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Receiver perception predicts species divergence in long-range communication

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The design of animal signals is believed to reflect the combined effect of the sensory system of receivers, the type of environment in which communication is being conducted, and the distance signals must travel in that environment. Although empirical studies have examined how each of these factors might separately explain the structure of signals used by animals within species, comparative evidence supporting the predicted interaction of the sensory system, environment and transmission range in the generation of species differences in communication is lacking. I studied the long-range visual displays used by male Caribbean *Anolis* lizards to advertise territory ownership. The type of movements included in advertisement displays was closely predicted by the motion detection capabilities of the visual system for a given distance and the compounding effects of environmental conditions at the time of display production. Furthermore, the motion detection of *Anolis* receivers predicted almost precisely the type of movements included in advertisement displays among closely related species from two separate island radiations. My study provides rare comparative evidence illustrating how the sensory system of receivers sets the minimum requirements for what constitutes an effective signal, given the transmission distance of signals, with further variance in signal structure resulting from the environmental conditions occurring at the time of communication.

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Effective communication is a formidable challenge faced by many animals. As social signals travel through an animal's habitat, background noise and other environmental factors invariably lead to signal degradation and attenuation that can severely limit both the detection and assessment of a signal by its intended receiver (Wiley & Richards 1982; Brenowitz 1986; Brumm & Slabbekoorn 2005; Wiley 2006). The distance over which communication occurs exacerbates the adverse environmental effects acting on animal signals, with reductions to signal fidelity being a particular problem for long-range signals (Wiley & Richards 1982; Naguib & Wiley 2001). Yet effective long-range communication is crucial for successful reproduction in many animals to attract mates (Brumm & Slater 2006; How et al. 2008; Naguib et al. 2008; Leonard & Hedrick 2010) or advertise territory ownership that determines access to mates (Kime et al. 2000; Peters & Evans 2007; Ord & Stamps 2008; Charles & Ord 2011). The strategies adopted by animals to facilitate long-range communication are well documented in acoustically communicating animals (e.g. changes to the amplitude, frequency and duration of vocalizations; reviewed by Brumm & Slabbekoorn 2005), with similar information becoming

available for other signal modalities, most notably visual signals (e.g. Ord et al. 2007; Peters et al. 2007; How et al. 2008; Fleishman & Pallus 2010). An important outcome from these studies is the recognition that it is not just the distance of communication and the environment that is important, but the sensory system of the receiver as well. On the one hand, long-range signals must include characteristics that resist degradation as they travel through the environment. On the other hand, signals must also sufficiently stimulate the sensory system of the receiver to elicit a response (Endler 1992; Ryan & Keddy-Hector 1992). Classic examples of how receiver senses can dictate signal design include the tuning of male mating calls to the female auditory apparatus in frogs (Ryan 1986; Gerhardt & Schwartz 2001; Wilczynski et al. 2001).

The lesson from such studies is that if we are to fully understand how animals resolve the problem of effective long-range communication, then we must consider the distance over which signals must travel, environmental factors acting on signals, and the sensory system used to detect signals. More generally, the types of stimuli readily detected by the sensory system of receivers should also lead to predictable variation in how signals are designed among closely related species whenever species communicate at different ranges and in different environments. Obtaining the behavioural and ecological information for the large number of species required to test this idea is difficult. Indeed, few studies have investigated the combined effects of receiver perceptual capabilities, distance and environment effects in creating signal

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divergence among species, despite a common belief that the interaction of all these factors are likely to be important in the evolution of signal design (Endler 1992; Basolo & Endler 1995). I report such a study here on the territorial advertisement displays of male tropical *Anolis* lizards from two separate island radiations on Jamaica and Puerto Rico.

Caribbean *Anolis* lizards offer an ideal model system for the study of long-range communication and the design of animal signals for several reasons. First, in an attempt to monopolize mating opportunities, adult males establish territories that overlap the home ranges of females (Stamps 1983). Resident males advertise territory ownership and discourage territory intrusions from other males using elaborate body movements or headbob displays, which are often accompanied by the extension of a throat fan or dewlap. To be effective as territorial advertisements, these visual displays must be conspicuous to multiple male and female receivers at a range of distances in the surrounding environment (Ord et al. 2007). Long-range communication is therefore a crucial component of the reproductive success of adult males in *Anolis* lizards. Second, both the production and detection of male advertisement displays are dependent on the level of visual noise generated by windblown vegetation and the available light in the environment. To compensate for poor viewing conditions resulting from distracting environmental motion and low light, male lizards of many *Anolis* species increase the speed of display movements (Ord et al. 2007, 2010). Robot playback experiments on one species have also confirmed that high-speed displays enhance display detection at typical neighbour distances (Ord & Stamps 2008). Furthermore, much (but not all) of the variation among *Anolis* species in display speed, as well as several other display characteristics, is explained by differences in visual noise and light levels experienced by lizards advertising territory ownership in different habitats (Ord et al. 2010, 2011). Typical male neighbour distances do vary widely among *Anolis* species as well (Ord et al. 2010; Charles & Ord 2011), and neighbour distance within at least one species seems to influence the speed of movements included in advertisement displays (Ord & Stamps 2008). However, the extent to which variation in neighbour distance affects differences in the production and design of territorial advertisement displays, both within and between species, has not been fully investigated.

Finally, and most importantly for the purposes of the current study, the motion detection capabilities of *Anolis* lizards have now been quantified for two species (Fleishman 1986; Pallus et al. 2010). This makes it possible to estimate the type of movement that should be most effective at grabbing the attention of receivers at a given distance. In this study, I used the available information on *Anolis* motion detection to bracket the likely optimum speeds at which Jamaican and Puerto Rican *Anolis* lizards should perform display movements, given the typical distance to territorial neighbours. I tested whether males within species performed displays at these expected speeds and the extent to which fluctuations in visual noise and ambient light that also affects signal detection explained deviations from those optimum speeds. I then evaluated a series of evolutionary models to identify the nature of the relationship among species between neighbour distance and divergence in display speed, and whether that relationship could be explained by the probable motion detection capabilities of receivers.

METHODS

Data Collection

Details on the methods used to obtain data on display speed, visual noise and habitat light can be found in Ord et al. (2007; see

also Ord 2008). Briefly, I surveyed the majority of *Anolis* species on the islands of Jamaica and Puerto Rico, and in some instances replicated my observations on two populations for four species. I treated replicate populations separately in all analyses, and will refer to species and populations collectively as taxa throughout this article. The data set covered 16 taxa (representing 12 species; see Supplementary Material, Fig. S1). Display data were obtained by videorecording adult male lizards on their territories for 20–30 min, during which time most males performed several advertisement displays (displays that were not clearly directed to a particular conspecific in the environment). Video was recorded on high-quality digital tape (miniDV). Clips of individual displays were exported from tapes and analysed using computational motion analysis in the MatLab-based program AIM (Analysis of Image Motion; Peters et al. 2002). The program's 'define Region of Interest' option was used to separate motion corresponding to the displaying lizard from that occurring in the background of the image. Display movement and background motion (i.e. visual noise) were summarized separately as the maximum speed recorded over the video sequence, which was then averaged across all clips for a given lizard for use in statistical analyses. Habitat light was measured at the end of videorecording at the site of first display using an LI-250A hand-held light meter with an LI-190SA Quantum Sensor positioned parallel to the ground. I took the average of two readings corresponding to the approximate position of the left and right eye of the lizard. Light data were measured as $\mu\text{mol}/\text{m}^2/\text{s}$ and was log-transformed for statistical analyses. The distance to all adult male neighbours observed during the 20–30 min period of videorecording and within sight of the focal lizard was measured with a tape measure from the site of first display. I took the average of the distances to all surrounding male neighbours for a given focal lizard as a measure of the typical distance over which advertisement displays were most likely to be viewed by receivers. I focused specifically on male neighbour distance, as the majority of female receivers can be expected to be within the territory of the resident male or those of his male neighbours, and consequently to be encompassed within the range estimated for adult male neighbours.

Motion Detection

I used findings from behavioural experiments quantifying motion detection in *Anolis* (Fleishman 1986; Pallus et al. 2010) to estimate the probable optimum speed at which lizards should perform display movements to maximize detection by territorial neighbours at a range of distances. These experiments showed that the detection of a moving stimulus approximating the up-and-down motion of an advertisement display is maximized at a visual angle of 0.2–0.4° (with detection declining outside this range), and this was consistent for two distantly related *Anolis* species (the mainland grass anole, *A. auratus*; Fleishman 1986; the Cuban brown anole, *A. sagrei*, a species that is also invasive to Jamaica, e.g. Fig. S1; Pallus et al. 2010). Visual models of motion perception in *Anolis* further support this 0.2–0.4° range for optimal motion detection (Fleishman & Pallus 2010; Pallus et al. 2010). Combined with evidence from an electroretinographic study of several Puerto Rican anole species (*A. gundlachi*, *A. cristatellus* and *A. pulchellus*; Fleishman et al. 1995), motion perceptual capabilities in the *Anolis* genus seem highly conserved among species. The optimal movement of advertisement displays that a male lizard performs should therefore be similar regardless of species, and computable if receiver distance is known for a species.

To be clear, Fleishman (1986) and Pallus et al. (2010) made specific predictions on display detection based on an estimate of the optimum amplitude of abrupt movements that elicited

responses by lizards in laboratory experiments. That is, motion detection was dependent on both high-speed (abrupt) and high-amplitude movement, but the studies specifically inferred motion detection as a function of display amplitude, not speed per se. This is because the ‘abrupt’ movement typically included in *Anolis* advertisement displays occurred over time frames that were likely to be too rapid for the vertebrate eye to resolve the speed of movement. Instead, such movements are perceived as seemingly instantaneous displacements. The attribute affecting detection was therefore the magnitude or distance of the displacement, or in the context of territorial displays, the amplitude of abrupt display movements (Fleishman & Pallus 2010). Yet speed and amplitude are not necessarily linked during display production; nor are they necessarily always equally important for the detection of advertisement displays. For example, a lizard might gradually raise his head in a high-amplitude movement of low speed, but distant inattentive territorial neighbours would be unlikely to detect this movement because of its low speed. In other words, the speed of display movements becomes important for display detection when those movements are performed over longer periods.

I focused on the maximum speed of advertisement displays, which corresponded to abrupt body movements occurring over 33–66 ms; that is, over one to two video frames (see Figures in Ord et al. 2007 and Fleishman & Pallus 2010). As calculated by the AIM program (and as the vertebrate eye would perceive such movements), the estimated speed of such abrupt movements should be equivalent to the motion amplitude of the display. I confirmed this by measuring the maximum amplitude of displays performed by 20 adult male lizards of *A. gundlachi* from display-action-pattern graphs that trace the displacement of the head over time (see Ord et al. 2007 for details). Amplitude was measured in millimetres and was the height the lizard lifted his head above the substrate during a territorial display. In all cases, the maximum amplitude of a display corresponded to abrupt movement occurring over 33–66 ms. I then correlated maximum amplitude, averaged across all displays performed by a given individual, and maximum speed for the same display sequence, as estimated by the AIM program (measured in mm/s), again averaged across all displays for a given individual. There was a strong correlation between maximum display amplitude and maximum display speed (Pearson’s product-moment correlation: $r = 0.62$, $t = 3.32$, $df = 18$, $P = 0.004$), with the relationship being roughly one to one (that is, a slope not statistically different from 1; 95% confidence intervals 0.34–1.33). Maximum speed was therefore proportional to motion amplitude.

With this in mind, it was possible to estimate the optimum speed, S_{\max} (or the amplitude of motion), for a given visual angle of movement, θ (in degrees), viewed at a given distance, d (in mm), using:

$$S_{\max} = 2d \left(\tan \frac{\theta}{2} \right) \quad (1)$$

With this equation, I was able to compute the maximum headbob speed for 0.2° and 0.4° to determine the lower and upper bounds of the display speed that should effectively grab the attention of territorial neighbours at progressive 1 m increments from the displaying lizard.

Implicitly, equation (1) assumes that the optimum speed for the detection of the headbob display is a continuous function of viewer distance. Charles & Ord (2011) found that *Anolis* species with average neighbour distances greater than 5 m were significantly more likely to possess a conspicuous tail crest, which was predicted to facilitate the detection of the territorial advertisement display more generally. It is possible, then, that the relationship between display detection and neighbour distance is instead reflected as

a threshold. That is, the detection of display movement is more likely to be compromised at receiver distances greater than 5 m, perhaps because the adverse effects of visual noise or habitat light on motion perception become especially acute at these distances. I considered the possibility of a threshold effect for receiver distance in my analyses (see next section).

I did not include dewlap extensions in my analyses, because these movements were generally of lower speed than headbob displays (Ord et al. 2010; see Discussion).

Statistical Analyses

I used the lme4 package v0.999375-31 (Bates 2008) in R v2.9.1 (R Development Core Team, The R Foundation for Statistical Computing, Vienna, Austria) to fit a mixed model to first test whether lizards within taxa increased headbob speeds with increased neighbour distance. The model included a random intercept and random slope for taxon (for discussion of mixed model design in the context as it is applied here, see Ord et al. 2010), and a fixed effect that corresponded to whether lizards belonged to taxa in which the average neighbour distance was greater than the putative threshold of 5 m (lizards of taxa with neighbours that were on average closer than 5 m were coded as ‘0’, and those lizards from taxa with neighbours that were on average greater than 5 m were coded as ‘1’). I used the interaction term between the taxon threshold and actual neighbour distance recorded for a given lizard to consider differences in the way lizards performed displays as a function of neighbour distance above and below the 5 m cutoff.

I then tested whether the speed of advertisement displays was optimal by computing the residual of a lizard’s display speed from the lower bound of 0.2° visual angle, which seems to be the minimum level of movement required to effectively grab the attention of a receiver (Fleishman 1986; Pallus et al. 2010). This analysis also provided a direct test of the consequences of environmental conditions on display performance while controlling for distance effects on perception. A residual value below zero infers that a lizard displayed at speeds below that expected for effective communication; a residual of zero indicates that a lizard displayed at exactly the minimum speed required for effective communication; a residual above zero infers a lizard displayed at speeds greater than the minimum required for effective communication, given the average distance of its territory neighbours. In the latter instance, I predicted that the compounding effects of high visual noise and low habitat light would explain why lizards displayed at speeds greater than that apparently required based solely on the distance of their territory neighbours. Specifically, I applied a mixed model that included a random taxon effect for visual noise and light to determine: (1) whether the mean residual for taxa differed significantly from zero (indicated by a significant intercept); and (2) whether deviations from a mean residual of zero were explained by differences in visual noise and ambient light experienced by lizards within taxa. The mixed model applied was similar to the model evaluating the influence of neighbour distance on display performance more generally, with a random effect for taxon and fixed effects of noise and light. Island origin of taxa was also included as a fixed effect and its interaction with both noise and light considered, because it has previously been shown that lizards from each island differ in the extent that they tailor display performances for enhanced detection, depending on prevailing environmental conditions at the time of display (e.g. Ord et al. 2010).

For all mixed models, I report effect sizes in the form of t values and 95% confidence intervals of intercepts and slopes. Confidence intervals that do not overlap zero are equivalent to statistically significant differences at $P < 0.05$.

Finally, I investigated the evolutionary implications of receiver distance on taxon divergence in display speed by assessing the fit of several alternative evolutionary models using the SLOUCH v1.2 program implemented in R (Hansen et al. 2008). Each model differed in how receiver distance might have influenced variance in headbob speed between taxa: (1) display speed increased linearly with neighbour distance (the 'linear regression' model); (2) display speed increased at progressively greater increments with neighbour distance (the 'polynomial regression' model; i.e. $y = x + x^2$); (3) display speed only increased in lineages estimated by maximum likelihood to have neighbour distances farther than 5 m (the 'threshold: likelihood' model); (4) display speed only increased in lineages estimated by parsimony to have neighbour distances farther than 5 m (the 'threshold: parsimony' model); or (5) display speed is unrelated to neighbour distances (the 'null' model). Maximum likelihood reconstructions of neighbour distance were estimated using the phylogenetic generalized least squares algorithm in COMPARE v4.6b (Martins 2004; see Fig. S1). Parsimony reconstructions of neighbour distance were estimated using Mesquite v2.72 (Maddison & Maddison 2009) based on terminal taxa coded as '0' or '1' depending on whether their average neighbour distances were less than or greater than 5 m, respectively. I evaluated the evidence in support of each of the five models using Akaike's Information Criterion with a correction for small sample size, AIC_c . The model with the lowest computed AIC_c value is considered the model of 'best' fit, although any model within two AIC_c units of this lowest model is considered equally supported by the data (i.e. $\Delta AIC_c < 2.0$; Burnham & Anderson 2004). To further evaluate the relative likelihood of each model, I computed model weights, AIC_w , to determine the level of evidence in favour of a given model relative to the other four models tested (Johnson & Omland 2004).

SLOUCH uses an Ornstein–Uhlenbeck model of evolution that incorporates the extent that trait evolution has been free to vary adaptively (reflected in the parameter $t_{1/2}$) and the influence of stochastic factors (v_y) during evolutionary diversification. Low phylogenetic signal is reflected by $t_{1/2}$ values that approach 0 (i.e. trait characteristics have not been retained from evolutionary ancestors), whereas high phylogenetic signal corresponds to large values of $t_{1/2}$ ($t_{1/2}$ can range from 0 to ∞). Low values of v_y suggest that stochastic forces resulting in nonadaptive phenotypic variation have been weak (v_y has a range from 0 to ∞). I report the range of $t_{1/2}$ and v_y within two likelihood units that by convention are considered to be estimates that fit the data equally well. In the context of a threshold effect for receiver distance, SLOUCH estimates the likelihood that lineages with neighbours farther than 5 m have converged towards a common display type characterized by high speed, relative to lineages with neighbours closer than 5 m. Within-taxon variance associated with taxon values were incorporated in all models.

I used the phylogeny created by Nicholson et al. (2005) based on 1483 aligned base pairs of mitochondrial DNA sequences (additional information on branch lengths for this tree are given in Losos (2009)). Statistical support for species nodes in the subsection of the phylogeny that I used were strong, with most Bayesian posterior probabilities at or above 90% and bootstrap support in parsimony analyses greater than 80% (Nicholson et al. 2005). For species in which I sampled two populations, I set branch lengths based on the minimum population divergence estimated among *Anolis* species on Jamaica (Jackman et al. 2002; see also Ord et al. 2010).

RESULTS

Within taxa, variance in display speed among lizards was not directly correlated with neighbour distance (Table 1), but displays

Table 1

Linear mixed model of the maximum display speed performed by adult male *Anolis* lizards from Jamaica and Puerto Rico as a function of the average distance to territory neighbours and whether lizards belong to taxa above or below the 5 m distance threshold

Variable	β (lower CI, upper CI)	t
$N_{\text{lizards, taxa}}=232, 16$		
Intercept	22.22 (18.16, 26.27)	10.74
Neighbour distance	-0.01 (-0.74, 0.72)	-0.02
Threshold	6.21 (0.70, 11.72)*	2.21
Neighbour distance*threshold	0.00 (-0.88, 0.87)	-0.01

Slopes with 95% confidence intervals (CI) that did not overlap zero are indicated with an asterisk and were considered statistically significant. See text for other details.

were significantly greater than the minimum speed likely required to grab the attention of territorial neighbours given the distance of those neighbours (Table 2). Specifically, residuals of display speed were significantly greater than the lower bound necessary for effective communication (i.e. the model intercept was significantly greater than zero; Table 2). Lizards therefore performed advertisement displays at speeds generally higher than required. These deviations from minimum effective speed were explained by the level of visual noise and habitat light experienced by lizards (Table 2). For example, plots for representative taxa (Fig. 1a) show that lizards generally performed displays at speeds above the minimum required for detection by neighbours (indicated by the dashed line). These plots illustrate that lizards increased the speed of their displays above this minimum as a function of increased visual noise and reductions in ambient light, environmental conditions known to exacerbate signal detection in lizards (e.g. Ord & Stamps 2008; Peters 2008).

Moreover, the 0.2–0.4° visual angle that is likely to correspond to the optimum range of movement for reliable detection by receivers clearly bracketed the speed of advertisement displays performed by different taxa, given the distance of their territorial neighbours (Fig. 1b). Only one species fell outside of this optimum region, *A. krugi*, and at a display speed greater than expected considering the proximity of its territorial neighbours (under 3 m). The 95% confidence intervals (CI) of neighbour distance for this species did extend into the computed optimum range (1.5–3.9 m; Fig. 1b), so this may reflect measurement error in neighbour distance for this species rather than a biological anomaly. In any respect, 33–39% of the variance in display speed among taxa was explained by receiver distance (Table 3). There was some evidence

Table 2

Linear mixed model of the deviation of the maximum display speed performed by adult male *Anolis* lizards from the minimum required for detection, as a function of visual noise and habitat light

Variable	β (lower CI, upper CI)	t
$N_{\text{lizards, taxa}}=231\ddagger, 16$		
Intercept	6.22 (0.97, 11.47)*	2.32
Visual noise	0.69 (0.28, 1.10)*	3.32
Ambient light	-3.15 (-5.28, -1.03)*	-2.91
Island origin	1.07 (-2.34, 4.48)	0.62

Display speed was computed as the residual from the 0.2° visual angle estimated to be the minimum level of movement needed for reliable detection by receivers (Fleishman 1986; Pallus et al. 2010). Slopes with 95% confidence intervals (CI) that did not overlap zero are indicated with an asterisk and were considered statistically significant. Interaction terms of island with light and noise were not significant (island*noise: $\beta = 0.92$ (-0.13, 1.97), $t = 1.72$; island*light: $\beta = 1.22$ (-3.53, 5.97), $t = 0.50$) and dropped from the final model. A residual greater than zero indicates that a lizard performed advertisement displays at speeds higher than required for effective communication given the distance of its territorial neighbours.

† One lizard was removed from the analyses because it was associated with an extreme outlier estimate of light.

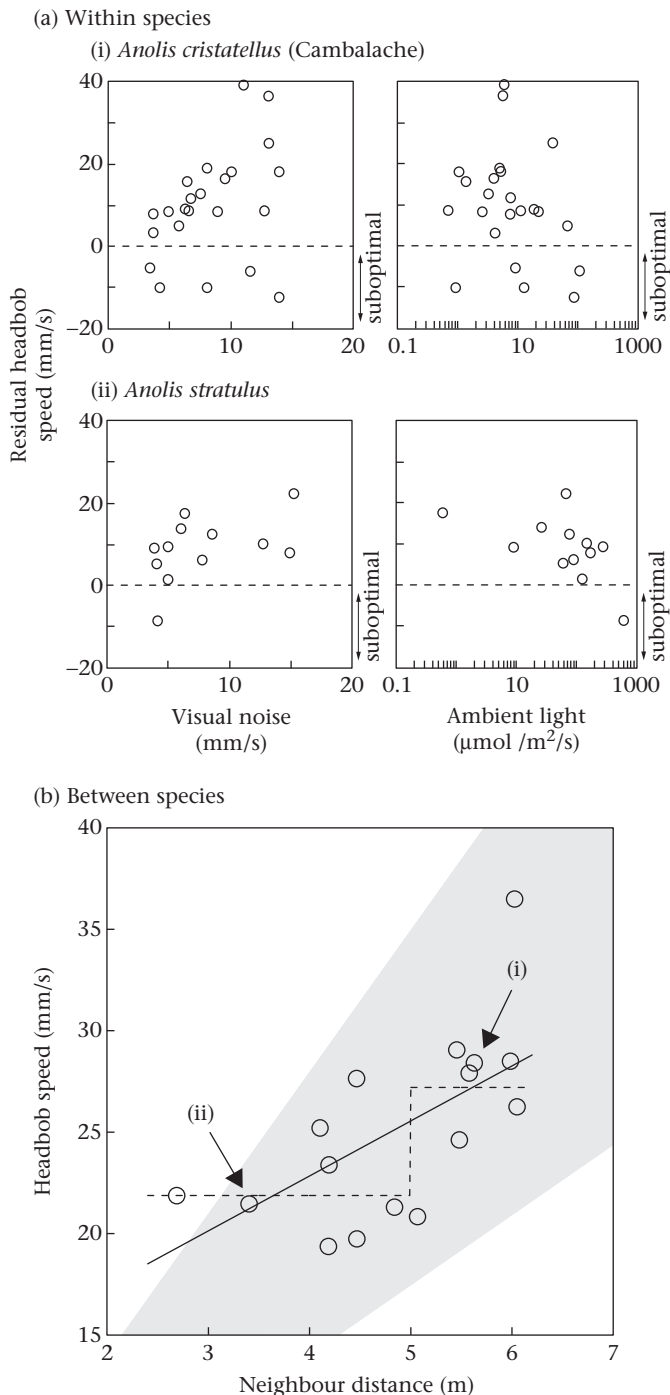


Figure 1. The speed of headbob movements used by male *Anolis* lizards to advertise territory ownership is tailored to the likelihood that those displays will be detected by territory neighbours. (a) Two representative species (*Anolis cristatellus* and *A. stratulus*), illustrating the relationship between environmental conditions that reduce visibility and deviations in display speed from the minimum speed required for detection by neighbours given their distance. Each point corresponds to the residual speed from the minimum level of movement that effectively grabs the attention of a receiver (0.2° visual angle; Fleishman 1986; Pallus et al. 2010). Lizards generally performed displays at speeds greater than would be expected based purely on neighbour distance (i.e. most values were greater than zero). This was because lizards had to further compensate for reduced display detection resulting from visual noise (distracting movement from windblown vegetation) and poor habitat light. That is, deviations in speed increased linearly with increased visual noise (panels to the left) and reductions in light (panels to the right). (b) Illustration of how, on average, the speed of advertisement displays among taxa fall almost exclusively within the optimum range for detection by territory neighbours. Here, points represent the means for individual taxa from Jamaica and Puerto Rico. Superimposed in grey is the range of speeds expected to

suggesting the existence of a threshold effect for receiver distance with the 'threshold: likelihood' model being the best supported of the five models evaluated (Table 3; in this model, the 95% CIs of the adaptive optima for the speed of displays for taxa with neighbours farther than 5 m was computed as 24.9–29.5 mm/s, whereas the optima for taxa that displayed to neighbours closer than 5 m was computed as 19.4–24.3 mm/s; see also Fig. 1b). The 'linear regression' model was the second most supported model (Table 3; intercept = 12.00 (95% CIs: 3.68–20.33), $\beta = 2.71$ (1.01–4.40); see also Fig. 1b). Regardless of the specific nature of the relationship (threshold or linear), the speed of advertisement displays has apparently increased as a function of receiver distance and in a manner consistent with what would be expected given the type of movements readily detected by *Anolis* lizards.

DISCUSSION

The sensory system of *Anolis* lizards has played an important role in determining how territorial males perform advertisement displays. In particular, the perceptual abilities of receivers has probably set a minimum speed at which display movements must be performed to be conspicuous. Given that moving the body up and down during displays must be energetically expensive (e.g. Brandt 2003; Perry et al. 2004) and might also be used by predators to localize lizards (see Ord & Stamps 2008), displays should not be performed at speeds much higher than this minimum. Indeed, it is quite remarkable how closely the average speed of advertisement displays of almost all taxa examined matched the expected range of movement that should be optimal for detection by the visual system of *Anolis* lizards (Fig. 1b; Fleishman 1986; Pallus et al. 2010). There was nevertheless considerable variance around these taxon averages, with lizards within taxa often performing displays at speeds greater than apparently necessary for the distance of their territory neighbours (Fig. 1a). Yet this is also explained by how lizards probably detect display movement under different conditions. Although the distance to territory neighbours determines the minimum speed required for an effective advertisement display, the level of visual noise and ambient light at the time of display will further reduce the visibility of display movements (Ord & Stamps 2008; Peters 2008). My analyses showed that those lizards performing displays at speeds higher than the minimum required probably did so because they were also coping with high visual noise or poor light (Table 2; Fig. 1a).

The motion detection capabilities of *Anolis* lizards offer some additional insight into previously reported differences in display behaviour between species from Jamaica and Puerto Rico. Although the range of headbob speeds used in advertisement displays by species on each island are similar (Ord et al. 2010), Puerto Rican species are capable of tailoring both the speed and duration of their displays according to fluctuations in visual noise and light; that is, the displays of Puerto Rican *Anolis* are contextually plastic (Ord et al. 2007, 2010). Puerto Rican species have also been shown to time the production of advertisement displays to coincide with periods when environmental conditions are at their most favourable for communication (Ord et al. 2011). In contrast, displays of Jamaican species are neither contextually plastic nor strategically

be optimal, based on the minimum and maximum level of movement that is most readily detected by these lizards (0.2 – 0.4° visual angle; Fleishman 1986; Pallus et al. 2010). Also shown are the trend lines associated with the two most supported evolutionary models listed in Table 3. The dashed line assumes the evolution of headbob speed abruptly increased in taxa with territory neighbours farther than 5 m (the 'threshold: likelihood' model; see also Fig. S1), whereas the solid line reflects a situation in which the evolution of headbob speed increased in a continuous, linear fashion with neighbour distances (the 'linear regression' model).

Table 3
Levels of support for five alternative models summarizing the potential evolutionary relationship between the speed of territory advertisement displays performed by *Anolis* lizards and the average distance of territory neighbours

Evolutionary model	AIC _c	ΔAIC	AIC _w	% r^2	$t_{1/2}$ (support region)	v_y (support region)
$N_{\text{taxa}}=16$						
Threshold: likelihood	94.46	0.00	0.40	33.5	8.5 (0.0–38.0)	7.5 (4.0–18.0)
Linear regression	94.83	0.37	0.33	38.7	10.0 (0.0–∞)	4.5 (0.0–230.0)
Threshold: parsimony	95.98	1.52	0.18	36.5	0.0 (0.0–37.0)	8.5 (2.5–18.0)
Null	97.39	2.93	0.09			
Polynomial regression	113.88	19.43	0.00			

See *Methods* for description of parameters. The phylogeny used for analyses is shown in *Fig. S1*.

timed to avoid adverse environmental conditions. Instead, these species seem to rely on the inclusion of rapid dewlapping as part of their advertisement displays (Ord et al. 2011). In support of this hypothesis, the speed of Jamaican dewlap extensions are within the optimum range of 0.2–0.4° (specifically, 22–32 mm/s), whereas this is only true for the headbob displays of Puerto Rican species. This is also consistent with previous findings from robot playback experiments that showed dewlap extensions performed at speeds comparable to headbob movements were equally effective at enhancing the detection of the advertisement display (Ord & Stamps 2008).

Interaction terms between island origin and plasticity in display deviations were not statistically significant in the current study (see *Table 2*; i.e. both Jamaican and Puerto Rican taxa seemed to tailor residuals in display speed to fluctuations in visual noise and light). However, this probably reflects differences in statistical power between this and previous studies (current study: $N_{\text{lizards}} = 231$; Ord et al. 2010: $N_{\text{lizards}} = 389$). Inspection of regression slopes estimated separately for Jamaican taxa showed plasticity in display was low, if not absent. The results reported in *Table 2* are therefore apparently almost entirely driven by plasticity in Puerto Rican taxa.

In light of this display plasticity (at least on Puerto Rico), it is uncertain whether the variation among taxa in headbob speed shown in *Fig. 1b* reflects an evolutionary or plastic response to differences in receiver distance between taxa. Assuming the average distance to receivers within a population is consistent across generations (which should result in stabilizing selection on display speed; see below), any event that brings a permanent shift to receiver distances (e.g. the invasion of a new environment) should prompt a corresponding evolutionary change in mean display speed (note: displays might still be plastic around this mean response to accommodate momentary fluctuations in visual noise and light; i.e. *Table 2*; Ord et al. 2010). I suspect that evolutionary change is responsible for at least some of the variance in display speed associated with receiver distance. Evolutionary change in mean display speed has been previously documented in these lizards as a function of habitat light, indicating that headbob speed has evolved in response to other factors affecting display detection (Ord et al. 2010). Moreover, the average distance to territory neighbours is generally consistent from year to year within species (e.g. *A. gundlachi* at El Verde, 2005: 3.3–6.4 m (95% CIs), $N = 12$ (male territory holders); 2006: 4.7–7.2 m, $N = 14$; 2007: 4.2–7.1 m, $N = 14$; 2009: 4.1–6.1 m, $N = 12$), suggesting that receiver distance is probably consistent across generations as well, providing the opportunity for stabilizing selection on an optimum mean display speed to occur. Conversely, in the absence of fluctuations in neighbour distance, plasticity in relation to receiver distance will serve no adaptive function. Plasticity would therefore have either not evolved in the first place, or ultimately become lost if there were costs associated with being plastic. Nevertheless, future studies will need to confirm that lizards do not learn the range of appropriate display speeds to perform based on the responses elicited from receivers

(learning being the most likely source of plasticity in communication; see Ord et al. (2007) for discussion).

In any respect, the Caribbean *Anolis* lizards present an excellent example of how the sensory system of receivers, the range over which signals must be transmitted, and the properties of the environment interact to generate predictable variation in long-range communication among closely related taxa. If these variables can be adequately measured in more groups, it should be possible to explain with some confidence, not only the way in which animals communicate with one another within populations, but why functionally equivalent signals often differ among closely related species. Presently, studies that attempt to investigate the evolutionary causes of divergence in animal communication generally do not consider the interaction of potential causal factors with receiver perception (e.g. Ord et al. 2002). This is probably pragmatic, because measuring perception capabilities can be difficult and labour intensive. Unfortunately, without this information, our broader understanding of how evolutionary diversification in animal signals occurs is limited, but it may also lead to misleading inferences on the extrinsic factors affecting signal detection.

Had I not considered the detection capabilities of receivers, it would have appeared that display speed was not dependent on receiver distance within taxa (*Table 1*). Robot playback experiments on these lizards have confirmed that distance does reduce the detection of display movements independently of environmental conditions (Ord & Stamps 2008). This would have implied that the displays of lizards with distant territory neighbours would often fail to adequately attract the attention of receivers. Yet the reality was quite different. Once the motion detection capabilities of neighbours was factored into the analysis, it became clear that the majority of lizards actually performed advertisement displays that were probably highly detectable given the typical distance of their neighbours (i.e. the intercept estimate in *Table 2* was significantly greater than zero; see also *Fig. 1a*).

Selection can also act directly on the sensory system itself to produce adaptations in receiver perception that differ among closely related species. For example, the visual system of fish is tailored to the light environment in which species live, and this in turn influences the types of visual stimuli that are viewed as conspicuous among species (Cummings 2007; Seehausen et al. 2008). It is intuitive to expect the coevolution of animal signals to 'exploit' the biases of the sensory system, and there is considerable empirical evidence to support this assertion (e.g. Ryan 1986; Gerhardt & Schwartz 2001; Wilczynski et al. 2001). Changes in receiver perception might therefore be assumed to always correspond with changes in signal design. However, this need not be the case. If sensory systems adapt to facilitate the detection of relevant stimuli in certain environments (e.g. food items, social partners, potential predators), this will tend to reduce selection on signals as a function of the environment. Closely related species will tend not to differ in aspects of their communication. Instead, habitat-dependent changes in receiver perception would obviate the

need for change in the structure of signals. This is quite different from a situation in which the conspicuousness of signals is not affected by the environment (which is probably rarely, if ever, true). Rather, evolutionary change in the sensory system compensates for the potential masking effects of acute environmental conditions. In the case of *Anolis* lizards, the motion detection capabilities of receivers are remarkably consistent among species (Fleishman 1986; Fleishman et al. 1995; Pallus et al. 2010). Colonization of new habitats and changes in receiver distance in this group have subsequently led to divergence in the speed of territory displays among species (Ord et al. 2010; this study).

Any attempt to explain macroevolutionary patterns of phenotypic diversity is complicated by the fact that evolution is a multivariate process; multiple parallel and opposing selection pressures act on animal phenotypes as a whole to create the diversity we see in the natural world. The study of animal communication is no different. Indeed, a large body of theory exists highlighting the multifaceted nature of animal communication (reviewed by Bradbury & Vehrencamp 1998). Our challenge now is to integrate these myriad factors at broad phylogenetic scales, while also considering the nature of signal variation within species. This is a daunting task, but one that should become increasingly possible in the coming years. It supports the argument for a long-term study of model systems in which detailed information from experimentation and observation on select species can be translated to broad phylogenetic scales to retrace the trajectory signal evolution (e.g. *Anolis* lizards: Fleishman 1986; Fleishman et al. 1995; Ord & Stamps 2008; Pallus et al. 2010; Ord et al. 2010; túngara frogs: Ryan & Rand 1990, 2003; Ron 2008; Akre et al. 2011).

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.anbehav.2011.10.016.

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