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Signal transmission and function in the complex displays of Puerto Rican *Anolis* lizards

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Complexity is an important feature of signalling systems, with many organisms incorporating multiple signalling components into their communicative displays. However, why this complexity evolves remains poorly understood. One possible explanation is that different signal components optimize information transmission in different environmental contexts. We used models of signal attenuation to compare how information decays with distance across five distinct signal components in the complex visual displays of Puerto Rican *Anolis* lizards. We predicted that different signal components would differ in their suitability for short- versus long-distance communication. Consistent with this prediction, attenuation distances generally differed among signal components, suggesting that multicomponent displays may facilitate information transmission across different signalling contexts. Attenuation distance also varied considerably among species. To understand why, we examined how environmental factors influence interspecific variation in signal efficacy for each signal component. Specifically, we examined the effects of average receiver distance, ambient light and background visual noise on modelled signal performance across the 10 species of *Anolis* that occur on Puerto Rico. We found that species experiencing higher levels of visual noise exhibited greater attenuation distances for alert, headbob and dewlap movements, whereas species inhabiting brighter environments displayed alert and headbob signals that attenuated over shorter distances. In addition, species that display to receivers at greater distances showed greater attenuation distances for headbob displays. These results highlight how multiple environmental pressures interact to shape the design and functional performance of complex, multicomponent visual signals, and present a framework for exploring the ecological and evolutionary drivers of such signals across taxa.

Animal communication depends on the successful transmission of information from signaller to receiver. For a signal to be effective, it must travel through the environment and stimulate the receiver's sensory system in a way that allows detection and interpretation. The signalling environment therefore plays a central role in shaping signal design. For example, receiver distance determines how much a signal degrades as it propagates (Akçay & Beecher, 2019; Lloyd, 1971; Ord, 2012; Rosenthal et al., 2004), ambient light influences the detectability and discriminability of visual features such as colour and pattern (Fuller, 2002; Hancox et al., 2013; Kranz et al., 2018; Leal & Fleishman, 2004; Maan & Cummings, 2012; McNaught & Owens, 2002; Medina et al., 2017), and background visual noise (e.g. wind-blown vegetation) can distract from both static and motion-based cues

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(Endler, 1993; Ord et al., 2007; Rosenthal, 2007). Because these environmental factors vary across space, time and ecological context, selection is expected to favour signals that maintain efficacy under diverse conditions. This idea forms a core component of the sensory drive framework (Endler, 1992), which emphasizes interactions among environmental conditions, signal properties and receiver perception as drivers of signal evolution.

One proposed solution to these environmental constraints is the evolution of complex, multicomponent signals. Rather than relying on a single trait, many animals use displays composed of multiple elements, such as behaviour, colour or sound (Ay et al., 2007). Although multicomponent displays are widespread, we still have a limited understanding of how environmental variation shapes their structure and function. One possible explanation for such complexity is provided by the efficacy trade-off hypothesis (Hebets & Papaj, 2005), which proposes that different signal components can serve complementary roles when no single component performs well across all conditions. Here, we refer to this idea as the efficacy optimization hypothesis, as the term 'trade-off' typically implies that an increase in one trait necessitates a decrease in another (Garland et al., 2022), which may not be strictly true for signal components. An example of the efficacy optimization hypothesis can be found in the Mediterranean fruit fly, *Ceratitis capitata*, in which males release long-distance pheromones to attract females to a lek and use short-range visual and acoustic signals to facilitate localization and female choice (Benelli et al., 2014). Such components may convey either redundant or distinct information while collectively improving overall signal performance. While several studies have examined the effects of individual environmental variables on particular signal traits (Fleishman et al., 2009; Kranz et al., 2018; Ryan & Rand, 1990), there has been little investigation of how various environmental pressures shape the efficacy of the different signal components within a complex display.

A key functional axis along which signal components may differ is the distance between the signaller and the receiver. As signals propagate, information is progressively lost with increasing distance from the signaller due to limits on sensory resolution and environmental degradation, a process known as signal attenuation (Endler, 1992). In visual systems, attenuation reflects declines in detectability or discriminability with increasing distance, driven by constraints on spatial and temporal acuity (Caves et al., 2018). Models of visual detection provide a powerful framework for characterizing this process by predicting the distance over which a given signal component remains effective (Ord, 2012; Vorobyev & Osorio, 1998). Attenuation distance thus offers a biologically meaningful measure of signal efficacy that links morphology and behaviour to functional performance under natural conditions (Endler, 1993). Despite its relevance, attenuation distance has rarely been used to compare different components of complex visual displays or to test how environmental variation shapes signal performance across species. Examining attenuation therefore provides an opportunity to advance our understanding of how multicomponent signals evolve in response to ecological constraints.

Anolis lizards provide an ideal system for investigating how factors related to signal transmission drive the evolution of complex, multicomponent signals. Anoles rely heavily on visual communication, exhibit extensive interspecific diversity and occupy heterogeneous habitats that vary in light environment, structural complexity and signalling distance (Muñoz et al., 2023). On Puerto Rico, a largely monophyletic fauna of 10 *Anolis* species occupy a wide range of ecological contexts, from open, brightly lit habitats to shaded, visually cluttered forests. These species communicate using a multicomponent visual display involving headbob movements and extensions of a colourful and diversely patterned throat fan, the dewlap (Rand & Williams, 1970). Headbobs involve the up-and-down movement of the lizard's head and body during typical species-specific displays, and dewlap movements involve the extension and retraction of the dewlap. Species also signal with 'alerts', which are exaggerated four-legged push-up movements that often precede species' typical headbob and dewlap extension movements. The headbobs, dewlap extensions and alerts represent behavioural (i.e. dynamic) signals, while dewlap colour patterns (including pattern complexity and colour contrast) are static signals. All five of these components are thought to contribute to species recognition and social interactions during territorial and mating evaluations (Baeckens et al., 2018; Leal & Fleishman, 2002; Losos, 1985; Macedonia et al., 2013; Ord & Martins, 2006; Williams et al., 1977), and the successful execution of these functions requires effective communication across variable viewing distances. Because signaller–receiver distance can range from centimetres to metres even within a single interaction, multicomponent displays may have evolved to ensure effective communication across this range (Bradbury & Vehrencamp, 2011; Hebets & Papaj, 2005).

Although the basic structure of the display is conserved across the *Anolis* radiation, the design of individual components varies markedly, with species differing in the speed and structure of their display movements, as well as in dewlap colour contrast and pattern complexity (Fleishman et al., 2009; Losos, 2009; Nelson & Ord, 2022; Nicholson et al., 2007; Ord & Martins, 2006; Williams & Rand, 1977). This diversity is widely thought to reflect adaptation to differences in the signalling environment. For example, average distances between signallers and receivers may vary among species due to differences in territory size or population density, potentially favouring signals that remain effective over species-specific ranges (Philibosian, 1975). Similarly, ambient light conditions and levels of background motion differ across the average habitats that species occupy, influencing the relative effectiveness of chromatic versus motion-based cues. In bright, open environments, colour and pattern may be especially salient, whereas in dim or visually noisy habitats, exaggerated movements or temporally conspicuous displays may be favoured (Ord et al., 2007). In summary, the interspecific diversity observed in anole display components likely reflects differences among species in the ecological and sensory challenges they face, leading to the expectation that attenuation distances of individual signal components will vary across species and environments.

In this study, we investigated how environmental variation shapes the efficacy of complex, multicomponent visual signals in Puerto Rican *Anolis* lizards by quantifying signal attenuation distance (Fig. 1). We addressed two main questions. First, do different components of the *Anolis* display exhibit predictably different attenuation distances, consistent with the idea that components facilitate information transfer over different ranges? We focused on five components: two static signals, dewlap pattern complexity (fine-scale spatial information) and within-dewlap colour contrast (coarse-scale pattern information); and three dynamic signals, the display speeds of headbobs, dewlap extensions and alert movements. Due to the exceptional sensitivity of anoles to motion, and known limits on their spatial acuity, we predicted that dynamic components would remain detectable over greater distances than static components. Among dynamic signals, we expected alert displays to have the greatest attenuation distance, as they are often directed towards nonspecific receivers during territory advertisement. In contrast, we predicted that static components,

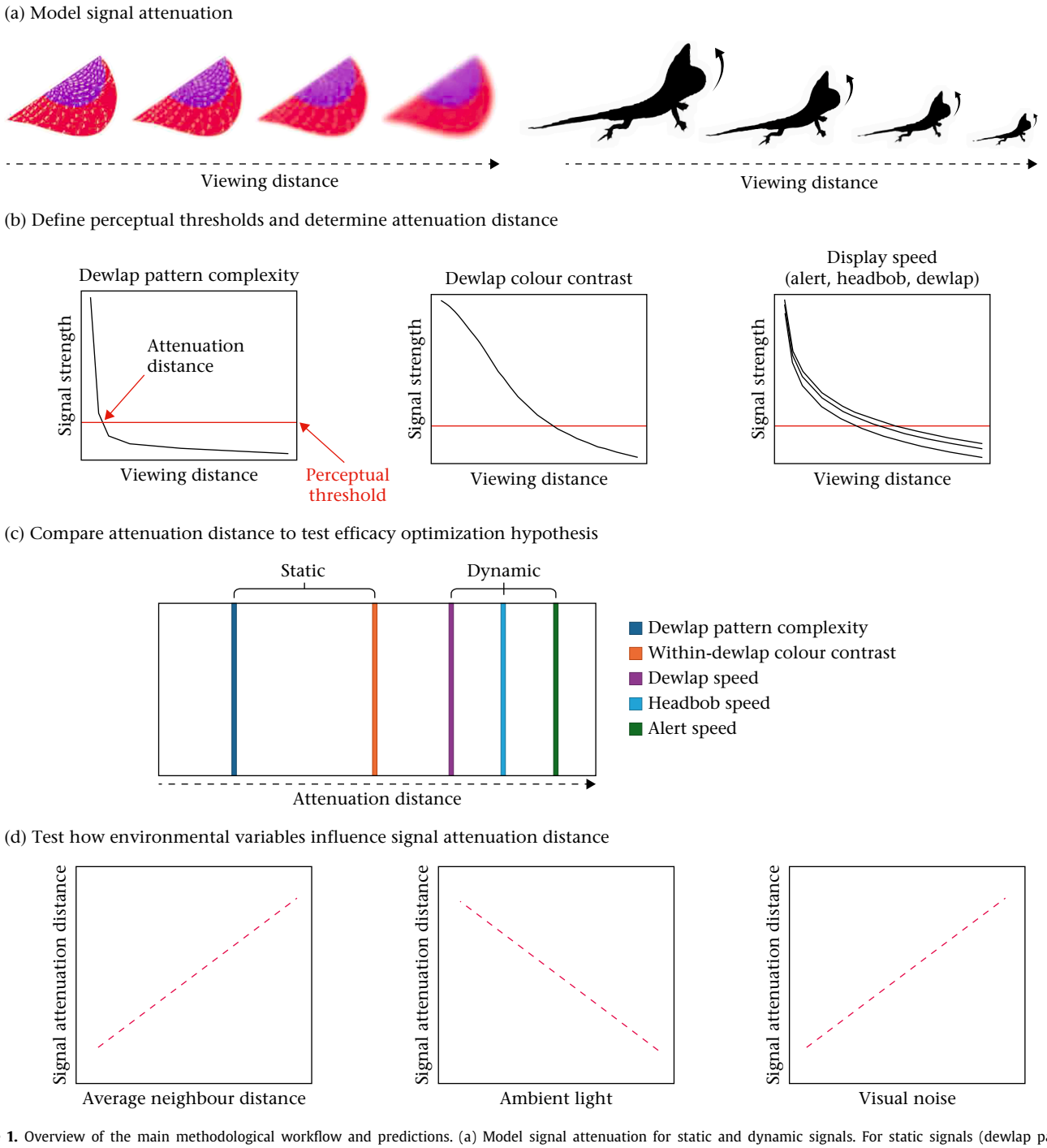

Figure 1. Overview of the main methodological workflow and predictions. (a) Model signal attenuation for static and dynamic signals. For static signals (dewlap pattern complexity and colour contrast), blur dewlap images using 0.08° minimum resolvable angle to model loss of spatial detail as viewing distance increases. For dynamic signals (alert, headbob, dewlap speed), calculate the minimum signal speed needed to catch neighbours' attention at increasing distances, using 0.25° visual angle of movement. (b) Define perceptual thresholds and determine attenuation distance. For dewlap pattern complexity, calculate the average distance at which the signal degrades to within 10% above the assumed asymptote of 10 m. For dewlap colour contrast, just noticeable difference (JND) predicts whether two similar colours are likely to be discriminable based on the signal-to-noise ratios of each channel in tetrachromatic visual systems. Define the perceptual threshold as JND value of 2, representing the midpoint of the range over which colours become distinguishable. Signal strength is the log ratio between the signal value and the perceptual threshold. For display speed (alert, headbob, dewlap), determine the point at which the signal crosses 0 after taking the log ratio between the real display speed and the minimum detectable speed. (c) Compare attenuation distance to test efficacy optimization hypothesis: (1) predict that signal components will differ in attenuation distances; (2) plot signal attenuation distance values; (3) use *t* test to compare attenuation distances between signal components. (d) Test how environmental variables influence signal attenuation distance using PGLS regression, repeated for each signalling component (prediction figures above).

particularly dewlap pattern complexity, would attenuate rapidly with distance due to their reliance on fine spatial detail, whereas within-dewlap colour contrast would persist over somewhat longer distances.

Second, we explored how interspecific variation in the attenuation distance of signal components relates to the signalling environment. Specifically, we evaluated whether attenuation distance is associated with average receiver distance, ambient light levels and

background visual noise. We expected that species experiencing greater signalling distances would exhibit signal components with lower spatial attenuation rates, as signals used over longer ranges must remain detectable across greater distances (Ord, 2012). Similarly, low light environments and high levels of visual noise are known to reduce signal detectability, which should select for signals that enhance contrast and transmission under challenging viewing conditions (Bian et al., 2025; Ord & Stamps, 2008). Accordingly, we predicted that species inhabiting dim or visually noisy environments would exhibit signal components that degrade less with distance, maintaining detectability despite environmental constraints. By integrating models of visual detection with comparative data on signal design and ecology, this study provides an exploratory, functionally grounded assessment of how multiple environmental factors interact to shape the evolution of complex visual displays.

METHODS

Ethical Note

Novel research presented in this paper was authorized by the University of Toronto Local Animal Care Committee (Animal Use Protocol 20011469) and the Departamento de Recursos Naturales y Ambientales of Puerto Rico (Permit 2021-IC-047). Fieldwork was conducted in numerous sites across Puerto Rico. Below we describe the approaches we used in our study as they relate to animal welfare (see Ord et al., 2007, 2010 for analogous information for the published behavioural data included in our study).

We sampled 10 adult male anoles per species to ensure that we accounted for within-species signal variation. We captured lizards using standard techniques described in McDiarmid et al. (2012). Briefly, we captured lizards by hand or by use of an extendible pole with a self-closing loop of dental floss attached to the end, a widely used method that poses negligible risk to the lizards.

Once captured, lizards were placed individually in opaque cloth bags and kept in an insulated cooler (up to 40 lizards at a time in a 57-litre cooler). Because lizards were only kept for short periods (nearly all were released within 24 h, and none were kept longer than 48 h), and to minimize stress associated with additional transfers between novel environments, we did not move lizards to cages. We monitored the temperature in the cooler at regular intervals to ensure that the temperature stayed between 17 °C and 25 °C so that the lizards did not overheat. Once data were collected, we released all lizards unharmed at the original site of capture.

To facilitate data collection, we briefly anaesthetized lizards in the field laboratory with isoflurane. Anaesthesia helped to prevent movement during full-spectrum imaging, which requires the alignment of two sequential photographs, and to reduce the likelihood of handling-induced colour change (metachrosis) during measurement (we visually monitored lizards for metachrosis and did not collect data from metachrotic skin patches). We used an open-drop isoflurane chamber consisting of a 1000 mL clear-sided jar containing a cotton ball housed inside a histology cassette treated with 0.1 mL of isoflurane, yielding a ~2% gas concentration in the chamber. Once placed in the jar, lizards were watched very closely and removed from the chamber as soon as they were successfully anaesthetized (initially evident by slumped posture and lack of righting response; confirmed by lack of response to a light pinch to the tail or toe). We handled lizards for brief periods (<4 min at a time) and monitored them for signs of distress, such as gaping, darkening of colour, lethargy or abnormal posture; we ceased work with distressed lizards and allowed them to recover. Lizards fully recovered from the anaesthesia within 15–30 min. We did not euthanize any animals during this study.

Data Collection

Data for this study were derived from two sources. The colour pattern data (i.e. static signal components) were gathered specifically for the present study from field-collected images in 2021. All other variables (dynamic display components and environmental variables) were derived from a single underlying data set collected in 2006 (Nelson et al., 2022; for additional information, see also Ord, 2012; Ord et al., 2007, 2010). Information about the data collection for each source is detailed below.

Dewlap colour pattern

We captured 10 adult male lizards for each of the 10 Puerto Rican *Anolis* species in July and August of 2021, with sampling occurring at 13 localities distributed across the island. To measure pattern in a colour space that includes all wavelengths visible to anoles, we followed the full-spectrum imaging procedures of Troscianko and Stevens (2015). We took RAW format images of anoles using a Canon EOS 7D camera with full-spectrum quartz conversion and fitted with a Nikkor EL 80 mm lens under full-spectrum illumination via two tubular metal halide lamps with their protective ultraviolet (UV) coating removed (Iwasaki EYE Colour Arc MT70FD 70 W E27) and diffused through polytetrafluoroethylene sheets (0.5 mm thickness). These lamps emit spectra that simulate daylight illumination (Troscianko & Stevens, 2015). The camera rig was secured to a custom-fabricated portable copy stand and pointed downwards to capture images. We placed lizards in lateral aspect underneath the camera on a grid paper background (10 × 10 mm squares) and manually extended their dewlaps with forceps. Spectralon white and greyscale diffuse reflectance standards (99%, 75%, 50% and 2%) were included in each image for reflectance calibration. Each lizard dewlap was imaged twice (Fig. 2), first using the Baader UV-IR-CUT filter (only capturing wavelengths between 400 and 700 nm) and then using the Baader U filter (only capturing UV light, 300–400 nm). To minimize the possibility of camera or specimen movement between image captures, we fitted the camera with a ZWO five-position, 2-inch/50 mm electronic filter wheel that allowed the filter to be switched between photographs without being touched (and potentially displaced) by the operator. To automate the image capture process, we used Astro Photography Tool (version 4.50) to create an imaging plan that takes each image using the desired filter wheel position (i.e. UV-IR-CUT or U filter) and associated camera settings (e.g. ISO). See Supplementary Fig. S1 for a photograph of the imaging set-up. We then used the Image Calibration and Analysis Toolbox (micaToolbox; Troscianko & Stevens, 2015) in ImageJ (Schneider et al., 2012) to align the UV and visible spectrum images of each lizard to create multispectral image stacks, which we standardized to represent the stimulation of each photoreceptor of the *Anolis* visual system using the normalized photoreceptor absorption calculated for *Anolis cristatellus* (Loew et al., 2002) (note that spectral sensitivities are generally conserved within the genus; Fleishman et al., 2020; Loew et al., 2002). Dewlap pattern complexity and within-dewlap colour contrast were measured for each male from standardized, visual system-corrected images.

Dynamic display movements

We next compiled data on headbob, dewlap and alert movements making up the dynamic displays of territory-holding males for eight of the 10 *Anolis* species on Puerto Rico (all but *Anolis cuvieri* and *Anolis occultus*) from a previously published data set (Nelson et al., 2022). Details on the methods used to obtain display movement data can be found in Nelson et al. (2022) (see also Ord, 2012; Ord et al., 2007, 2010). Briefly, those authors recorded communicative displays of adult male lizards in their territories for 20–30 min. To quantify speed, we separated display movement

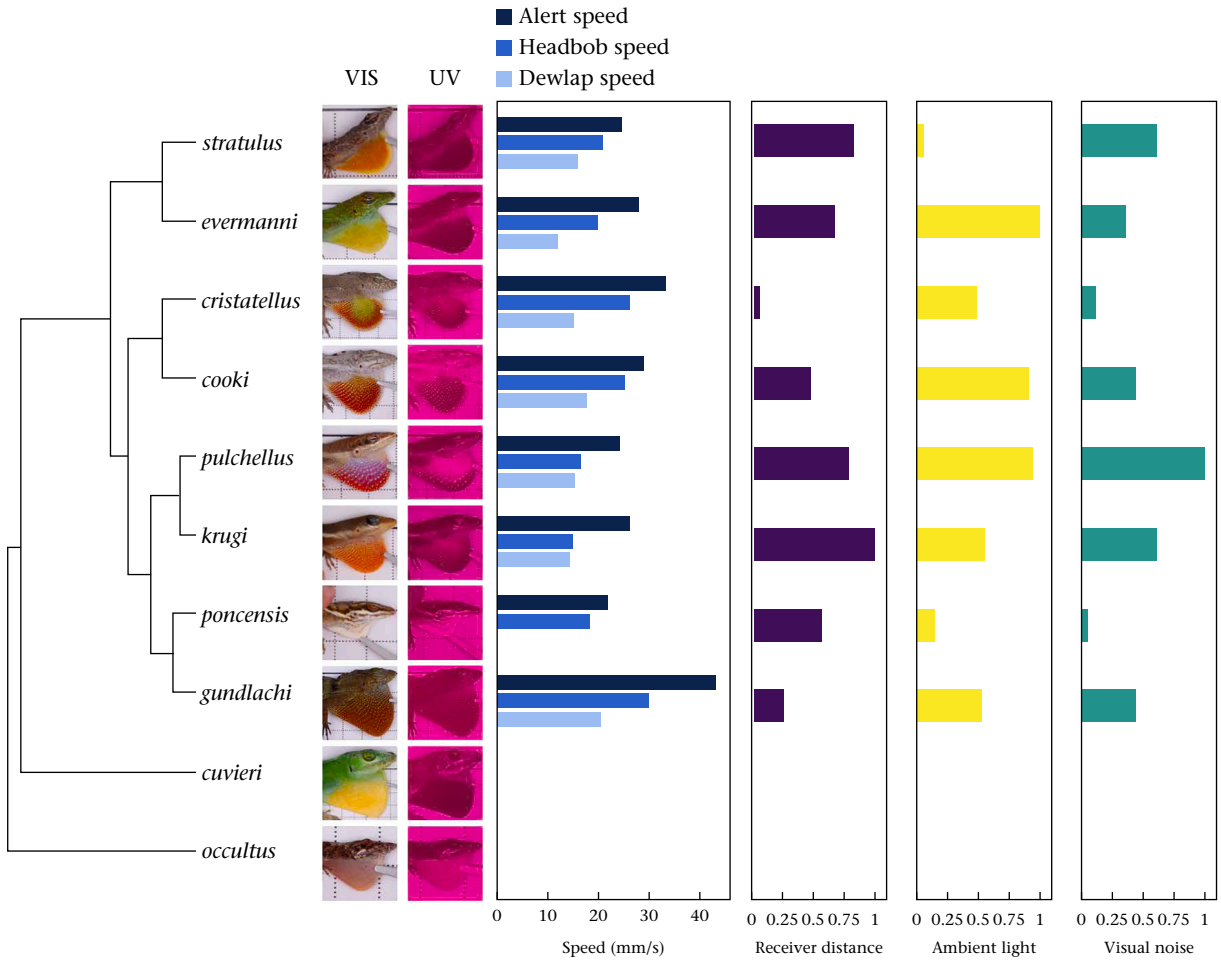

Figure 2. Phylogeny of sampled *Anolis* species (from Mahler et al., 2016), with images of the male dewlaps taken with a visible light filter (400–700 nm; left images) and a UV filter (300–400 nm; right images). Visible-light images approximate how dewlaps are perceived by the human visual system. In the UV images, light regions indicate UV-reflective areas, whereas dark regions indicate little or no UV reflectance. Visible and UV images were combined during post-processing to generate multispectral representations of dewlap coloration. The first set of horizontal bars shows average display speeds (mm/s) for alert, headbob and dewlap movements. The second set of horizontal bars shows the average receiver distance, ambient light level and visual noise for each species; values were log-transformed and minimum–maximum values were scaled between 0 and 1. Dynamic signal and environmental data were not available for *A. occultus* or *A. cuvieri*.

from background movement using the MATLAB-based program AIM (Analysis of Image Motion; Peters et al., 2002) and recorded the maximum display speed from the video sequence. Maximum speed isolates brief, high-velocity display movements, which are the features most relevant for eliciting orienting responses and peripheral motion detection in receivers (Ord et al., 2007), and therefore provides a biologically meaningful measure of display speed. Wherever possible, movement data were collected from 5 to 10 individuals per species; however, this was not feasible for all signal components or species, whereas it was possible to collect larger samples in other cases. Because the dynamic signal data were collected from different individuals than those used for the static signal measurements, we made efforts to select individuals from the same or ecologically similar populations studied in Ord et al. (2010) wherever possible. We note that dewlap speed could not be reliably quantified for *Anolis poncensis* due to its small dewlap, the movement of which is tightly coupled with body movement. This species was therefore excluded from dewlap speed analyses but retained for other display components where data were available.

Environmental variables

Environmental data were obtained from previously published studies (Nelson et al., 2022; see also Ord, 2012; Ord et al., 2007, 2010) and were collected concurrently with the aforementioned video recordings of dynamic displays for the same eight Puerto Rican *Anolis* species (i.e. excluding *A. cuvieri* and *A. occultus*). As described in those publications, average receiver distance was calculated as the mean distance between a displaying male and its visible male neighbours, averaged across individuals within each species (for details, see Ord, 2012). Habitat light was measured at each display site using a LI-250A hand-held light meter equipped with a LI-190SA Quantum Sensor, positioned at the lizard's head height and parallel to the ground (Ord et al., 2010). For each species, the mean light level across individuals was used as a measure of average ambient light. Background visual noise was estimated as the speed of windblown vegetation visible in the video backgrounds using MATLAB, and was also averaged across individuals to produce species means (Ord et al., 2010).

Modelling Signal Degradation, Perception Thresholds and Attenuation Distance

Viewing distances used

To investigate signal degradation, we modelled each signal component at 12 viewing distances between 0.1 and 10 m, starting with distances of 0.1, 0.5 and 1 m, and then at intervals of 1 m for the remaining distance. Robot playback experiments suggest that

display movements are unlikely to be effectively detected beyond 10 m by most conspecific anole receivers (Ord & Stamps, 2008). Below we describe the specific modelling procedures for each signal component.

Modelling spatial acuity for static signals

To model how the dewlap colour pattern might appear at increasing viewing distances, we used the AcuityView package (Caves & Johnsen, 2017) implemented in ImageJ as part of the Quantitative Colour Pattern Analysis framework (QCPA; van den Berg et al., 2020). AcuityView blurs images to approximate the amount of spatial detail that can be resolved given the size of the subject and the receiver's visual acuity and viewing distance. Fleishman et al. (2017) used anatomical data for *Anolis carolinensis* (Makaretz & Levine, 1980) and behavioural experiments on *Anolis sagrei* to estimate the minimum resolvable angle for central fovea vision in anoles as 0.08. As *Anolis* retinal anatomy has been shown to be highly conserved across species (Fite & Lister, 1981; Loew et al., 2002; Underwood, 1970), we expect this value to be a suitable estimate for Puerto Rican anole species. For all acuity transformations of each image, we quantified two colour pattern variables: within-dewlap colour contrast (coarse-scale pattern information) and dewlap pattern complexity (fine-scale pattern information).

Within-dewlap colour contrast

To measure within-dewlap colour contrast, we selected two regions on the dewlap for each individual (these regions corresponded to the different colour patches for species with bicoloured dewlaps and the left and right of the dewlap for species with single-coloured dewlaps). We then calculated the just noticeable difference (JND) between these two regions using QCPA (van den Berg et al., 2020). JND predicts whether two similar colours are likely to be discriminable based on the signal-to-noise ratios of each channel in tetrachromatic visual systems (Vorobyev & Osorio, 1998). JND values between 1 and 3 are considered a threshold range where colours are distinguishable, with values <1 indicating that colours are completely indiscriminable and values >3 indicating colours are discriminable under good lighting conditions (Siddiqi et al., 2004). After testing several values within this range, we chose the midpoint, 2, as our perception cutoff value (we present results using other cutoffs in the Supplementary Material section S3). To model how the perception of colour contrast degrades over distance, we calculated a log ratio between the calculated JND and the assumed perception threshold value of 2 for each individual. We plotted the log ratios as a function of distance to assess how perception of colour contrast decays with increasing distance between signal and receiver. As we used a log ratio on the *Y* axis, positive numbers along the signal degradation curve indicate the two colours are discriminable and negative numbers indicate the two colours are indiscriminable (for a discussion of the assumptions and potential limitations of these methods see Supplementary Material section S2).

Dewlap pattern complexity

To measure pattern complexity, we used DEWPAT (Sanderson et al., 2025) to compute average dewlap wavelet detail coefficients (i.e. high-frequency content) for all acuity transformations of each image (see Sanderson et al., 2025 for details). Briefly, for an image, wavelet detail coefficients represent areas of the signal containing high levels of detail (changes occurring over short spatial intervals). In contrast to other signal components in this study, no perceptual threshold has been established for pattern complexity. Therefore, we derived a complexity threshold that reflects the average complexity value among Puerto Rican anoles at which 90% of the complexity information originally in the dewlap has been lost due to diminishing acuity with increasing distance. We interpret this amount as corresponding to an effective loss of the biological information encoded in the complexity of a visual signal (see Supplementary Material section S4 for an exploration of the effect of using other loss thresholds, including one that corresponds to the complexity 'half-life'). To compute this threshold, for each individual anole dewlap in our sample, we first calculated the difference between the first detail wavelet coefficient value (i.e. the value measured at 0.1 m viewing distance) and the final detail wavelet coefficient value (i.e. the value measured at 10 m viewing distance), representing the signal decay from 0.1 m to 10 m. We treat the detail wavelet coefficient value at 10 m as an effective distant asymptote, as complexity information is nearly completely lost by this distance in all samples (Ord & Stamps, 2008). We then calculated 10% of this difference and added this to the final wavelet coefficient value (i.e. the value measured at 10 m viewing distance), giving us an individual-specific perceptual threshold. We then averaged these thresholds across all individuals of all species to obtain a single perceptual threshold for pattern complexity in *Anolis* (available evidence suggests that visual acuity is generally conserved across anole species, supporting our use of a single threshold; Fite & Lister, 1981). For each species curve, we then calculated the attenuation distance as the distance from the receiver (i.e. the *x* value) at which the curve crosses the average perceptual threshold. The result is the distance at which the signal degrades to within 10% above the 10 m value, which we consider to be effectively asymptotic. As with colour contrast, we calculated a log ratio between the calculated pattern complexity and the approximated perception threshold value for each individual. We plotted the log ratios as a function of distance to assess how pattern complexity perception decays with increasing distance between signal and receiver. As we used a log ratio on the *Y* axis, positive numbers along the signal degradation curve indicate pattern information exceeds our defined perception threshold and negative numbers indicate pattern information falls below this threshold.

Dynamic display movements

Previous behavioural experiments (Fleishman, 1986; Pallus et al., 2010; Steinberg & Leal, 2013, 2016) and electroretinographic studies (Fleishman et al., 1995) have quantified the visual motion perception capabilities from a handful of *Anolis* species (see also Fleishman & Pallus, 2010; Pallus et al., 2010). In all cases the minimum amplitude needed to elicit a response was a ~0.25° visual angle of movement (see also the *Anolis* visual models employed in Fleishman & Pallus, 2010; Pallus et al., 2010). As with the minimum resolvable angle estimate above, these studies suggest that motion perception capabilities are similar across anole species, regardless of habitat type or evolutionary history (Steinberg & Leal, 2016; see also Fleishman et al., 2017). Here we calculated the minimum signal speed that should effectively grab the attention of receivers ($S_{\min}$) at a given viewing distance (d) using 0.25° visual angle of movement (Steinberg & Leal, 2016) and the following equation modified from Ord (2012):

$$S_{\min} = 2d\left(\tan\frac{0.25}{2}\right) \quad (1)$$

To model how signal information in empirical display movements degrades over distance, we first standardized these movements by the minimum detection thresholds for the examined range of signalling distances. Specifically, we calculated the log ratio between the actual lizard display movement speed and the minimum detectable speed ($S_{\min}$) at each distance (in metres)

between 0.1 m and 10 m for each display movement (alert, headbob, dewlap) for each individual. We then plotted the log ratios over distance to assess how speed perception degrades over distance. As we used a log ratio on the *Y* axis, positive numbers along the signal degradation curve indicate the movement speed is detectable and negative numbers indicate movement speed is no longer detectable.

Statistical Analysis

We conducted all statistical analyses in R version 4.0 (R Core Team, 2025). To test whether distinct signal components differ in attenuation distance (as predicted by the efficacy optimization hypothesis), we compared the attenuation distances between signalling components. We calculated the attenuation distance of each signalling component from each individual's respective signal attenuation plot (i.e. the distance at which the signal curve passed the perceptual threshold line), then averaged attenuation distance values across individuals within each species and calculated species-level standard errors (SE). We plotted the species-level attenuation distances and visually inspected the values to determine the general trend, then compared each combination of signal components using paired phylogenetic *t* tests. As a means of focusing on the magnitude of biological significance, we based our interpretation of results on effect sizes and their associated 95% confidence intervals, assessing the extent to which estimated effects could be distinguished from zero. We used pairwise tests rather than a phylogenetic ANOVA because the number of species differed among component comparisons, and each test was therefore conducted on the overlapping set of species for that specific pair of signal components. We note that analyses based on species means can only reveal species-level evolutionary patterns, and that these analyses do not shed light on potentially interesting patterns that may exist within species or in species-level trait variances.

To explore how the signalling environment may influence attenuation distance, we used a multiple regression approach to model signal component attenuation distance as a function of each species' average receiver distance, average ambient light and average visual noise. Specifically, we fitted phylogenetic generalized least squares (PGLS) regression models that explicitly incorporate sampling error (SE) in the dependent variables using the 'pgls.SEy' function from the R package phytools version 2.5-2 (Revell, 2024), assuming a Brownian motion error structure to account for shared evolutionary history. We conducted this analysis using the attenuation distance of each signal component as the response variable, with the exception of within-dewlap colour contrast. Because the colour contrast values for species with monochromatic dewlaps were negligibly small (i.e. they began below the perceptual threshold), we were only able to calculate attenuation distances for the five species with bicoloured dewlaps. Therefore, instead of testing how environmental variables affect the attenuation distance of this signal attribute, we tested how they affect within-dewlap colour contrast directly, as colour contrast is strongly correlated with colour contrast attenuation distance. This approach allowed us to include species with monochromatic dewlaps in this analysis. All response variables were natural log-transformed and *z* score standardized prior to analysis.

Given the practical constraints of our sample sizes ($N = 8–10$ species per signal component), drawing strong conclusions about linear relationships can be challenging. However, our goal was to explore potential predictors of attenuation distance using a conservative comparative framework while remaining mindful of these constraints. Accordingly, because the estimation of phylogenetic signal as a free parameter in phylogenetic regression is unreliable with very small data sets (Revell, 2012), we assumed a simple Brownian motion model of trait evolution for our PGLS analyses (i.e. assuming Pagel's $\lambda = 1$). To assess the sensitivity of our inferences to this assumption, we also evaluated models that did not incorporate phylogenetic structure (i.e. Pagel's $\lambda = 0$); these results were biologically very similar and are presented in the Supplementary Material. As with the *t* test analyses described above, we focused our interpretation of results on effect sizes and their associated 95% confidence intervals, assessing the extent to which estimated effects can be distinguished from zero.

Phylogeny

For all phylogenetic comparative analyses, we used the relative time-calibrated phylogeny of Mahler et al. (2016). This tree is the maximum clade credibility topology from a 100 000 tree sample of the posterior distribution of a BEAST analysis of 95 *Anolis* species and two outgroups using data for five nuclear genes. We pruned this tree to just the *Anolis* species found on the main island of Puerto Rico; because this tree was missing the species *A. poncensis*, we grafted that species onto this tree as the sister taxon of *Anolis gundlachi* (following Gamble et al., 2014) using the 'bind.tip()' function in phytools (Revell, 2024).

RESULTS

We observed substantial variation in attenuation distance among different signal components, consistent with the idea that different components of complex displays are used in different contexts (Fig. 3, Table 1). On average, alert movements could be detected at the furthest distance, followed by headbob, then dewlap movements, and finally dewlap pattern complexity. The attenuation distance of colour contrast varied among species and seemed to rely heavily on the juxtaposition of UV-reflecting and non-UV-reflecting colour patches. These patterns were robust to alternative choices of perceptual threshold for pattern complexity (section S4 of the Supplementary Material). Across all tested thresholds, the relative ordering of attenuation distances among signal components was unchanged for all species except *Anolis pulchellus.* At the lowest threshold (5%), the attenuation distance of dewlap pattern complexity increased for *A. pulchellus,* exceeding that of dynamic signal components, although colour contrast remained the most long-range signal. Importantly, pairwise phylogenetic comparisons among signal components were consistent across all tested thresholds, with no changes in statistical outcomes. Patterns of colour contrast attenuation were more sensitive to alternative choices of perceptual threshold than other signal components (see Supplementary Material). However, across all tested thresholds, species with juxtaposed UV-reflecting and non-UV colour patches consistently exhibited the greatest colour contrast attenuation distances.

Environmental variation was associated with patterns of signal attenuation for dynamic (i.e. alert, headbob and dewlap movement) but not static (i.e. dewlap complexity and colour contrast) display components. Species experiencing higher levels of visual noise showed greater attenuation distances for alert, headbob and dewlap displays, with positive slope estimates and 95% confidence intervals that excluded zero (Fig. 4). Similarly, species inhabiting brighter environments exhibited alert and headbob (but not dewlap) signals that attenuated at shorter distances, as indicated by negative slope estimates with confidence intervals not overlapping zero (Fig. 4). Species that display to receivers at greater distances showed greater attenuation distances for headbob displays (positive slope; confidence intervals not overlapping zero),

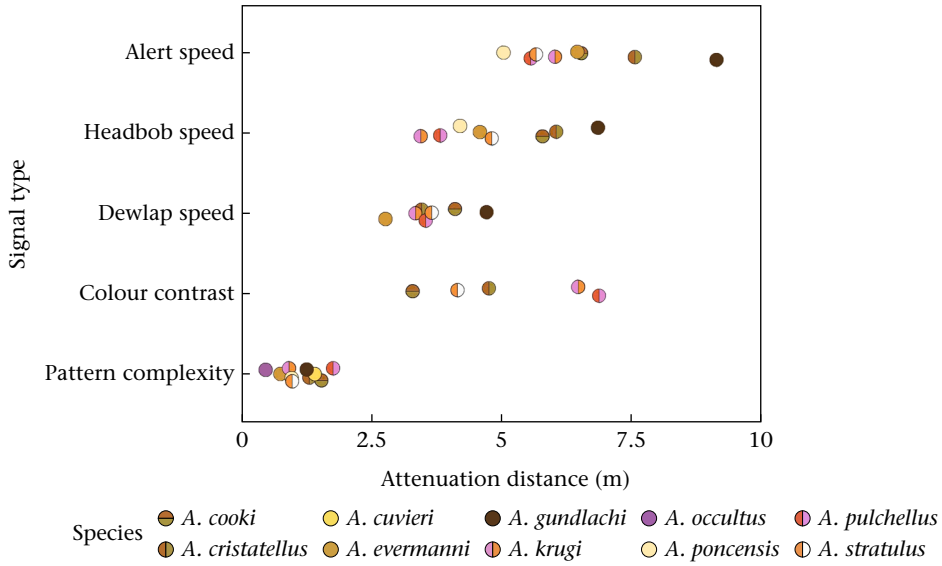

Figure 3. Species differences in maximum attenuation distance (*X* axis) per signal type (*Y* axis bins). Each dot colour represents a different *Anolis* species from Puerto Rico (dot colour reflects the approximate colour of the species' dewlap; note that five species have bicoloured dewlaps). Points were vertically jittered to reduce overlap. Note that for some species we did not have data for all signal components.

but not for any other display components (Fig. 4). Slope estimates for both dewlap pattern complexity attenuation distance and within-dewlap colour contrast distance had confidence intervals that substantially overlapped zero for all environmental predictors, indicating no robust association. When models were rerun without assuming phylogenetic structure in the residuals ($\lambda = 0$), results were very similar overall, with just two noteworthy discrepancies. First, confidence intervals for the effect of ambient light on headbob attenuation slightly overlapped zero in the nonphylogenetic analysis, although the estimate of the effect remained very similar. Second, the effect of receiver distance in the nonphylogenetic model greatly overlapped zero, and its estimated positive slope was noticeably lower than in the phylogenetic model (see Supplementary Material). The full set of model results, including those where $\lambda = 0$, is provided in the Supplementary Material.

DISCUSSION

In this study we investigated whether complex, multicomponent displays evolve to facilitate information transfer at different viewing distances and then asked how environmental variables influence signal attenuation. We found that maximum attenuation distance differed among signal components, as predicted by the efficacy optimization hypothesis, which proposes that distinct signal components should vary in effectiveness over specific communication distances. Our analysis of interspecific signal component variation revealed that environmental conditions were important predictors of signal attenuation for dynamic, but not static, display components. Specifically, species experiencing higher levels of visual noise exhibited greater attenuation distances for alert, headbob and dewlap movements, whereas species inhabiting brighter environments displayed alert and headbob signals that attenuated over shorter distances. In addition, species that display to receivers at greater distances showed greater attenuation distances for headbob displays. In contrast, attenuation distance of our static signal components, dewlap pattern complexity and within-dewlap colour contrast, showed no robust association with any environmental predictor. Together, our findings suggest that different components of complex displays may evolve in response to distinct distance-based signalling demands, with dynamic signal components potentially evolving to compensate for poor viewing conditions.

Variation in the attenuation distances of different signal components likely reflects the distinct functions they assume in anole communication, with dynamic signals best suited for long-range detection and static signals for close-range interactions. Of the five signal components we examined, alert speed exhibited the

Table 1
Results from phylogenetic paired *t* tests comparing attenuation distance between signalling components

Model	Estimate	*t*	*df*	95% CI
Alert speed vs headbob speed	1.473	2.559	6	0.345, 2.601[a]
Alert speed vs dewlap speed	3.124	4.168	5	1.655, 4.593[a]
Alert speed vs dewlap complexity	5.346	4.516	6	3.026, 7.667[a]
Alert speed vs within-dewlap colour contrast	1.335	1.326	3	-0.638, 3.309
Headbob speed vs dewlap speed	1.531	2.870	5	0.486, 2.577[a]
Headbob speed vs dewlap complexity	3.873	4.793	6	3.021, 4.517[a]
Headbob speed vs within-dewlap colour contrast	-0.006	-0.005	3	-2.433, 2.420
Dewlap speed vs dewlap complexity	2.486	6.016	5	2.070, 2.823[a]
Dewlap speed vs within-dewlap colour contrast	-1.222	-1.247	3	-3.140, 0.697
Dewlap complexity vs within-dewlap colour contrast	-3.624	-4.235	3	-5.301, -1.947[a]

Dynamic components: alert speed, headbob speed and dewlap speed. Static components: fine-scale dewlap pattern complexity and within-dewlap colour contrast.
[a] Confidence intervals (CIs) that did not overlap zero.

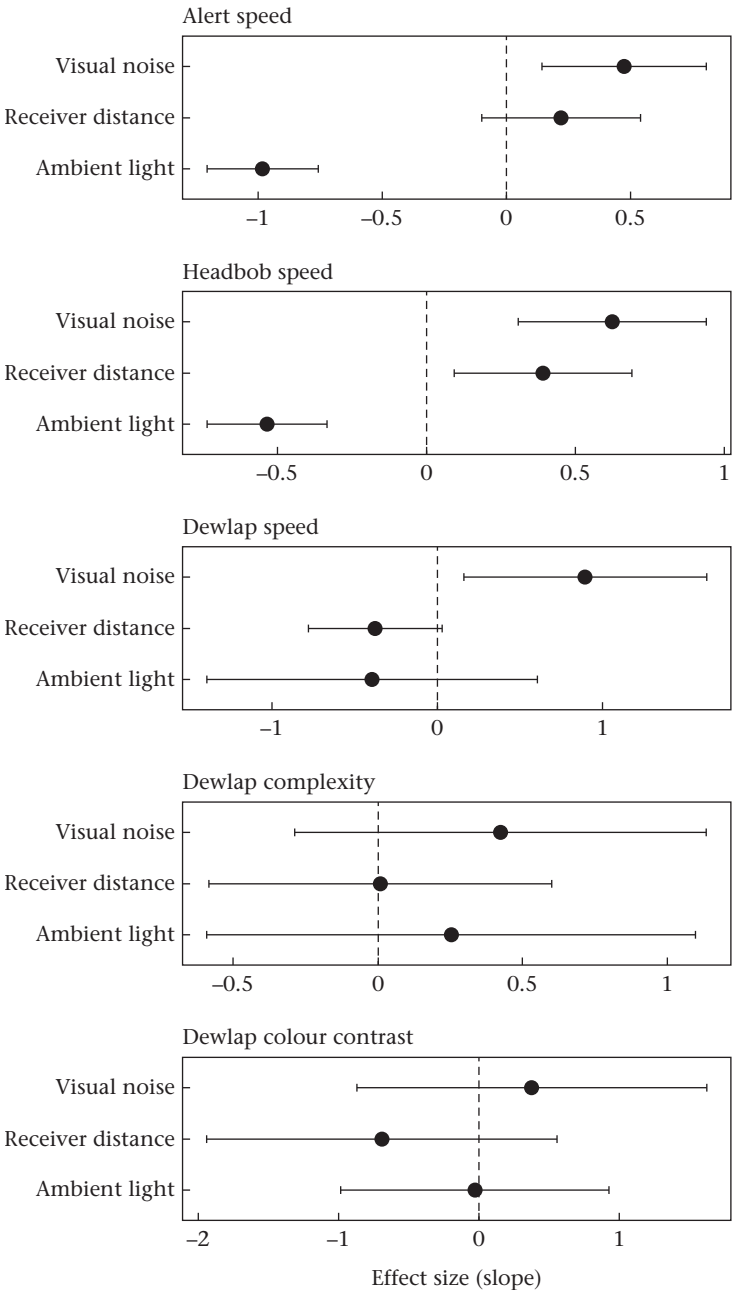

Figure 4. Effect sizes (with 95% confidence intervals) of three environmental predictors (visual noise, receiver distance, ambient light) on the attenuation distance of five *Anolis* signal components: alert speed, headbob speed, dewlap speed, dewlap pattern complexity and within-dewlap colour contrast. Points represent estimated effect sizes from phylogenetic multiple regression models, and horizontal bars indicate 95% confidence intervals, illustrating the magnitude and direction of each predictor's influence on signal traits.

farthest attenuation distance, suggesting that alert-specific push-up displays are detectable over the longest ranges (Fig. 3). This result is unsurprising, as alert displays are typically directed towards nonspecific receivers during territorial advertisement (Ord, 2012; Ord & Stamps, 2008). Male anoles defend territories of varying sizes (Muñoz et al., 2023), and because alert signals are not directed towards specific receivers, they should theoretically be detectable across the entire territorial range. Of the other dynamic display components, headbob speed showed the second-greatest attenuation distance, on average, followed by dewlap speed, although we note that these two signal components were similar in estimated attenuation distance in some species (Fig. 3). By contrast, dewlap pattern complexity exhibited the shortest attenuation distance across all species, and the results for within-dewlap colour contrast were mixed and highly dependent on the presence of UV colour patches.

Our finding that dynamic signal components exhibited moderate to high attenuation distances compared to the static components aligns with our knowledge of the *Anolis* visual system. Anoles have tetrachromatic colour vision, enabling them to perceive a wide range of colours, including those that extend into the ultraviolet range (Fleishman et al., 2022). Although anoles exhibit relatively high spatial acuity compared to other reptiles, they are nonetheless only able to discern fine-scale visual details at

close range (Fleishman et al., 2017, 2020). While anoles can detect static visual features, their dynamic acuity is estimated to be three times higher than their spatial acuity (Fleishman, 1986; Steinberg & Leal, 2016), making their visual system highly specialized to detect motion. Like raptors and some other bird species, anoles possess bifoveal vision, allowing them to track moving objects over wide angles, aiding in prey capture and motion-based communication (Fite & Lister, 1981; Fleishman, 1992; Fleishman et al., 1997). The interplay between these static and dynamic visual capabilities likely contributes to the evolution of complex signalling in anoles. Their relatively high spatial acuity enables them to discern intricate dewlap patterns, which may convey critical information during close-range interactions, such as mate choice or rival assessment (Driessens et al., 2015; Fleishman et al., 2020; Losos, 2009). However, the effectiveness of these static signals diminishes as distance increases due to inherent limits in spatial processing. Dynamic signals, which include motion-based displays such as push-up and headbob movements, may compensate for this limitation by enhancing signal visibility over longer distances, particularly in conditions where static signals might be obscured or less discernible such as shaded forest habitat, which is where many of these species are found (Fleishman, 1992).

While signal use is clearly shaped by perceptual limits, it is also shaped by trade-offs associated with production costs and ecological risks. Although all visual components in anoles require active display (e.g. the static colour pattern is shown via dynamic extension of the dewlap), long-range communication typically involves the addition of faster and more exaggerated movements, such as alert push-ups and rapid headbobs, which are used more frequently at greater signalling distances (Ord & Stamps, 2008). These high-velocity movements are likely to be more energetically demanding (Dresp-Langley, 2014), suggesting that display composition may shift with distance as a way of balancing efficacy and cost. Consistent with this idea, alerts are selectively deployed under conditions where increased detectability is likely to be necessary, implying that there is a cost associated with their deployment. If there were no cost, then every display should start with an alert to increase the odds of eliciting a receiver response (Ord & Stamps, 2008). Of course, energetic costs are likely not the whole story, as there may also be costs related to predation (i.e. if a signal is more conspicuous at a distance, it will be more conspicuous to both conspecifics and predators). For example, in *Draco* lizards there is a hypothesized trade-off between dewlap size and chromatic conspicuousness. Dewlaps with high chromatic contrast may be highly detectable not only to conspecifics but also to avian predators with excellent colour vision and high spatial acuity. To reduce predation risk, *Draco* species are thought to rely on relatively large dewlaps that increase detectability through surface area and motion, while maintaining comparatively low chromatic contrast that limits long-distance visibility to predators (Klomp et al., 2016). This combination illustrates how different signal components can be tuned to balance efficacy and risk. More generally, multicomponent displays may allow anoles to optimize signal transmission across diverse ecological contexts, ensuring effective communication across variation in receiver distance and environmental conditions.

Nonetheless, while our comparative results demonstrate clear differences among signal components in their attenuation and detectability across environmental conditions, they do not provide direct evidence of adaptive optimization. Demonstrating this would require showing that particular components are not only more effective under specific conditions, but are favoured relative to alternatives and confer a functional advantage in relevant signalling contexts (Chittka & Briscoe, 2001). Moreover, the efficacy of individual components may not be independent within the lizard's full display. For example, dynamic components such as dewlap movement may enhance the detectability of static colour signals by facilitating receiver orientation (Ord & Stamps, 2008; Peters & Evans, 2003; Számadó, 2015), suggesting that component performance cannot be fully understood when considered in isolation. If such synergies can increase detectability, our modelled attenuation estimates may be best understood as theoretical minima. However, the reverse could also be true, for example, if the movement of the dewlap during a display hinders a receiver's ability to distinguish its fine-scale pattern elements (Tan & Elgar, 2021). Future work integrating receiver responses, experimental manipulations of multicomponent displays and measures of signalling success across ecological contexts will be necessary to test whether different signal components are indeed specialized for, or favoured in, particular communicative environments. As such, our results are best interpreted as evidence for differential signal efficacy across components, providing a foundation for future tests of adaptive hypotheses.

An interesting pattern that emerged from our results is that UV coloration contributes disproportionately to within-dewlap colour contrast. We found that colour contrast between UV-reflecting and non-UV-reflecting patches dramatically increased the effectiveness of the dewlap as a long-distance signal, whereas adjacent non-UV patches did not. For example, *A. pulchellus* and *Anolis krugi*, which possess dewlaps with UV patches and non-UV patches, showed the highest colour contrast attenuation distances (these distances even surpassed alert speed). This pattern is consistent with findings from other taxa, in which the juxtaposition of UV-reflective and non-UV colour patches produces disproportionately large increases in chromatic contrast to the receiver's visual system (Hausmann, Arnold, Marshall, & Owens, 2003). Interestingly, *A. pulchellus* specializes on open grassy habitats, which tend to have high ambient UV light, long sightlines and substantial background motion from windblown vegetation. These conditions may favour signals that maintain chromatic contrast over long distances and remain detectable against visually noisy backgrounds. However, other relatively open-habitat species like *Anolis cooki* and *A. cristatellus* have two adjacent UV-poor dewlap colour patches and exhibited much lower attenuation distances.

While attenuation distance patterns reveal how different signal components perform across viewing distances, understanding what drives this variation requires considering the environments in which signals are used. By far the best-supported pattern in our data was that variation in long-distance dynamic signals (alert and headbob speed) among *Anolis* species appears to be shaped by the need to compensate for poor viewing conditions caused by low ambient light and high visual noise. Species from darker habitats (e.g. *A. gundlachi*) tended to exhibit dynamic signals with greater attenuation distances, suggesting that motion-based signals evolved to counteract the rapid loss of chromatic and spatial information in dim light (Fialko, 2023; Ord et al., 2007). Likewise, species experiencing high levels of background motion showed longer-range alert, headbob and dewlap signals, consistent with the idea that increased motion contrast helps these displays stand out against visually noisy backgrounds (Bian et al., 2025), a result that is concordant with intraspecific patterns described by Ord (2012). In the latter study, individuals of a given species tended to perform displays at speeds higher than the minimum necessary for effective detection by territorial neighbours, and these excess speeds were strongly predicted by environmental constraints such as low ambient light and high visual noise (Ord, 2012). Our interspecific analyses suggest that these same environmental pressures

not only modulate signal performance within species but also help shape the evolutionary patterns in long-distance dynamic signals that we observe among species. This continuity across evolutionary scales suggests that the dynamic displays in *Anolis* may be driven by long-standing constraints imposed by habitat structure and light environment.

Signal attenuation is not unique to visual communication; signals across all sensory modalities degrade as they are transmitted through the environment (Groot et al., 2024). Indeed, many of the patterns we have described here resemble patterns observed in other types of signals in other taxa. Acoustic signals, for example, lose amplitude and are distorted by the medium through which they travel (e.g. air or water) as well as by surrounding vegetation (Morton, 1975; Naguib & Wiley, 2001), while chemical signals diffuse and degrade over distance, reducing their potency (Wyatt, 2014). Similar constraints affect vibrational communication, whereby signal fidelity depends heavily on substrate type and distance (Cocroft & Rodríguez, 2005). These transmission challenges are commonly framed through the concept of signal-to-noise ratio: environmental noise reduces the contrast between a signal and its background and increases the likelihood of missed detections (Wiley, 2017). Theoretical and empirical work across taxa shows that such noise has consequences for communication. Across modalities, organisms often respond by increasing signal conspicuousness or by using multicomponent or multimodal displays that provide redundancy or exploit alternative sensory channels when one component is particularly susceptible to noise. For example, environmental noise elevates detection thresholds and constrains the distance at which acoustic signals can be recognized, often selecting for heightened amplitude, altered frequency structure or temporal adjustments in vocalizations (e.g. Brumm & Slabbekoorn, 2005; Slabbekoorn & den Boer-Visser, 2006; reviewed in Wiley, 2017). In this context, the tendency for *Anolis* species in dim or noisy habitats to use more extreme dynamic displays (e.g. rapid alert or headbob movements) is consistent with a general pattern in which animals increase signal conspicuousness to maintain an adequate signal-to-noise ratio under challenging environmental conditions.

Headbob displays were the only signal component for which species-level variation in attenuation distance was positively associated with average receiver distance, such that species that typically signal to more distant receivers exhibited headbob movements that propagated farther. This pattern suggests that headbob displays may be particularly sensitive to typical signalling distances experienced during social interactions. While headbobs are species typical and are a frequently expressed component of anole displays, other dynamic components may be subject to different functional and selective pressures. Alert displays, for example, do not always precede species-typical headbob displays and are often expressed in response to poor environmental viewing conditions (Ord & Stamps, 2008). By contrast, the lack of a relationship between dewlap movements and average receiver distance suggests that dewlap movement speed is not primarily shaped by selection for long-distance signal transmission (an idea further supported by its low attenuation distance). Instead, perhaps dewlap movements function mainly to enhance apparent body size or to facilitate assessment of dewlap colour and pattern, roles that may be most relevant at closer viewing distances (Fleishman et al., 2017).

Conclusion

Our study breaks new ground by examining attenuation across a variety of different components of a highly complex visual display repertoire. By doing so we have been able to examine the potential transmission consequences of the evolution of complex, multicomponent signals. We have demonstrated that different signal components are detectable at different viewing distances in *Anolis* lizards, which is consistent with the efficacy optimization hypothesis and shows that signals may evolve to ensure information is conveyed across different contexts. Our analyses revealed that ambient light and visual noise influence the attenuation of dynamic signal components, suggesting that these environmental variables have played an important role in shaping broad evolutionary patterns in the efficacy of dynamic visual signals. While we accounted for key aspects of anole visual perception, including tetrachromatic colour vision, motion detection, spatial acuity, and variation in ambient light and background visual noise, other components of visual performance (e.g. certain aspects of contrast sensitivity) may also influence signal detectability. Such factors represent important directions for future research. Overall, our findings underscore the importance of environmental efficacy in shaping signal evolution and support the idea that complex displays allow animals to maintain effective communication across diverse or variable sensory environments. Our attenuation distance models provide a useful tool for estimating signal transmission over different distances and we hope that they will allow other researchers to compare signal components (e.g. colour and acoustic signals) in other taxa (e.g. birds, spiders, etc.). More broadly, our results highlight how environmental constraints can differentially shape the evolution of individual components within complex displays, and provide a comparative framework for investigating multicomponent signal evolution across sensory modalities and taxa.

Author Contributions

Jillian A. Sanderson: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Zifang Xiong:** Writing – review & editing, Data curation. **Edita Folfas:** Writing – review & editing, Data curation. **Alejandro A. Laboy González:** Writing – review & editing, Data curation. **Zachary K. Lange:** Writing – review & editing, Data curation. **Alexander H. Murray:** Writing – review & editing, Data curation. **Efrén A. Ortiz Jiménez:** Writing – review & editing, Data curation. **Luke O. Frishkoff:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Data curation. **Terry J. Ord:** Writing – review & editing, Validation, Resources, Methodology, Formal analysis, Data curation, Conceptualization. **D. Luke Mahler:** Writing – original draft, Supervision, Resources, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Data Availability

The data and R scripts used for this project are archived in Mendeley Data (https://doi.org/10.17632/ds3xh36kgr.1).

Inclusion and Diversity Statement

Our study was conducted by a mixed-gender team of scientists who were residents of Canada, the United States, Australia and Puerto Rico, where the study was performed.

Declaration of Interest

None.

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Supplementary Material

Supplementary material associated with this article is available at: https://doi.org/10.1016/j.anbehav.2026.123683.

The Supplementary Material has not been copy-edited and the content, formatting and file functionality are the sole responsibility of the author(s).

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