

## Convergent evolution in the territorial communication of a classic adaptive radiation: Caribbean *Anolis* lizards



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To demonstrate adaptive convergent evolution, it must be shown that shared phenotypes have evolved independently in different lineages and that a credible selection pressure underlies adaptive evolution. There are a number of robust examples of adaptive convergence in morphology for which both these criteria have been met, but examples from animal behaviour have rarely been tested as rigorously. Adaptive convergence should be common in behaviour, especially behaviour used for communication, because the environment often shapes the evolution of signal design. In this study we report on the origins of a shared design of a territorial display among *Anolis* species of lizards from two island radiations in the Caribbean. These lizards perform an elaborate display that consists of a complex series of headbobs and dewlap extensions. The way in which these movements are incorporated into displays is generally species specific, but species on the islands of Jamaica and Puerto Rico also share fundamental aspects in display design, resulting in two general display types. We confirm these display types are convergent (the consequence of independent evolution on each island) and provide evidence that the convergence was driven by selection for enhanced signal efficiency. Our study shows how adaptation to common environmental variables can drive the evolution of adaptive, convergent signals in distantly related species.

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Convergent evolution is the independent origin of similar phenotypes in distantly related species. When convergence results from natural selection, it provides some of the best evidence for adaptive evolution in nature because it represents replicated examples of the same, or at least very similar, adaptation arising from separate selection events. Most examples of convergent evolution involve morphological traits (e.g. Taylor & McPhail 2000; Rosenblum 2006; Losos 2009), but any aspect of the phenotype can be the target of selection and subsequently has the potential to exhibit convergence. Animal behaviour is no exception, and there are a number of compelling cases of behavioural convergence. Notable examples include strategies of maternal care shared between ungulates and macropods (wallabies, wallaroos and kangaroos; Fisher et al. 2002), the array of similar web patterns in distantly related Hawaiian spiders (Blackledge & Gillespie 2004), the common design of echolocation calls in diverse lineages of bats (Jones & Holderied 2007), and the high-pitched 'seet' alarm call produced by some songbirds (Marler 1955). Yet identifying

behavioural examples of convergent evolution has been challenging: behaviour is often difficult to quantify because of its complexity and variability within individuals as compared to other phenotypic characteristics like morphology. Nevertheless, for these same reasons, behaviour can also provide valuable insights into the circumstances that promote convergent evolution in complex phenotypes that can vary within as well as across species.

An attractive candidate for the study of behavioural convergence is animal communication because it is a predictable target of selection from the environment. Indeed, how properties of the environment affect the propagation of animal signals has been a topic of long-standing interest to researchers of animal communication (e.g. Alexander 1962; Marler 1967; Morton 1975). There is now a strong body of signal detection theory (Wiley 2006) that outlines how animals should produce signals to maximize reception and assessment in difficult environments (e.g. habitats that are noisy). By extension these models also predict that the type of environment in which animals communicate should dictate the type of signals that the animals produce. This should lead to adaptations that drive signal convergence when distantly related species occupy very similar environments (Endler 1992). Habitat-dependent convergence in the design of animal signals should therefore be common, but few studies have investigated this

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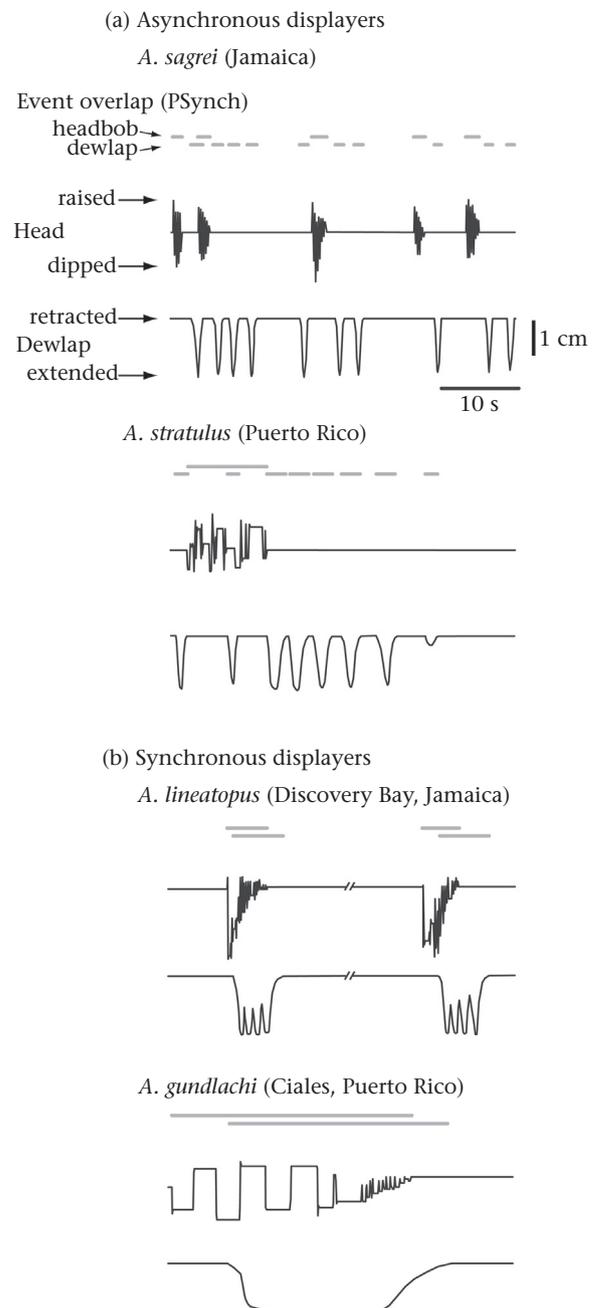
phenomenon explicitly and robust examples are subsequently rare. Here, we provide a test of habitat-dependent convergence in the behavioural displays of 12 species of *Anolis* lizards from two separate island radiations on Jamaica and Puerto Rico.

There are several important reasons why we might expect signal convergence in *Anolis* lizards. Anoles communicate using movement-based visual displays composed of two discrete components: vertical movements of the body, known as headbobs or pushups, and extensions of an expandable throat fan, called a dewlap. Males use these displays to advertise continued territory occupancy and to deter intrusions (Jenssen 1977; Ord 2008). As most potential receivers are located far from the signaller (Ord 2012), anole displays are particularly susceptible to environmental degradation (Ord & Stamps 2008). *Anolis* advertisement displays are therefore under considerable selection pressure to remain conspicuous. In particular, lizards living in poorly lit or windy environments in which there is frequent, distracting motion from windblown vegetation (high ‘visual noise’) compensate by enhancing the speed of display movements or extending the duration of displays (Ord et al. 2007, 2010). This predicts convergence in display characteristics among species living in comparable light and visual noise conditions between islands.

Another reason to anticipate convergence in the territorial displays of Jamaican and Puerto Rican anoles is the abundant evidence of the convergence of other traits among species on these and other islands. *Anolis* lizards of the Greater Antilles (which includes Jamaica and Puerto Rico) provide a classic example of convergent morphological evolution, in which the same set of ecomorphs has evolved independently on each island. These ecomorphs are named according to the area of the environment or microhabitat in which species are typically found and include grass-bush, trunk-ground and trunk-crown specialists (plus three other ecomorph types that are not the focus of this current study; see Losos et al. 1998). Much of the convergence within ecomorphs reflects adaptations that increase locomotor performance in a given microhabitat (reviewed in Losos 2009). However, there are indications that display rates may also have converged within ecomorphs (Losos 1990), in addition to the degree of overlap among male territories, which tends to increase from grass-bush (low overlap), trunk-crown (moderate overlap) to trunk-ground (high overlap; Johnson et al. 2010).

The current study focuses on a general aspect of communication: the extent to which animals with different signal components rely on each of those components for communication in the same functional context. Although all of the anoles on Jamaica and Puerto Rico use dewlaps and headbobs in their territorial advertisement displays, pilot studies suggested that species might differ in the extent to which they emphasize these two components. For instance, *Anolis stratulus* repeatedly ‘pumps’ the dewlap (many dewlap extensions of short duration), but rarely does so in conjunction with headbobs, while *Anolis gundlachi* performs a series of headbobs, while keeping the dewlap extended throughout the headbob display (Fig. 1). However, it was unclear whether these display types occur on both islands, and if so, whether they are related to ecomorphs or to differences in signalling conditions (light levels/visual noise).

We began by devising an index, PSynch, to quantify the nature of the relationship between the dewlap and headbob components in an anole’s advertisement display, and then asked whether this index was correlated, across taxa, with other display characteristics. Next, we mapped these display phenotypes onto the phylogeny of Jamaican and Puerto Rican lizards to confirm that convergence was involved for at least one of the display types (the other display type could be ancestral). Finally, we tested two nonexclusive hypotheses to explain the convergence: (1) display phenotypes differed among



**Figure 1.** Convergent display types performed by male *Anolis* lizards on Jamaica and Puerto Rico. Lines in black are display-action-pattern graphs of representative displays that depict movement of the head up-and-down (top line) and the extension of the dewlap in-and-out (bottom line) over time. Lines in grey show the extent of headbob movements and dewlap extensions overlap. (a) Asynchronous displays were mostly made up of frequent extensions of the dewlap that rarely overlapped with headbob movements (proportion of synchronized dewlap and headbob movements, PSynch:  $\mu_{\text{taxon}}$ : *A. sagrei* = 1.7%; *A. stratulus* = 15.9%). (b) Synchronous displays were made up of headbobs and dewlap extensions, but most movement was concentrated in the headbob portion of the display (PSynch:  $\mu_{\text{taxon}}$ : *A. lineatopus* = 68.9%; *A. gundlachi* = 74.5%). Videos of these display sequences are provided in the Supplementary Material. These videos highlight that species that use asynchronous displays also tend to have small, colourful dewlaps, whereas species that use synchronous displays tend to have large, pale coloured dewlaps.

ecomorphs, implying that morphological and behavioural traits evolved together in response to selection in different microhabitats; and (2) display phenotypes were associated with ambient light, visual noise and distance to receivers (Ord et al. 2010; Ord 2012), suggesting that certain types of displays have evolved to

improve signal detection in challenging environments. We tested both hypotheses because ambient light, visual noise and receiver distance were not uniquely associated with particular ecomorphs; e.g. two different ecomorphs live in the same sunny environment on Jamaica (*Anolis sagrei*, a trunk-ground anole; *Anolis grahami*, a trunk-crown anole) and the same shady habitat on Puerto Rico (*A. gundlachi*, a trunk-ground anole; *Anolis evermanni*, a trunk-crown anole).

## METHODS

### *Sampling and Video Analysis*

Sixteen populations of male *Anolis* lizard, belonging to 12 species, were surveyed across Jamaica and Puerto Rico (see [Supplementary Table S1](#)). These species form two separate clades (independent radiations) on each island and include most of the species in each clade (11 of the 13 species on both islands). We also included *A. sagrei* on Jamaica, an invasive species from Cuba, as a 12th species in our survey because of its close phylogenetic affiliation to the Jamaican endemics (see [Results](#), [Fig. 3](#)). Two species on Puerto Rico (*Anolis cuvieri* and *Anolis occultus*) were not included in our study because they did not belong to the Puerto Rican radiation. Rather, these two species arose from two separate colonization events and were phylogenetically far removed from the all of the species found on both Jamaica and Puerto Rico (*A. cuvieri* was affiliated with one of several distantly related clades from Hispaniola, while *A. occultus* was affiliated with a clade at the base of the Caribbean phylogeny). For four species, two populations that were geographically separated by at least 10 km were examined ([Table S1](#)). These populations were treated as separate taxa in analyses because there was informative variation in both display behaviour and environmental conditions affecting signal detection for different populations of the same species that might provide insights on the relative roles of evolution and within-individual variability in phenotypic convergence.

Sampling consisted of video recording free-living adult males on their territories for 25–30 min, followed by measurements of habitat light and neighbour distances. Video recordings were made at various times of day from 0530 to 1830 hours, with consecutive video trials conducted out of visual range of previous trials (see [Ord et al. 2010](#)). Areas where lizards had been previously recorded were not revisited to ensure that individuals were not inadvertently sampled twice. Data on display behaviour were then compiled from separate clips exported from recorded video that depicted male lizards performing territorial advertisement displays. Visual noise occurring in the backgrounds of these clips was also measured using computational motion analysis (see below). Habitat light was recorded at the end of video recording trials using a LI-250A handheld light meter and a LI-190SA Quantum Sensor (from LI-COR Biosciences, Inc., Lincoln, NE, U.S.A.) positioned at the site where the lizard was first observed to display. Receiver distance was determined by averaging the distances from the site of first display to all conspecific adult male neighbours within the line of sight of the focal lizard that had been noted during the 25–30 min recording period. A single investigator (T.J.O.) recorded all video and collected all light and neighbour distance measurements. More details on sampling are given in [Ord et al. \(2010\)](#) and [Ord \(2012\)](#).

Display clips were used to estimate several key variables expected to covary with environmental conditions that affect signal detection ([Wiley & Richards 1982](#); [Brumm & Slabbekoorn 2005](#)): the intensity, duration and rate of production (see [Ord et al. 2010](#)). Signal intensity was measured as the maximum speed of movements included in territorial advertisement displays and was quantified using Analysis of Image Motion (AIM; [Peters et al. 2002](#)).

This software was also used to quantify the maximum speed of environmental motion, or visual noise, occurring in the background of video clips. Signal duration was measured for dewlap and headbob display bouts to the nearest video frame (~33 ms for the NTSC, National Television System Committee, video format) using the time-codes of clips in iMovie HD version 5.0.2. Duration was measured as the length of time (s) from the start of the first movement to the end of the last movement. Signal rate was measured as the average number of dewlap and headbob bouts of display per min.

Movement is only one aspect of the dewlap display. Both the size and colour of the dewlap are believed to be influential in conveying information to conspecific receivers (e.g. [Vanhooydonck et al. 2005](#); but see [Henningsen & Irschick 2012](#)) and for the overall detection of the advertisement display (reviewed by [Fleishman 2000](#)). We measured dewlap size as the area of the dewlap when fully extended in display clips using the software ImageJ v.1.42q (National Institutes of Health, Bethesda, MD, U.S.A., <http://rsbweb.nih.gov/nih-image/>). Three measurements of dewlap area were taken from different display clips for each adult male and were converted from pixels<sup>2</sup> to mm<sup>2</sup> using a calibration value obtained at the time of video recording (an object of known size was placed in-frame at the site where a lizard had displayed; see [Ord et al. 2007](#)). These three measurements were averaged for each male, and then averaged again across all adult males for a given taxa. Snout–vent length (SVL) was also estimated from videos by measuring the distance from the tip of the lizard's nose to the base of its tail (the majority of lizards were not caught following video recording, so data on actual SVL were not available in most instances). As with dewlap measurements, three separate clips were used to obtain SVL measures and averaged to provide a single mean SVL for each male. This was then averaged a second time across all male lizards to compute an average taxon SVL. We used the residuals from the phylogenetic regression of taxon mean log-transformed dewlap area and taxon mean log-transformed SVL to compute a size-corrected estimate of dewlap size for comparative analyses.

Information on dewlap colour was compiled from [Fleishman \(2000\)](#), which summarizes several indices of dewlap colour for 11 of the 12 species included in our study (11 of 16 taxa; all species except *Anolis poncensis*, one of the few anole species with a greatly reduced dewlap; see below). All seven Puerto Rican species examined by Fleishman were from the same populations surveyed by our study (those near El Verde and Bahía de la Ballena; [Table S1](#); L. T. Fleishman, personal communication). For the Jamaican species, two of the four species (*Anolis lineatopus* and *A. sagrei*) were surveyed at the same site near Discovery Bay ([Table S1](#); L. T. Fleishman, personal communication). However, Fleishman computed values for these two species based on pooled estimates of males surveyed at this location and two other populations around the island. The remaining two Jamaican species (*Anolis opalinus* and *A. garmani*) were also sampled at several different locations, but none of these locations overlapped with our study. For all the Jamaican species, we followed Fleishman's general assumption that dewlap colour varies less within species than it does between species.

[Fleishman \(2000\)](#) summarized dewlap colour in three ways: chroma (the radiance amplitude at 450 nm divided by the radiance amplitude at 650 nm); hue (the 'cut-on' value,  $\lambda_c$ , or the wavelength at which the radiance amplitude was halfway between the amplitude of 450 and 650 nm); and UV reflectance (the radiance amplitude at 360 nm divided by the radiance amplitude at 650 nm). Modelling and empirical experiments reported by [Fleishman \(2000\)](#) showed that, in poor light (e.g. full shade), the detection of the dewlap was enhanced by colours of high chroma (colours that converge on white), high UV reflectance, and in general by low hue.

Finally, we devised an index to quantify the way in which dewlap extensions were coordinated with headbobbing movements during territorial advertisement displays. This index, PSynch (the proportion of synchronized dewlap and headbob movements), measures the probability that lizards will extend the dewlap when they perform headbobs. A value of 0% would indicate that bouts of dewlap extension never overlapped bouts of headbobbing. Conversely, a value of 100% would indicate that bouts of dewlap extension always overlapped bouts of headbobs (Fig. 1). To distinguish between these two extremes, and based on the relationship of PSynch to other display characteristics (see Results, Fig. 2), we use the term ‘asynchronous’ displays to refer to species that emphasized dewlapping in their displays (PSynch < 50%) and the term ‘synchronous’ displays to refer to species that emphasized headbobbing in their displays (PSynch > 50%).

*Anolis poncensis* was unusual because it was one of a handful of anoles with a greatly reduced dewlap (Fig. S1). Indeed, the dewlap was so small that it was extremely difficult to determine whether males were extending the dewlap at all, despite close inspection of high-quality video footage. The level of variance associated with estimates of PSynch and dewlap size for this species was consequently far greater than that of all other taxa examined (e.g. Fig. S1). Furthermore, the functionality of such a tiny dewlap as a signal was questionable. Rather than exclude the species from our study, we adopted the conservative approach of repeating our analyses with and without *A. poncensis*.

### Statistical Analysis

#### Quantifying the display characteristics correlated with PSynch

We began our investigation by first testing hypotheses about relationships between PSynch and other display characteristics that were either previously shown to be important in anole displays (speed, duration, dewlap size and the colour of the dewlap; Fleishman 2000; Ord et al. 2010), or expected to be related to PSynch (frequency of dewlap and headbob movements). We did so by using bivariate phylogenetic regression analyses (see ‘Testing the adaptive convergence of display’ below) and used *r* values computed by these analyses that were greater than 0.5 to identify signal characteristics associated with differences in PSynch among taxa. For instance, if a high value of PSynch indicated an emphasis on headbobbing, we would expect a positive relationship between headbob speed and PSynch; conversely, if a low value of PSynch indicates a reliance on dewlapping, we would expect to observe a negative relationship between PSynch and dewlap bout rate.

#### Assessing stimulus–response relationships (SRRs) involving PSynch

A difficulty specific to the study of behavioural evolution is that behaviour typically varies within individuals as an immediate response to the external stimuli that impinge on those individuals when they express behaviour. For over a century, ethologists and psychologists have studied the functional relationships between external stimuli and immediate behavioural responses to those stimuli, which we can call stimulus–response relationships (SRRs). Recent studies have demonstrated that when SRRs can be described using linear functions, the behaviour of individual animals can be modelled using a reaction norm approach, in which each individual’s SRR is characterized by an intercept and slope (Dingemans et al. 2010; Stamps & Groothuis 2010a). In turn, the slope of an individual’s SRR can be used to estimate the ‘contextual plasticity’ of that individual. Contextual plasticity is a specific type of behavioural plasticity that differs in a number of important ways from other types of behavioural plasticity (e.g. developmental or phenotypic plasticity; Stamps & Groothuis 2010a, b). For instance, contextual plasticity is typically studied by observing the responses

of individual animals to different stimuli over short periods of time, whereas studies of behavioural developmental plasticity typically involve matched groups of animals with the same genotype, reared under different sets of environmental conditions, and then tested using a standard behavioural assay (Stamps & Groothuis 2010b).

We have previously shown that some components of the *Anolis* advertisement display are contextually plastic, that is, they vary within individuals as a function of short-term (minutes to hours) fluctuations in ambient light and visual noise (Ord et al. 2007, 2010). Furthermore, because different individuals from the same population have SRRs with similar slopes and intercepts, it is possible to characterize a mean SRR for the individuals in a given taxon using observations of different individuals sampled at the same locality over several days (Ord et al. 2007; T. J. Ord, unpublished data). We have also demonstrated how random regression models can be used to model linear reaction norms and estimate the mean SRR for a given taxon, and how the intercepts generated by these models can be used to control for SRRs in subsequent phylogenetic comparative analyses (Ord et al. 2010). We used this approach to estimate whether PSynch varied within taxa as a function of short-term fluctuations in ambient light or visual noise and, if so, to control for this variation in order to study convergent evolution in PSynch. We did not assess SRRs of PSynch in relation to receiver distance because, within each taxon, the average distance to territorial neighbours was comparable for different males within each study area and was stable across the periods when the males were sampled. This made it difficult to detect variation in behaviour within or across individuals in PSynch as a function of distance to neighbours (see also Ord 2012).

Reaction norms were computed by fitting a random regression using the lme4 package v.0.999375–40 in R v.2.13.1 (R Development Core Team, The R Foundation for Statistical Computing, Vienna, Austria). Taxon identity was included as a random effect, and habitat light and visual noise were included as continuous-variable fixed effects. Island origin was included as a covariate because previous studies showed that some display characteristics were contextually plastic as a function of light levels or visual noise in Puerto Rican lizards, but not contextually plastic in taxa from Jamaica (Ord et al. 2010). Interaction terms between island origin and light and visual noise were initially included to test for the presence of island-specific SRRs involving PSynch. Interactions that were not significant were excluded from the final model.

The analysis estimated several biologically relevant parameters: the within-taxon slope (an estimate of the slope of the SRR, or contextual plasticity, of the individuals in that taxon); the within-taxon intercept (an estimate of that taxon’s ‘baseline’ response to a standardized set of conditions); and the average of the within-taxon slopes (a weighed estimate of the average slope of the SRR for all of the taxa analysed). Of importance for evolutionary analysis, when comparing behavioural characters that are contextually plastic within individuals, analyses based on within-taxon intercepts and slopes can be more informative than analyses based on the mean values for each taxon. This is because the mean will vary as a function of the external stimuli that surrounded the individuals from a given taxon at the time of measurement. For example, imagine that all of the species in a lineage have identical SRRs (same intercepts and same slopes), but the taxa were sampled under different sets of external stimulus conditions. In that case, a phylogenetic analysis based on the mean value for each taxon (the traditional approach) would erroneously interpret any relationship between these mean values and the external stimuli where each taxon was sampled as evidence of evolutionary change. In contrast, an analysis based on the within-taxon intercepts would reveal no phylogenetic relationship between the intercepts and the external stimulus, because all of the taxa would have the same intercept. An

analysis based on within-taxon intercepts would therefore correctly indicate that the differences among taxa in mean values reflect a shared SRR, coupled with differences in external conditions at the time of measurement, for the taxa in that data set. Conversely, if none of the species in a taxon were contextually plastic (the SRRs of every taxon were characterized by slopes of zero), then the within-taxon intercepts would be the same as the taxon means. In that case, phylogenetic regressions based on intercepts and means would recover the same relationship between display behaviour and the external stimulus. A detailed discussion and graphical illustration of the philosophy of using within-taxon intercepts to replace taxon mean values in comparative analyses of traits that vary in response to external stimuli within individuals are provided in Ord et al. (2010).

If SRRs with nonzero slopes were present, we computed the within-taxon intercepts for use in subsequent phylogenetic analyses by refitting the random regression model with only the environmental variable found to correlate with PSynch. This focused analysis provided a more precise estimate of the within-taxon SRR intercept in the absence of noninfluential environmental variables included in the original multiple regression. These estimates of within-taxon intercepts were then used in phylogenetic analyses to assess variance among species in 'baseline' variation in PSynch.

#### *Testing the adaptive convergence of display*

We used the SLOUCH program v.1.2 (Hansen et al. 2008) implemented in R for all phylogenetic analyses (including bivariate regressions used for identifying correlations between PSynch and other display characteristics). The program uses maximum likelihood to estimate phylogenetic inertia, specifically the phylogenetic half-life ( $t_{1/2}$ ), and stochasticity ( $v_y$ ) in the evolutionary diversification of a phenotypic characteristic. It then incorporates these estimates in subsequent analyses of putative selection pressures. Both  $t_{1/2}$  and  $v_y$  range in value from zero (no phylogenetic inertia or stochasticity) to infinity (any value  $\geq 1000$  infers extensive phylogenetic inertia or stochasticity). The program models evolution as an Ornstein–Uhlenbeck (OU) process in which the phenotype evolves towards some optimum value via Brownian motion, and, if reached, is kept at or near this optimum via stabilizing selection. Phylogenetic inertia affects how rapidly the phenotype can evolve towards this optimum (as well as the strength of selection), while stochasticity determines the extent to which the phenotype can effectively track the trajectory to and around this optimum. Predictor variables are included in the analysis to test putative sources of selection and to calculate the value corresponding to the optimal adaptive phenotype. In instances in which a phenotypic characteristic is not under selection, there will be no optimum value for the characteristic, and variance among species is simply the outcome of Brownian motion (neutral evolutionary change resulting from drift).

SLOUCH offers two analyses: the first models fixed phenotypic optima (e.g. in response to an environment that is constant over evolutionary time), while the second models moving phenotypic optima (e.g. that track an environment that changes over evolutionary time). We used the fixed optima analysis to test the ecomorph hypothesis: that ecomorphs have different display types (defined by PSynch; e.g. trunk-crown anoles have relatively low PSynch values, whereas trunk-ground anoles have relatively high PSynch values). To apply this analysis, we had to first reconstruct the grass-bush, trunk-ground and trunk-crown ecomorphs onto the phylogeny and did so following the maximum likelihood reconstructions of the Greater Antillean ecomorphs by Losos (2009). Ambiguous basal nodes were assigned as 'ancestral' (see also ecomorph reconstructions of Butler & King 2004). These

reconstructions were mapped manually (replicating precisely the likelihood reconstructions of Losos 2009) onto the phylogeny using Mesquite v.2.74 (Maddison & Maddison 2010) and exported to SLOUCH using a custom written script. We also applied a null model that assumed variance in PSynch among taxa was unrelated to ecomorphology. To fit this model, the entire phylogeny was mapped as 'ancestral' (Butler & King 2004). We compared the relative support for the ecomorph and null models using Akaike's Information Criterion correction for small sample size, AICc: a model was considered to fit the data better if its AICc value was at least two units lower than the other model (Burnham & Anderson 2002; see Ord & Gracia-Porta 2012 for discussion of AICc in a phylogenetic context).

To test the signal detection hypothesis, we used the moving optima analysis to assess whether habitat light, visual noise or transmission distance explained variance in PSynch among taxa. The analysis computes the correlation between each of the environmental variables and PSynch in two ways. The 'evolutionary' regression reports the intercept and slope estimates that incorporate phylogenetic inertia and stochastic effects in the evolution of PSynch. The 'optimal' regression reports the intercept and slope estimates as if PSynch were unaffected by phylogenetic inertia or stochastic effects, that is, the optimal relationship in which selection has been the only factor influencing the evolution of PSynch. Hansen et al. (2008) cautioned against interpreting the optimal regression if the number of taxa included in the analysis is low ( $< 30$ ). This is because implausible parameter values can be computed when uncertainty in the estimated values of  $t_{1/2}$  and  $v_y$  is large, and this uncertainty is accentuated by small sample sizes. We focused only on the outcome of the evolutionary regression and report support regions for  $t_{1/2}$  and  $v_y$  as the range of values within two log-likelihood units of the best estimate.

The ecomorph and signal detection hypotheses were not mutually exclusive. A comparison of the relative contribution of each in explaining variance among species in PSynch was not straightforward because modelling a fixed and moving adaptive optima could not be included in the same analysis (this is why each analysis is a separate option in SLOUCH). However, it was possible to include categorical and continuous variables within the moving adaptive optima analysis. Doing so effectively performs a phylogenetic ANCOVA. To this end, we scored ecomorph as a dummy variable and included it in a model with habitat light (which was found to be the primary variable associated with differences in PSynch among taxa in tests of the signal detection hypothesis). We then compared the support for this model with models that only included ecomorph or habitat light using AICc.

An estimate of within-taxon variance was included in most SLOUCH analyses to account for uncertainty in taxon values. For analyses of taxon means, we used the variance associated with the computed means, while for analyses of within-taxon intercept values, the variance computed for the average within-taxon intercept was used for all taxa because separate estimates for each taxon intercept were not computed by lmer4 (see Bates 2008). Variance estimates associated with measures of dewlap colour were not reported by Fleishman (2000) and could not be included in our analyses.

The phylogeny we used was from Nicholson et al. (2005), reproduced in Losos (2009) with branch lengths set proportional to time (see also Mahler et al. 2010). It was based on 1483 aligned base pairs of mitochondrial DNA sequences. We manually trimmed the phylogeny down to the species of interest using Mesquite. All nodes in this smaller tree were well supported with Bayesian posterior probabilities at or above 90% for most nodes. The topology and relative branch lengths of the pruned phylogeny were consistent with a recent phylogenetic analysis using an extensively expanded

set of gene sequences for a subset of species (Alföldi et al. 2011). Populations within taxa were positioned on the phylogeny with branch lengths set to the minimum population divergence estimated for *Anolis* species on Jamaica (Jackman et al. 2002).

## RESULTS

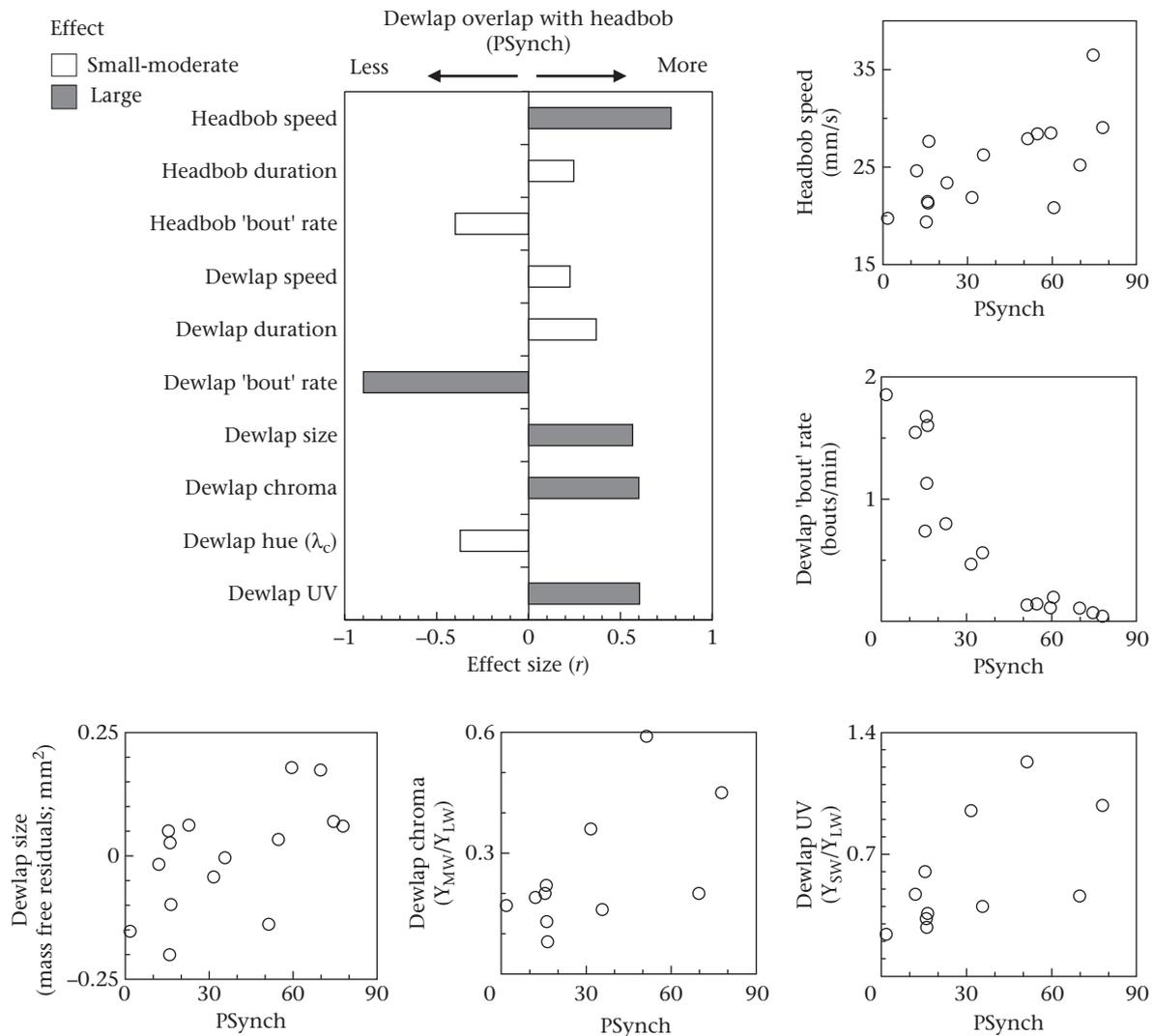
### *PSynch* and Other Characteristics of Territorial Displays

Our bivariate phylogenetic analyses supported our initial hypothesis that taxa with low values of *PSynch* relied on repeated dewlap extensions for territorial advertisement, and conversely, that taxa with high values of *PSynch* relied more on headbobbing in the same situation. Large, positive effect sizes were found between *PSynch* and headbob speed, dewlap size, dewlap chroma and dewlap UV reflectance, and a large negative effect size was found between *PSynch* and dewlap bout rate (Fig. 2). That is, taxa at the ‘asynchronous’ end of the continuum (taxa with low values of *PSynch*) had displays characterized by frequent extensions of a

relatively small, colourful dewlap (i.e. of low chroma; e.g. see Supplementary Material, Movies S1, S2) with low UV reflectance. Their headbob movements were generally slow and rarely occurred at the same time as dewlap extensions. In contrast, taxa at the ‘synchronous’ end of the continuum (taxa with high values of *PSynch*) performed rapid headbob movements and extended the dewlap less often. Their dewlaps were typically large, pale in colour (e.g. see Supplementary Movies S3, S4) and had high UV reflectance, and, if used, were typically extended at the same time as headbob movements.

### *SRRs of PSynch* As a Function of External Stimuli

Although there was no indication that *PSynch* varied as a function of visual noise, the *SRRs* for *PSynch* as a function of ambient light tended to have negative slopes in a random regression model that included all taxa (Table 1). In a second analysis that omitted *A. poncensis* (a species with a tiny dewlap; Supplementary Fig. S1), the confidence interval associated with the average within-



**Figure 2.** Covariance of signal characteristics as a function of the proportion of synchronized dewlap and headbob movements (*PSynch*) in *Anolis* lizards. Correlation coefficients were computed using a bivariate phylogenetic regression implemented in the program SLOUCH. One species was excluded from these analyses because it had a greatly reduced dewlap, making measurement of dewlap characteristics impossible (*A. poncensis* on Puerto Rico). Highlighted in grey are *r* values of large effect ( $r > 0.5$ ); the direct relationship of each of these variables with *PSynch* is illustrated in separate scatterplots. Taxa with low values of *PSynch* were termed ‘asynchronous’ displayers; taxa with high values were termed ‘synchronous’ displayers.

**Table 1**

Within-taxon variance in PSynch as a function of environmental conditions expected to influence signal detection in *Anolis* lizards

	$\beta$ (95% CI)	
	All taxa	Without <i>A. poncensis</i>
Intercept	47.36 (29.36, 65.35)	44.16 (25.75, 62.57)
Habitat light	-5.24 (-10.98, 0.51)	-6.14 (-12.13, -0.15)*
Visual noise	0.14 (-0.38, 0.67)	0.16 (-0.35, 0.68)
Island	-7.22 (-29.64, 15.19)	-3.06 (-23.25, 17.13)
$N_{\text{taxa, lizards}}$	16, 467	15, 456

PSynch: the proportion of synchronized dewlap and headbob movements. Results are shown for the mean reaction norm across all taxa. Separate reaction norms were computed for each taxon and are shown for habitat light in Fig. S1. Interaction terms between environmental variables and island were considered but failed to explain significant variance in PSynch among individuals and were excluded from the final model reported here.

\* Slope estimates that were statistically different from zero ( $P < 0.05$ ).

taxon slope for relationships between PSynch and light did not overlap zero (Table 1). These results indicated that similar SRRs were apparent in all of these taxa: when individuals from each taxon displayed under low light conditions (i.e. early in the morning or late in the evening) they exhibited higher values of PSynch (i.e. more emphasis on headbobbing) than when they displayed under brighter conditions (more emphasis on dewlapping). The interaction between the average within-taxon slope for habitat light and island was not statistically different from zero (all taxa, 95% CI: -7.04, 17.70; without *A. poncensis*: -6.64, 18.78), indicating that lizards from Jamaica and Puerto Rico had similar SRRs for PSynch as a function of ambient light levels (Fig. S2).

To control for the effects of SRRs in subsequent analyses of evolutionary change in PSynch, we conducted a second set of evolutionary regressions in which within-taxon intercepts for PSynch were used instead of each taxon's mean value for PSynch.

### Convergence of Display Phenotypes

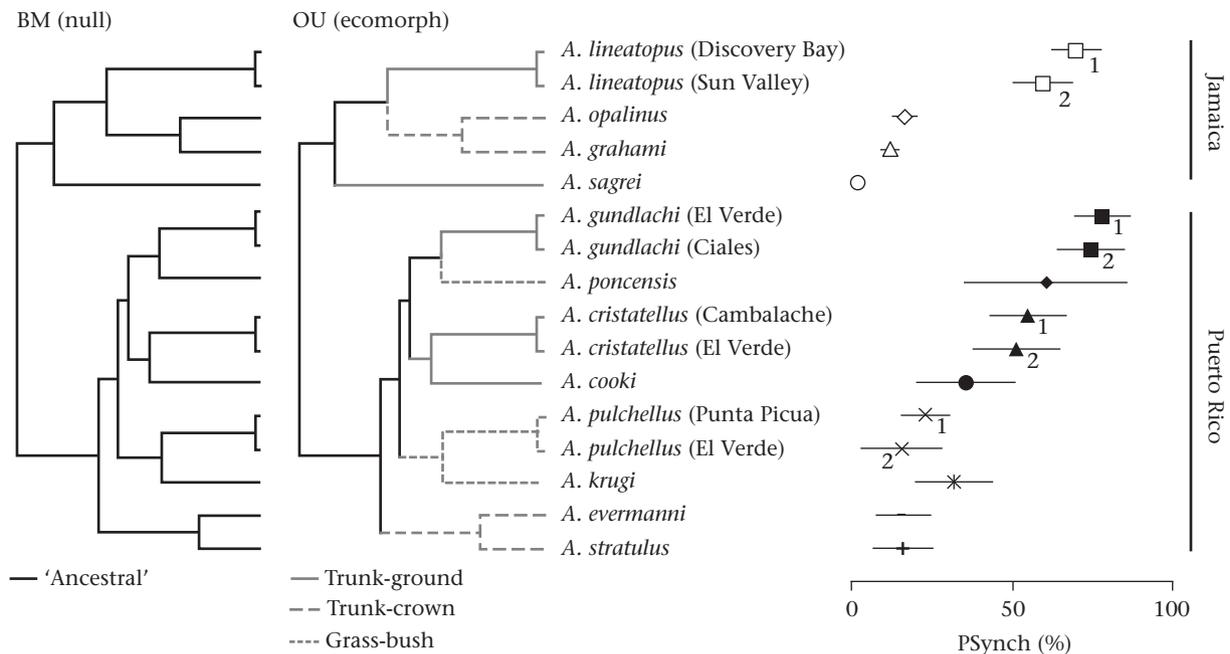
Plotting PSynch and within-taxon variance as confidence intervals onto the anole phylogeny indicated that synchronous and asynchronous phenotypes were found on both Jamaica and Puerto Rico (Fig. 3; note: within-taxon intercepts of PSynch that control for SRRs showed the same qualitative pattern as Fig. 3). This plot also shows that a wide range of PSynch values occurred across the taxa on both of the islands. On Jamaica, displays seemed to be clustered at two ends of the continuum: some taxa had relatively low values of PSynch (emphasis on dewlapping: *A. opalinus*, *A. grahmi* and *A. sagrei*), while others had relatively high values of PSynch (emphasis on headbobbing: *A. lineatopus*). On Puerto Rico, PSynch was distributed more evenly between these extremes: some species emphasized dewlapping (*A. pulchellus*, *A. evermanni*, and *A. stratulus*), others emphasized headbobbing (*A. gundlachi* and *A. poncensis*), and still others had intermediate types of displays (*Anolis cooki*, *Anolis krugi* and *Anolis cristatellus*).

Within islands, closely related taxa tended to exhibit similar values of PSynch (Fig. 3). For example, *A. evermanni* and *A. stratulus*, two close phylogenetic relatives on Puerto Rico, both relied heavily on dewlapping in their displays. Similarly, two close phylogenetic relatives on Jamaica, *A. opalinus* and *Anolis grahmi*, both emphasized dewlapping in their displays. In most instances, close relatives with similar display types were also the same ecomorph, so this phylogenetic pattern might reflect similarities in microhabitat among closely related taxa.

### Evidence of Selection

#### Ecomorph hypothesis

The ecomorph model tested whether the adaptive convergence in morphology previously shown between ecologically similar species on each island extended to PSynch. In all cases, the ecomorph model was supported over the null model, irrespective of



**Figure 3.** Optima models contrasted with the observed variation among *Anolis* taxa in the proportion of synchronized dewlap and headbob movements (PSynch). BM (null) refers to a model in which variance among taxa was solely the outcome of Brownian motion (in the absence of selection). The OU model assumed that different adaptive optima for PSynch existed for different ecomorph categories, with evolution proceeding via an Ornstein–Uhlenbeck process. Error bars for PSynch are 95% confidence intervals. Open symbols correspond to species found on Jamaica; closed symbols correspond to those on Puerto Rico. Numbers next to symbols refer to populations sampled for a given species. Note: *A. sagrei* is an invasive species from Cuba and is not a member of the monophyletic clade that originated on Jamaica; *A. poncensis* has a greatly reduced dewlap that is miniscule in comparison with other *Anolis* taxa (see Fig. S1).

whether models were fitted to mean values of PSynch or to within-taxon intercepts (estimates of PSynch that controlled for SRR as a function of habitat light), and whether or not *A. poncensis* was included in the analyses (Table 2). Generally, trunk-crown species (*A. opalinus*, *A. grahami*, *A. evermanni* and *A. stratulus*) and grass-bush species (*Anolis pulchellus* and *A. krugi*) performed a territorial advertisement display tending towards the asynchronous end of the continuum, whereas trunk-ground ecomorphs (*A. lineatopus*, *A. gundlachi*, and *A. cristatellus*) performed displays towards the synchronous end of the continuum.

However, these relationships between ecomorphs and display type did not apply to all of the species in the analyses (Fig. 3). *Anolis poncensis*, a grass-bush anole with an unusually small dewlap (see Fig. S1), performed a display that was closer to the synchronous end of the continuum than it was to the asynchronous end. Conversely, the trunk-ground anoles *A. cooki* and *A. sagrei* performed advertisement displays that were closer to the asynchronous end of the continuum. Phylogenetic inertia in PSynch might account for the mismatch between ecomorph and display type in *A. poncensis* and *A. cooki* (see Fig. 3). However, this explanation is unlikely to account for the emphasis on dewlapping in *A. sagrei* displays, because *A. sagrei* is an invasive species from Cuba, where most of its relatives are trunk-ground anoles (Losos 2009).

Taken together, there was some support for an association between ecomorphology and the PSynch. However, the relationship was imperfect, suggesting that other factors might have contributed to display evolution.

#### Signal detection hypothesis

In analyses that included habitat light, visual noise and receiver distance (i.e. distance that displays must travel through the environment), the leading predictor of PSynch among taxa was the type of light environment in which taxa communicated (Table 3). This

**Table 2**  
Support for optima models of PSynch in *Anolis* lizards

Model applied	AICc	$r^2$	$t_{1/2}$ (support region)	$v_y$ (support region)
<b>Mean phenotype</b>				
All taxa				
OU (ecomorph)	138.1	0.79	$\infty$ (0, $\infty$ )	980 (25, $\infty$ )
BM (null)	145.1	0.00	150 (0, 325)	$\infty$ (300, $\infty$ )
$N_{\text{taxa}}$	16			
Without <i>A. poncensis</i>				
OU (ecomorph)	133.4	0.75	30 (0, $\infty$ )	90 (20, $\infty$ )
BM (null)	135.7	0.00	120 (0, 310)	$\infty$ (240, $\infty$ )
$N_{\text{taxa}}$	15			
<b>Baseline phenotype</b>				
All taxa				
OU (ecomorph)	139.1	0.84	975 (0, $\infty$ )	550 (0, $\infty$ )
BM (null)	147.9	0.00	125 (0, 350)	$\infty$ (300, $\infty$ )
$N_{\text{taxa}}$	16			
Without <i>A. poncensis</i>				
OU (ecomorph)	134.5	0.82	370 (0, $\infty$ )	270 (0, $\infty$ )
BM (null)	138.5	0.00	110 (0, 340)	$\infty$ (280, $\infty$ )
$N_{\text{taxa}}$	15			

PSynch: the proportion of synchronized dewlap and headbob movements. AICc: Akaike's Information Criterion corrected for small sample size. Results are shown for analyses run on species means and within-taxon intercept values that estimate the baseline phenotype (intercept for the stimulus–response relationships, SRRs, for each taxon). Models were applied using SLOUCH (Hansen et al. 2008). The parameter,  $t_{1/2}$ , or the phylogenetic half-life of PSynch reflects the extent to which the phenotype of ancestors influences those of descendant taxa with values approaching  $\infty$  corresponding to high phylogenetic inertia in PSynch. The influence of stochastic factors on PSynch evolution is summarized by  $v_y$ , with large values (e.g. >100) indicating that PSynch 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 a fitted model is given by  $r^2$ .

**Table 3**

PSynch among *Anolis* taxa as a function of variables expected to influence signal detection

	$\beta$ (95% CI)	
	All taxa	Without <i>A. poncensis</i>
<b>Mean phenotype</b>		
Intercept	26.52 (–30.22, 83.25)	21.44 (–27.67, 70.56)
Receiver distance	3.37 (–3.29, 10.04)	5.21 (–1.07, 11.49)
Habitat light	–18.54 (–32.54, –4.54)*	–27.62 (–41.74, –13.51)*
Visual noise	2.10 (–2.04, 6.24)	3.22 (–0.83, 7.27)
$r^2$	0.30	0.54
$t_{1/2}$ (support region)	280 (0, $\infty$ )	10 (0, $\infty$ )
$v_y$ (support region)	$\infty$ (80, $\infty$ )	90 (0, $\infty$ )
$N_{\text{taxa}}$	16	15
<b>Baseline phenotype</b>		
Intercept	18.95 (–50.84, 88.73)	13.09 (–43.77, 69.95)
Receiver distance	6.01 (–2.77, 14.79)	8.49 (0.65, 16.32)*
Habitat light	–10.06 (–27.34, 7.22)	–25.17 (–41.95, –8.39)*
Visual noise	0.87 (–4.39, 6.14)	2.84 (–2.06, 7.74)
$r^2$	0.15	0.51
$t_{1/2}$ (support region)	180 (0, 680)	10 (0, $\infty$ )
$v_y$ (support region)	$\infty$ (120, $\infty$ )	110 (0, $\infty$ )
$N_{\text{taxa}}$	16	15

PSynch: the proportion of synchronized dewlap and headbob movements. Results are shown for analyses run on species means and within-taxon intercept values that estimate the baseline phenotype (intercept of the stimulus–response relationships, SRRs, for each taxon). Models were applied using SLOUCH (Hansen et al. 2008). See Table 1 for parameter descriptions.

\* Slope estimates that were statistically different from zero ( $P < 0.05$ ).

was generally true regardless of whether analyses focused on mean taxon values or within-taxon intercepts. The relationship between PSynch and mean habitat light was weaker when SRRs within taxa were controlled for, but Fig. 4b shows *A. poncensis* as a prominent outlier in this analysis; the species occupies an unusually bright habitat for its recorded PSynch (note: the 95% CIs of the species mean value of PSynch were large for *A. poncensis* and did overlap lower values of PSynch more typical of taxa living in bright environments; Fig. 3). When *A. poncensis* was omitted, baseline PSynch was strongly, negatively correlated with habitat light (Table 3).

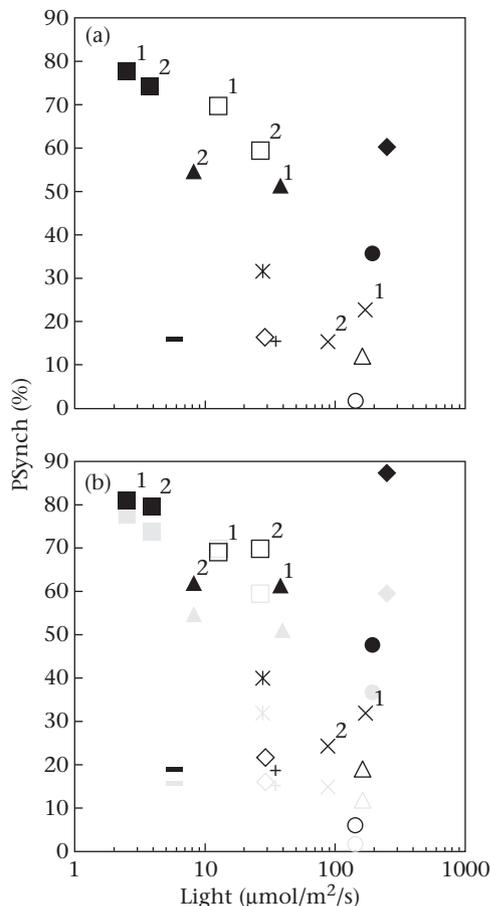
These analyses showed that displays emphasized headbobbing (high values of PSynch) when taxa communicated in low light environments but emphasized dewlapping (low values of PSynch) when taxa were in well-lit environments (Fig. 4). The baseline analysis without *A. poncensis* also reported a positive correlation between PSynch and the average receiver distance of advertisement displays (Table 3).

#### Relative support for the ecomorph and signal detection hypotheses

A model that combined both ecomorph and habitat light in a phylogenetic ANCOVA was poorly supported compared to alternative models that included only ecomorph or only ambient light, regardless of whether taxon mean values of PSynch or within-taxon intercepts controlling for SRR in PSynch were examined (Table S2). The alternative models that included only habitat light or only ecomorph were generally equally supported ( $\Delta\text{AICc} < 2.0$ ; Table S2). Hence, while the available evidence rules out a combined effect for ecomorph and habitat light on PSynch, it remains unclear which of these factors best accounts for display convergence in PSynch.

## DISCUSSION

When species with very different evolutionary histories are presented with the problem of communicating effectively in comparably challenging habitats, do they converge on similar solutions in signal design, or do they evolve alternative strategies



**Figure 4.** Variation in the proportion of synchronized dewlap and headbob movements (PSynch) among *Anolis* taxa as predicted by habitat light. Symbols correspond to those shown in Fig. 3. (a) Species means. (b) Within-taxon intercept values (intercept for the stimulus–response relationships, SRRs, for each taxon); grey symbols correspond to mean values shown in (a).

derived from different signalling precursors? The answer to this question is complex for *Anolis* lizards, and the results of the present study need to be placed first in the context of past work on this system.

Previous studies have revealed important differences between the territorial advertisement signals of Puerto Rican and Jamaican anoles. Puerto Rican male lizards use displays that vary within individuals (high contextual plasticity) to maintain a conspicuous signal under visually noisy or poorly lit conditions (Ord et al. 2007, 2010; see also Ord 2012). Their headbob displays are of long duration (Ord et al. 2010), and they strategically time display production to avoid windy periods when distracting motion from moving vegetation is high (Ord et al. 2011). In contrast, Jamaican lizards do not tend to alter their displays in response to short-term fluctuations in light or visual noise (Ord et al. 2010; but see also Table 1 and below), their headbob displays are of short duration (Ord et al. 2010), and they do not time their displays to exploit lulls in visual noise (Ord et al. 2011). Jamaican lizards also extend their dewlaps more rapidly than do anoles from Puerto Rico, a design characteristic that may help Jamaican lizards maintain a display that is detectable across a range of environmental conditions (Ord et al. 2011). Collectively, these differences in behaviour on the two islands represent alternative adaptive solutions to the common problem of producing an effective display in visually challenging environments (Ord et al. 2011).

Even so, the current study demonstrates convergence in another important aspect of display behaviour for anoles on the same two islands: the extent to which they rely on dewlapping versus headbobbing in their territorial advertisement displays. We first show that an index based on the relative timing of the dewlap and the headbob portion of the display (PSynch) provides a useful description of the emphasis on dewlap extensions versus headbobbing for each taxon (Fig. 2). We demonstrate that taxa with low values of PSynch (at the ‘asynchronous’ end of the continuum) have higher dewlap bout rates and slower headbob movements than species with high values of PSynch (at the ‘synchronous’ end of the continuum). PSynch was also positively related to dewlap size. This association might result from physical constraints (i.e. it may be more difficult to repeatedly and quickly extend and retract a large dewlap than a small one: see Bels 1990; Font & Rome 1990) or it might occur because headbobbing displays and large dewlaps both help increase display detectability in low light environments (see below).

We found evidence that the reliance on synchronous versus asynchronous displays were associated with the ecomorphs of *Anolis* taxa (Table 2). But we also found that taxa that displayed in low light environments were more likely to emphasize headbobbing (synchronous or high values of PSynch), whereas taxa that displayed in brightly lit environments were more likely to emphasize dewlapping (asynchronous or low values of PSynch; Table 3). Although our analyses indicated that models based on ecomorphs and ambient light were equally supported (Table S2), we suspect that light levels have been the primary force driving the convergence of display types on Puerto Rico and Jamaica. We make this inference for several reasons. First, within taxa, we found that PSynch was contextually plastic as a function of short-term fluctuations in light levels: individuals of taxa from both islands emphasized headbobbing more when displaying under low light conditions than when displaying under more brightly lit conditions. Second, experimental studies have shown that several of the display characteristics that covary with PSynch enhance signal conspicuousness under low light conditions. For instance, headbob speed, dewlap chroma and the UV reflectance of dewlaps have all been shown to enhance signal detection under low light (Fleishman 2000; Ord & Stamps 2008). We suspect that large dewlaps may also facilitate detection in dark environments (although the factors influencing the evolution of dewlap size are likely to be complex; Losos & Chu 1998). Third, there is currently no indication that different ecomorphs inhabit microhabitats that systematically differ with respect to conditions that might affect visual signal reception (Johnson et al. 2010). For instance, in our study, trunk-ground ecomorphs occupied a wide range of light environments: *A. sagrei* (well-lit) versus *A. lineatopus* (shady) on Jamaica, or *A. cooki* (well-lit) versus *A. gundlachi* (shady) on Puerto Rico. Finally, there is no indication that the function of these displays differ among ecomorphs; in all of these species, territorial advertisements are assumed to affect mate choice and male–male social interactions (Jenssen et al. 2001; Ord 2008).

Our results therefore suggest that habitat light has most likely contributed to both the evolution of alternative signal strategies, through the emphasis of different display characteristics on Jamaica and Puerto Rico (Ord et al. 2010, 2011; Ord 2012), and to convergent display phenotypes, through disruptive (or directional) selection within islands on a cluster of display characteristics that have led to shared display types between islands. Perhaps more important, we demonstrate that when studying the evolution of both within-island divergence and between-island convergence in communication signals in anoles, we need to control for stimulus–response relationships (SRRs) within individuals (Ord et al. 2010, Table 1, Fig. S2). In the current study, we found that the individuals

in virtually all of the taxa studied increased their emphasis on headbobbing under low light, and conversely, increased their emphasis on dewlapping under bright light (excluding *A. poncensis*; see below). However, even after we controlled for these SRRs within taxa, we still detected major differences across taxa in PSynch as a function of ambient light (Table 3, Fig. 4). Indeed, our evolutionary regression of within-taxon intercepts that controlled for SRRs recovered a slope several orders of magnitude greater than the average within-taxon slope ( $\beta_{\text{within-taxon, light}} = -6.14$ ;  $\beta_{\text{across-taxa, light}} = -25.17$ ; Table 1, Table 3). That is, the mean slope of the SRR of PSynch as a function of light for the individuals within each taxon was far lower than the estimated relationship between PSynch and light among taxa.

*Anolis poncensis* provides an important and instructive exception to the generalization that anoles in bright environments have low values of PSynch. This species has a greatly reduced dewlap, lives and displays under bright light conditions, and emphasizes headbobbing in its displays. Such a drastic reduction in the size of the dewlap is rare in *Anolis*. Indeed, a large dewlap is one of the defining characteristics of the genus and significant reduction in its size has only been reported for 11 of the ~400 *Anolis* species so far described (five species are grass-bush anoles including *A. poncensis*, two are trunk-crown anoles, while the rest exhibit no particular ecomorph; Losos 2009). The reason for the reduced dewlap of *A. poncensis* is unknown, but once it occurred, repeated extensions of such a diminutive dewlap would not necessarily increase the efficacy of this species' displays. Instead, despite its ecomorph and environment, *A. poncensis* emphasized components of its display (i.e. headbobs) that can reach distant recipients under challenging conditions for communication. In fact, the advertisement display of *A. poncensis* includes far more headbob movements than any of the other species examined on Puerto Rico (number of individual bobs included in a headbob display by *A. poncensis*, 95% CIs = 14.0, 23.7; mean number of individual bobs included in a headbob display by other Puerto Rican taxa = 6.9; T. J. Ord, unpublished data).

In other taxa, sunny environments have selected for displays that emphasized frequent extension of the dewlap (see also Ord & Martins 2006). Because *A. poncensis* is an exception to this rule, it presents a wonderful opportunity to compare the efficiency of the synchronous display versus the asynchronous display in brightly lit habitats. Such an experiment could be done with playbacks of different display types using a robotic lizard (Martins et al. 2005; Kelso & Martins 2008; Ord & Stamps 2008, 2009).

Although we have both experimental and comparative evidence that displays emphasizing headbobs might be advantageous in low light environments (Ord & Stamps 2008; Ord et al. 2010; this study), it is currently unclear whether displays at the other end of the continuum (i.e. those that rely more on frequent dewlapping) are favoured in well-lit environments, or whether they simply represent the retention of an ancestral display type. The asynchronous display might be considered to be adaptive if dewlaps with low UV and chroma that are rapidly extended and retracted contrast well against a high UV-reflecting and brightly lit background, and if this type of display is more conspicuous to recipients in sunny habitats than a display that emphasizes a series of rapid headbob movements. While this specific comparison has yet to be made, there is some evidence that the UV reflectance of the dewlap, and its subsequent detection, is related to the level of UV reflectance of backgrounds and intensity of ambient light (i.e. low UV-reflecting dewlaps contrast well with high UV-reflecting backgrounds in full sun species; Leal & Fleishman 2002; see also Fleishman 2000).

Historical influences, however, are also apparent in the distribution of PSynch; taxa do retain aspects of their phenotype from their evolutionary ancestors (Fig. 3). Determining what those

historical influences might have been is difficult. Closely related taxa within islands do tend to be the same ecomorph, and an ecomorph is the product of natural selection. That is, the historical influence on PSynch seen in Fig. 3 might reflect a correlation between display phenotype and ecomorph, with ecomorph being the product of stabilizing selection that tends to track phylogeny on a small scale. But again, for the reasons we outline above, we think that display convergence has been driven primarily by selection for enhanced detection in low light environments, and not by ecomorph per se. The evolutionary ancestor of the Puerto Rican radiation most likely performed a display that emphasized dewlapping, with phylogenetic reconstructions of PSynch recovering a value of 34.9% (confidence interval of 32.9–36.9%; reconstructions were computed using COMPARE 4.6b (Martins 2004) and the phylogenetic generalized least squares (PGLS) model outlined in Martins & Hansen (1997), with the adjustment to the computed standard errors from Rohlf (2001)). A similar low value of PSynch suggesting a reliance on dewlapping was also calculated for the ancestor of the Jamaican radiation (confidence interval: 28.7–34.0%, but this analysis did not include *A. sagrei*, an invasive species from Cuba). Playback experiments are the only means to adequately test the adaptive significance of the asynchronous display. However, a survey of other *Anolis* species on different islands would help resolve the origins of the synchronous versus asynchronous types of display on the anole phylogeny. Convergence by definition is the independent evolution of an adaptation (or similar phenotype more generally) in different taxa, and this has yet to be resolved for taxa that emphasize dewlapping (towards the asynchronous end of the PSynch continuum). Regardless, for at least taxa that emphasize headbobbing (those towards the synchronous end of the continuum) there were clear convergences in territorial display among species on Jamaica and Puerto Rico (Figs 3, 4).

Most examples of convergent evolution in behaviour either have not had a common selection pressure or have not had an independent evolutionary origin explicitly identified. Returning to those examples highlighted in the Introduction, similar web designs in Hawaiian spiders have clear independent origins on each island (Blackledge & Gillespie 2004), but why these convergent designs have evolved is unknown. A qualitative review of bat echolocation calls (Jones & Holderied 2007) presents a compelling argument for the independent origin of remarkably similar signal designs in different species groups, and several possible sources of selection are mentioned, but a formal test of the convergence hypothesis has yet to be done. Indeed, even for the remarkable similarity in the seet alarm calls produced by different species of songbird (Marler 1955), a classic textbook example of convergent behaviour (Alcock 2009), there is some evidence that predatory birds may have more difficulty hearing these calls than do nearby conspecifics (Klump et al. 1986), but no comparative study has examined whether seet calls have evolved in response to predation or the extent to which these calls originated independently in different species. The degree of territory overlap among conspecific male *Anolis* lizards, and to some extent display rate, is associated with ecomorphology, but the reasons for these convergences are unclear (Losos 1990; Johnson et al. 2010). One of the rare cases in which both an independent origin and viable selection pressure have been identified is the behavioural convergence of shared maternal care strategies between ungulates and macropods that have probably evolved in response to heightened predation risk (Fisher et al. 2002).

Our study offers a new example of adaptive convergence in animal behaviour. It also demonstrates that complex phenotypes can respond adaptively in multifaceted ways, and that recent evolutionary history can affect the expression of convergent phenotypes among closely related taxa (e.g. species like *A. poncensis*

and *A. evermanni* shared the display type of their immediate relatives, despite occupying very different habitats; Figs 3, 4). Subsequently, signals of some species may not always appear adaptively suited to their current environment. The likelihood of this will depend not only on the strength and consistency of selection over evolutionary time, but also on the amount of time that species have had to adapt to the changed conditions on colonizing a new environment.

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## Supplementary Material

Supplementary material for this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2013.03.037>.

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