



Original Article

Why does the complexity of functionally equivalent signals vary across closely related species?

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Received 19 August 2021; revised 4 April 2022; editorial decision 1 May 2022; accepted 3 May 2022

Animal signals are observed to vary widely in complexity among species, but why this should be the case—especially among closely related taxa—is unclear. Identifying the selective forces that drive these differences is important for understanding signal evolution, as well as the origins of communication more generally. We used a measure derived from information theory to quantify the complexity of visual territorial advertisement displays performed by males of closely related taxa of Puerto Rican *Anolis* lizard. In general, the information potential of visual displays appeared to be high compared with signals of other taxonomic groups (e.g., other lizards, birds). Nevertheless, there was still considerable variation in signal complexity among the *Anolis* taxa studied. We found a strong relationship between signal complexity and phylogeny for some aspects of the advertisement display traditionally thought to be important in species recognition. Other aspects of the display tended to vary independently of phylogeny, with differences in signal complexity among taxa reflecting the distance over which displays were typically viewed by territorial neighbors, and to some extent the number of sympatric congeners present in the environment. More generally, we highlight a little used, but tractable means of quantifying complexity in different species—and in different aspects of the same signal (the number, timing, and type of components)—that can reveal the evolutionary processes generating increases (or decreases) in communicative complexity.

Key words: color, ornament, Shannon–Wiener index, social complexity, territoriality, visual signal.

Complex animal signals have historically been considered to be those made up of many components resulting in large repertoires (Freeberg et al. 2012). Yet complexity can also include the properties of the individual components themselves (e.g., Benedict and Najar 2019), such as the number of notes, stridulations, or volume pulses produced in a particular call or the variety of motions included in an otherwise continuous movement used in a courtship dance. In many cases, researchers simply describe signals as “elaborate”, “sophisticated”, or “complex” in the intuitive sense and without formal definition or quantification. For example, many male birds are considered to perform elaborate songs, courtship dances, and show off conspicuously colored plumage to attract females (Andersson et al. 2002; Irestedt et al. 2009; Krakauer et al. 2009; Ligon et al. 2018). Male wolf spiders are similarly observed to perform sophisticated courtship displays that use a combination of visual and seismic signals, which can in turn be highly variable among closely related species (Rovner 1968, 1975; Hebets et al. 1996, 2013; Wilgers and Hebets 2011; Fialko 2018). Furthermore,

complex signals have been argued to improve opponent assessment among territorial males in lizards (Ord et al. 2001; Stuart-Fox and Ord 2004), to convey information on the level of threat posed by different types of predators in rodents and birds (Blumstein and Armitage 1997; Templeton et al. 2005) or to recruit others to the source of a food resource in bees (the waggle dance: von Frisch 1967; Esch 2012).

Despite this general interest in the complexity of animal signals, we have only a rudimentary understanding of the potential selective forces that lead to variation in signal complexity among closely related taxa. For example, the need to regulate an increasingly complex social system (Blumstein and Armitage 1997; Freeberg 2006), convey species identity (Seddon 2005; Ord and Garcia-Porta 2012; Freeberg et al. 2012) and—perhaps most obviously—needs arising from an increasing pressure for elaborate signals resulting from sexual selection (Andersson 1994; Johnstone 1995; Ord et al. 2001; Chen et al. 2013) are all factors that have been argued to drive the evolution of communicative complexity. However, the extent to which these factors explain why closely related taxa differ in signal complexity continues to be a rare focus of investigation. These factors are also specific to why complexity might increase in

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some species and not others, and does not consider negative selection pressures that might decrease communicative complexity.

In the first instance, communicative complexity has typically been linked to the evolution of social complexity (Freeberg 2006): as the number of social interactions increases among individuals in a population, an increasingly complex set of social signals are expected to evolve to effectively mediate those interactions (Freeberg and Lucas 2012; Pollard and Blumstein 2012). This hypothesis has often been examined in mammals, which are probably the most obvious examples of animals exhibiting complex societies in the form of group living: for example, spider monkeys (Symington 1988), ground-dwelling sciurid rodents (Blumstein and Armitage 1997), elephants (McComb et al. 2003), bats (Gustin and McCracken 1987; Wilkinson 2003), dolphins (Brager 1999; Connor et al. 2000) and whales (Dunlop et al. 2006). But there are examples of complex signals in non-group living taxa as well. Consider the substrate-borne vibration signals and visual ornamentation of jumping spiders (Elias et al. 2012), the complex combination of polarized, colorful ornaments and water-borne vibrations of male mantis shrimp (Chiou et al. 2008; Kleinogel and Marshall 2009) or the conspicuous headbob and dewlap movements of territorial male *Anolis* lizards (Ord and Martins 2006; Losos 2009). These are all complex signals in the form, number and types of components used, number of sensory modalities employed, or general repertoire size of signals produced, but none exhibit the type of social group living seen in many mammals.

Furthermore, properties of the environment that impact the detection or evaluation of animal signals has also been implicated in shaping the complexity of signal designs (reviewed by Hebets and Papaj 2005 and Freeberg et al. 2012). All signals must travel through the environment before reaching a receiver and any environmental condition that generates noise for the sensory systems of those receivers will inevitably degrade the discrimination of signals to a lesser or greater degree (Guilford and Dawkins 1991; Ord and Stamps 2008). For instance, background acoustic or visual noise from windblown vegetation and other sources can reduce the range of frequencies detected by birds (Slabbekoorn and Peet 2003; Brumm 2004; Luther 2009) and frogs (Goutte et al. 2016; Tennessen et al. 2016) or the types of visual displays seen by lizards (Peters 2008). Poor ambient light can similarly reduce the visibility of both color and motion signals (Ord and Stamps 2008; Fleishman et al. 2009). For these reasons, environmental conditions might be intuitively assumed to reduce signal complexity. But signals can become more elaborate to facilitate their transmission through the environment. For example, signals that incorporate components across signal modalities (e.g., a visual and seismic signal; Candolin 2003; Hebets et al. 1996, 2013; Elias et al. 2012) or add introductory alert components to an existing signal (Ord and Stamps 2008) have been shown to enhance signal detection in noisy environments and are instances where the number of components incorporated into the signal has increased (and are, therefore, arguably, more complex). Nevertheless, it remains unclear whether the environment is a widespread factor promoting signal complexity or one that reduces it (Ord et al. 2002; Ord and Garcia-Porta 2012).

It has also been suggested that the frequency of encounters with sympatric congeners might promote an increase in signal complexity to ensure accurate species recognition (Seddon 2005; Ord et al. 2011; Freeberg et al. 2012; Ord and Garcia-Porta 2012). For example, additional taxon-specific elements are incorporated into social signals to reduce errors in recognition that might lead to energetically costly or reproductively wasteful interactions (e.g.,

engaging with a heterospecific that is not competing for the same resource, or mating with an individual from the wrong species), while increasing overall signal complexity. For example, Caribbean anole lizards that encounter many sympatric heterospecifics tend to perform headbob displays with more bobs of varied duration (and interpreted to be more complex) than species that rarely encounter other species (Ord and Martins 2006). Yet it is also possible, and perhaps more likely, that animals communicating in a crowded community simply diverge in signal design away from those of congeners, which does not lead to any change in complexity (e.g., Kirschel et al. 2009) or potentially reduces complexity if identity is better conveyed by a simple signal. As with the case of the physical properties of the environment, it is unclear to what extent the need for accurate species recognition might induce increases (or decreases) in signal complexity.

Finally, sexual selection is the most likely factor that might promote the evolution of complexity in non-group living animals. There are many examples of the evolution of complex male courtship signals in response to female mate choice decisions (e.g., in the context of preferences for multi-component signals: Kime et al. 1998; Coleman et al. 2004; Elias et al. 2006; Reichert et al. 2017). But there are now an increasing number of studies that have begun to document a role for male-male competition as well: increasing competition among males for territories has selected for more accurate cues in opponent assessment in the form of increasingly more complex signal repertoires (e.g., the visual displays and number of ornaments in many lizards: Ord et al. 2001; Ord and Stuart-Fox 2006; Chen et al. 2013; Pérez i de Lanuza and Font 2016).

In general, however, variation in signal complexity among closely related species is likely explained by a number of competing selection pressures that result in the fundamental need for more complex signals on one hand (e.g., differences in social complexity or intensity of sexual selection across species) and factors that limit complexity on the other hand (e.g., species living in different habitats) or both (e.g., Ord and Martins 2006; Hebets et al. 2013). The origins of such diversity in signal complexity are especially interesting among closely related species because these species are more likely to be using signals for the same function (e.g., territorial defence) and share physiological, sensory, and cognitive attributes as well as a host of other factors through their shared evolutionary history. Studying the potential causes of variation in signal complexity among closely related species might therefore provide a particularly powerful means of understanding how and why signal complexity evolves more generally.

The most common method of measuring signal complexity continues to be counting the number of distinct signals making up a taxon's repertoire (e.g., Benedict and Najjar 2019), with the notion being large repertoires of distinct signals are more complex than small repertoires. As previously alluded to in the opening of our introduction, this method misses complexity in other aspects of communication, such as complexity in the design of individual signals that make up a repertoire and the degree of variation or unpredictability in how components are organized (McShea 1991). It also misses variation in the relative use of each element and instead counts all elements as equally important irrespective of their frequency. However, the frequency of use or abundance of elements has long been recognized as an important aspect of diversity (Magurran 2004; Sherwin et al. 2017).

The second less commonly applied method uses the Shannon–Wiener index, a measure of complexity (Wicken 1987) that is derived from information theory (Shannon and Weaver 1949; see

Spellerberg and Fedor 2003 for clarification on the historic confusion over the labeling of this index). Here, complexity is measured in explicit mathematical terms of “entropy” (see below) and used to infer the number of binary bits of information (Sanders and Ho 1981). The greater the number of distinct elements produced, and the more even is their abundance (frequency of use), the greater the number of possible distinct bits of information that can be encoded. Although the formulation of the index shares similarities to Boltzmann’s original gas-entropy equation, it is not a measure of entropy per se, rather complexity specifically (see Wicken 1987). The Shannon–Wiener index provides an objective, sophisticated means of quantifying communicative complexity, but requires detailed and often labor-intensive analysis of signals beyond simply counting elements making up a signal repertoire.

In this study, we used the Shannon–Wiener index to investigate the origins of complexity in the territorial advertisement displays of 11 closely related taxa of *Anolis* lizard on the island of Puerto Rico. These lizards were especially suited for this study because of the existence of a large video library of territorial displays (see Ord et al. 2010, 2016) accompanied by detailed information on both the social and physical environment (see Ord et al. 2010; Charles and Ord 2012 for further details) and phylogeny (Gamble et al. 2014). In particular, the level of competition for territories, the number of sympatric species likely to be encountered, and the type of environmental conditions impacting display detection are known to vary among the 11 taxa and have been previously shown to account for signal differentiation across these lizards (Ord et al. 2010; Charles and Ord 2012; Ord 2012). Furthermore, anole displays seem complex, consisting of multiple elements, including headbobs, pushups, an often multi-colored dewlap that in itself can vary in how it is extended and retracted during the display, plus the addition of different tail components. This group subsequently offers a rare opportunity to tease out the potential factors that drive variation in signal complexity among closely related species. Signal complexity in the genus as a whole has been found to vary across species based on counts of the number of modifier components (e.g., back arching, body raising/tilting) added to a core headbob and dewlap display (Jenssen 1977, 1978; Ord et al. 2001), but also the variety of movements used in the headbob display itself (Ord and Martins 2006). However, these previous attempts have failed to capture much of the diversity in display and the complexity of element arrangements and have also not examined how variation in display complexity might arise.

To this end, we began our investigation by first assessing the extent to which differences in the complexity of *Anolis* territorial displays among taxa might reflect phylogeny, which has been reported to be common in other systems (Ord and Garcia-Porta 2012). That is, variation in signal complexity across taxa is largely non-adaptive and reflects stochasticity in the evolution process that produces similarities in complexity among closely related taxa compared with distantly related taxa (i.e., high estimated phylogenetic signal). We also tested whether variation in complexity might be adaptive and instead reflect differences among taxa in the physical environment occupied (i.e., long range communication in visually difficult environments constrains—Ord et al. 2002—or selects for—Ord and Stamps 2008—signal complexity), the degree of sexual selection experienced (pressure for improved opponent assessment promotes increased signal complexity—Ord et al. 2001) and the need for accurate species recognition among taxa (with species identity cues conveyed best by simple or complex signals—Ord and Martins 2006). Our ultimate goal was to understand why closely related

taxa using visual signals in the same functional context (here, advertising territory ownership) vary in signal complexity and whether this variation might offer insights into the evolutionary origin of signal complexity in the group as a whole.

METHODS

Data collection

Temporal display movements

The headbob and dewlap displays of free-living male territorial owners for 11 taxa on Puerto Rico (belonging to 8 species with two populations surveyed for three of those species known to vary in display behavior and the environments occurred; for example, Ord 2012) were quantitatively analyzed using 475 video recordings taken from an existing video archive (see Ord et al. 2010, 2016). We analyzed 5–10 territorial displays for an average of 9 males per taxon (range: 6–10 males). Video recordings were only analyzed if the lizard was positioned perpendicular to the video camcorder and if the footage was steady. Individuals were selected depending on whether they had the appropriate number of recorded video clips (5 to 10; clips in which males moved position were not included). Headbob movements and dewlap extensions were mapped using ImageJ v.1.50i (Schneider et al. 2012) by manually tracking the change in the position of the head and the extension and retraction of the dewlap over time to construct Display-Action-Pattern (DAP) graphs (Carpenter et al. 1970; Jenssen 1977; Figure 1a). From these DAP graphs, we measured nine headbob and dewlap variables (Table 1a). These variables have been used in other comparative analyses of lizard displays (e.g., Martins 1993; Ord and Martins 2006) and have been shown to encompass most of the variability in display design among species (Ord and Martins 2006; see also Martins et al. 1998; Clark et al. 2015).

Display components and motifs

In addition to quantifying the way in which headbobs and dewlaps were used in display (previous section), we also categorized behaviors into eight different components: (1) headbob (2) two-legged pushup, (3) four-legged pushup, (4) dewlap extension, (5) tail raise, (6) tail arch, (7) tail curl or (8) tail flick (Table 1b). These components seemed to be combined in various ways to form 18 different “motifs” (Table S1). For example, a display component might be performed in isolation (e.g., a headbob without any dewlap extensions or tail components) or combined with one or two other components (e.g., pushups combined with a tail raise or arch).

Dewlap color

Dewlap color was examined from 99 video stills extracted from clips for each male lizard. These stills were only taken for fully extended dewlaps and when a lizard’s profile was positioned perpendicular to the video camcorder. From these stills (e.g., Figure 1a), the proportion of the dewlap covered by each distinct color was calculated using ImageJ software and used to calculate actual entropy (H ; see below).

Environmental and social factors

Average receiver distance (mean distance measured with a tape measure to all sighted male neighbors surrounding a given male, averaged across lizards within a given taxon; see Ord 2012 for details), average ambient light (taken at the site of first display and averaged across male lizards; Ord et al. 2010), average background

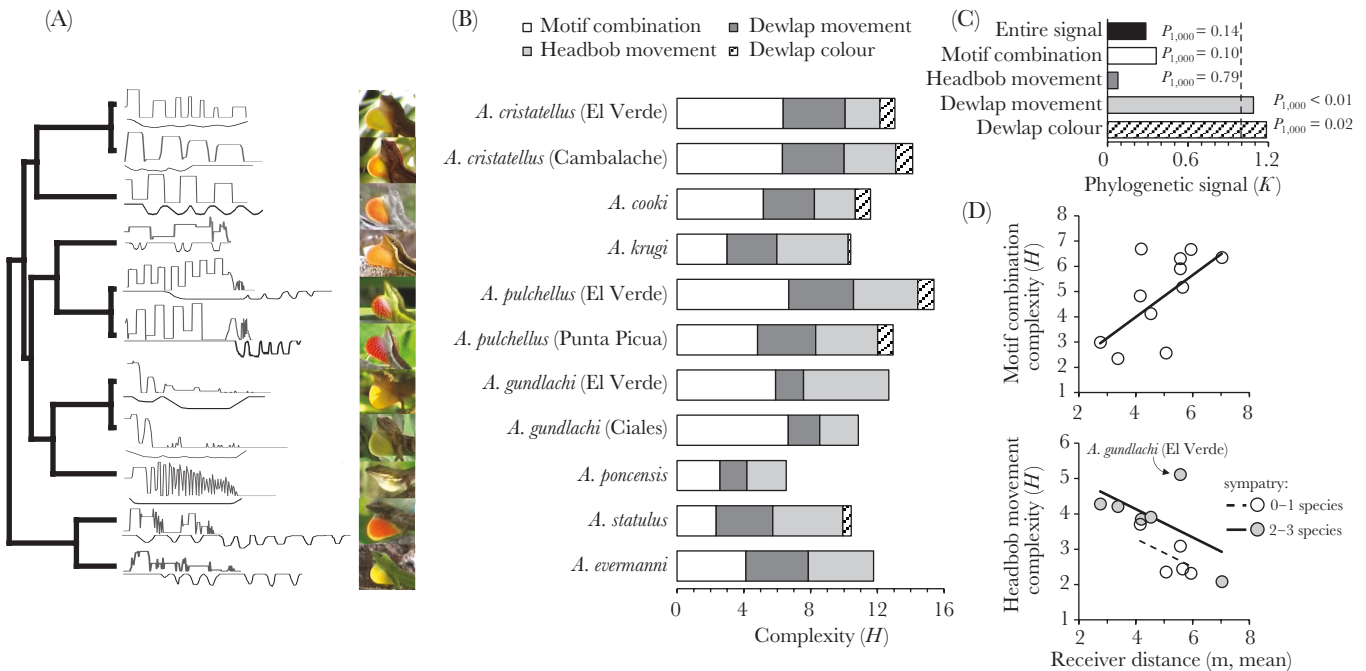


Figure 1

The phylogeny of signal complexity of territorial advertisement displays performed by male *Anolis* lizards on Puerto Rico. Representative Display-Action-Pattern (DAP) graphs (a) depict the taxon-typical vertical movement of the head and extension/retraction of the dewlap over time. Also presented are stills taken from video recordings used to create the DAP graphs that show the color and pattern of the male dewlap at full extension. The overall complexity (H) of signals (b) are provided as a stacked measure of all four signal characteristics combined (motifs, headbob and dewlap movements, and dewlap color). The estimated phylogenetic signal (K) of each component of complexity (c) is reported along side a P value computed from a 1000 randomizations of data across the tips of the phylogeny, whereas the dashed line corresponds to a K of 1 that is interpreted to be consistent with a Brownian motion model of evolutionary change along the phylogeny (K of 0 represents essentially instantaneous evolutionary change unrelated to phylogeny). The complexity (d) of the headbob movements and motifs used by territorial males was found to vary across taxa as a function of the distance to territorial neighbors, and to some extent the number of sympatric species encountered.

visual noise (generated by windblown vegetation and computed using motion analysis and averaged across males; Ord et al. 2010), average number of male neighbors (total number of surrounding male territorial holders, averaged across lizards; Charles and Ord 2012) and sex ratio (total number of male neighbors divided by the total number of observed females within a male's territory; Charles and Ord 2012) were taken from the data archive associated with the video recordings and were collected at the time each male lizard was recorded. These factors have either been found to influence the detection of displays in the environment (receiver distance, ambient light, and background noise; Ord et al. 2010, Ord 2012) or the level of competition experienced by males for territories (number of male neighbors and sex ratio; Charles and Ord 2012). We also used field notes of sympatric species observed in visual sight of lizards to provide two measures of sympatry: (1) total number of sympatric species and (2) a categorical measure of sympatry (split either side of the median number of sympatric species: none or one sympatric species versus two or more sympatric species, coded as 0 or 1, respectively).

Data analysis

Quantifying signal complexity

Temporal display movements (display variables; Table 1a), display components (Table 1b), and their motif combinations (Table S1) were converted to a common scale by splitting data into equal-sized range bins and calculating the proportion of times a certain display

characteristic occurred in each bin. This was done across all lizards within a given taxon. For example, the average duration of the headbob display performed by a male lizard was first computed by taking the mean duration across the 5–10 headbob displays recorded for that individual. This was repeated for all male lizards from all 11 taxa. Next, the minimum and maximum average duration of the headbob display was identified and used to calculate its range (e.g., the shortest average headbob display was 0.99 s by a male *A. pulchellus* from Punta Ricua, whereas the longest average headbob display was 44.47 s by a male *A. gundlachi* from El Verde, resulting a range of 43.48 s). This range was then divided into five time windows (“bins”) of equal duration (i.e., bins with a range of 8.69 s ($43.48\text{ s} \div 5$), such that the first bin ranged from 0.99 s to 9.68 s, the second from 9.69 s to 18.38 s, and so on). Individual lizards were scored depending on whether their average display duration lay within the bounds of a given bin (1 or 0 for “yes” or “no”, respectively). These data were then tallied and divided by the total number of lizards surveyed for a taxon to obtain the proportion of lizards with displays occurring within each time bin. The resulting sum of these proportions across bins for a given display characteristic, and within each taxon, equaled 1 (see Online Supplementary Information and Table S2 for a worked example). This conversion enabled Shannon–Wiener values to be computed for both discrete and continuous variables. It is an approach that has long been used in physics and engineering (e.g., Jaynes 2003), but does not seem to have been used by communication biologists. The common scaling provided by the approach attaches importance to each aspect of

Table 1**Display (a) variables and (b) components scored from video-recordings and Display-Action-Pattern graphs of territorial advertisement displays performed by male Puerto Rican *Anolis* lizards**

Characteristic	Description
(a) Display variables	
Headbob number (HBn)	Total number of individual headbob movements
Headbob duration (HBd)	Duration (s) of an individual headbob movement, recorded from the start of the upward movement to the following downward movement of the head/legs
Headbob interval (HBint)	Duration (s) of each “gap” between headbobs
Headbob amplitude (HBamp)	Proportional measure of amplitude (relative to the start height of the head as it was held above the substrate at the beginning of the display)
Headbob amplitude variation (HBvar)	Number of different headbob amplitudes per headbob movement
Dewlap number (DWn)	Total number of complete extensions and retractions of the dewlap
Dewlap duration (DWd)	Duration (s) of a dewlap display recorded from the start of a dewlap extension to the complete retraction of the dewlap
Dewlap pulse (DWpul)	Total number of times the dewlap was partially extended during a single dewlap display
Dewlap amplitude (DWamp)	Proportional distance that the dewlap was extended from the throat (relative to the maximum extension distance recorded for that display).
Dewlap interval (DWint)	Time (s) between the complete retraction of the dewlap to the start of a dewlap extension
Dewlap latency (DWlat)	Time (s) from start of the first headbob to the start of the first dewlap. Negative values indicate dewlap displays precede headbobs. Latency of the first dewlap from the first headbob
(b) Display components	
Headbob (Hb)	Up and down movement of the head and neck
Two-legged pushup (Ht)	Vertical movement of the forebody
Four-legged pushup (Hf)	Flexion of all four legs
Dewlap (Dp)	Extension and complete retraction of the dewlap
Tail raise (Mtr)	Base to the tip of the tail is straight and elevated horizontally above substrate
Tail arch (Mta)	Base to the tip of the tail is arched and elevated horizontally above substrate
Tail curl (Mtc)	Base to the mid-section of tail is straight and elevated horizontally above substrate, whereas the tip of the tail is curled
Tail flick (Mtf)	Back and forth horizontal movement of the tail

the display in proportion to how frequently it occurs in the display, relative to other taxa. Dewlap color data was not converted because it was already calculated as a proportion.

We selected five bins to make our scaling conversion (see [Online Supplementary Information](#)), but other bin numbers could have also been selected. To some extent, this choice influences the ultimate estimate of complexity in a similar way the precision of a measuring instrument will affect the resolution of the measure taken. Our choice of five bins was a practical one that we expected would provide a reasonable and standardized estimate of complexity across all taxa and display characteristics (NB: the median correlation between estimates computed using five versus three bins was $r_{\text{pearson}} = 0.90$ with a lower and upper quartile of 0.83–0.97, and our findings would be qualitatively unchanged regardless which bin number was selected).

The proportion data were entered into a calculation that is an adaptation of the Shannon–Wiener species diversity index (Shannon and Weaver 1949), H , to measure what has been termed the “Actual Entropy” of a signal system or the amount of potential information in a signal (see Martins 1994) using the following equation:

$$H = - \sum P_i (\ln P_i)$$

where P_i is the proportional occurrence of i th display characteristic within a taxon, summed across all characteristics (display variables, motif combinations, and dewlap colors). The base of the log term can be of any value and we arbitrarily used a natural-ln. To compare our estimates to those reported in the literature computed with other bases, we applied the following conversion:

$$H = \frac{H'}{\log_x(e)}$$

where x is the base used in the calculation of H' and e is the base of the natural-ln (i.e., 2.718281828459; NB: this comparison was made to other taxonomic groups as a means of assessing the relative complexity of the territorial displays of Puerto Rican *Anolis* lizards to other communication systems, which is a particular advantage of using the standardized measure of complexity provided by the Shannon–Wiener index).

Finally, we also computed the “evenness”, V , of information potential as it is distributed across display characteristics by applying a correction factor known as the “normalization to unity”:

$$V = \frac{H}{\ln N_c}$$

Here, N_c is the total number of characteristics making up the territorial advertisement display for a given taxon (all observed display variables, motif combinations, and dewlap colors). This correction has been interpreted in a variety of ways, such as a measure of code efficiency, degree of constraint in a signal system, or its level of redundancy (Martins 1994). In effect, however, it offers a measure of complexity that controls for the total number of separate characteristics making up a signal (e.g., repertoire size), as H will be a positive function of this number. We report these values in the [Supplementary Information](#) along with the outcomes of the associated phylogenetic analyses with environmental and social factors. However, we consider the number of characteristics making up a signal to be an important aspect of its complexity and consequently focus our investigation on H .

Assessing the influence of evolutionary history and environmental and social factors on signal complexity

First, we used phylogenetic reduced major axis regressions implemented in R v.4.0.5 (R Development Core Team 2018) and the

Table 2

Relations of complexity (H) among components of male territorial advertisement displays across 11 Puerto Rican *Anolis* taxa. Values above the diagonal are $r_{\text{phylogenetic RMA}}$ values, with the text below the diagonal highlighting the magnitude of effect

	Motif combination	Headbob movements	Dewlap movements	Dewlap color
Motif combination	–	–0.22	0.56	0.29
Headbob movements	Small	–	0.03	–0.19
Dewlap movements	Large	Small	–	0.50
Dewlap color	Small	Small	Large	–

phytools package v.0.7-70 (Revell 2012) to assess correlations among complexity measures of different display characteristics.

Second, we computed Blomberg's K statistic (Blomberg et al. 2003) using *phytools* to evaluate the extent to which variation in signal complexity reflects the underlying phylogenetic relationships among taxa. When K converges on 0, display complexity has been free to vary—potentially adaptively—independently of phylogeny, while values approaching 1 (or higher) imply complexity has evolved through incremental changes along the phylogeny in a process consistent with Brownian motion. Randomization tests based on 1,000 simulations of K were used to obtain a probability value that K could be statistically distinguished from 0.

Finally, we used a model fitting approach to determine the extent various combinations of environmental and social factors account for interspecific variation in signal complexity. Models were applied using phylogenetic Ornstein-Uhlenbeck (OU) regressions (Hansen et al. 2008) using the *phylolm* package version 2.6.2 (Ho and Ane 2014). Models included a range of predictor combinations that were grouped depending on whether factors were associated with signal reception (receiver distance, ambient light, and background noise) or intensity of territorial competition (male neighbors, sex ratio), in addition to two indices of sympatry (total number of congeners, low vs high sympatry). Models were ranked based on a second-order calculation of Akaike's Information Criterion (AIC_c) and compared against a null, intercept-only model. AIC_c values were then converted into ΔAIC_c scores relative to the best-supported model (the model with the lowest computed AIC_c value). We considered any model within $\Delta AIC_c \leq 2$ of the best-supported model and including a predictor variable with a computed t -value ≥ 1.95 as a credible model explaining interspecific variation in signal complexity. AIC_c values were also converted into AIC_w scores to provide a general comparison of the level support for each model relative to all other models considered (formulae reported in Burnham and Anderson 2002).

In all analyses, the phylogeny used was based on Gamble et al. (2014) and pruned to the 11 taxa of interest (Figure 1a), with populations within species set to an estimate of the likely minimum divergence time following Ord et al. (2010).

RESULTS

Signal complexity of *Anolis* territorial advertisement displays

Overall signal complexity (H ; inclusive of display variables, motif combinations, and dewlap colors) varied widely among the 11

Puerto Rican *Anolis* from 15.40 bits (the number of possible distinct bits of information that can be encoded)/display in *A. pulchellus* (at El Verde) to 6.54 bits/display in *A. poncensis* (Figure 1b).

We also computed complexity for each signal characteristic, with headbob and dewlap movements considered separately. The El Verde population of *A. gundlachi* had the highest complexity in the headbob movement of displays, 5.11 bits/display, although the Ciales population had one of the lowest, 2.32 bits/display (NB: population differences in headbob complexity were more subtle for *A. cristatellus*: 3.09 and 2.09 for El Verde and Cambalache, respectively). *A. pulchellus* (at El Verde) had the highest complexity in the movement of the dewlap extension/retraction of 3.87 bits/display (Figure 1b) compared with the lowest value again being *A. poncensis* at 1.62 bits/display (*A. poncensis* has a tiny dewlap that is barely visible during display; see Ord et al. 2013). The El Verde population of *A. pulchellus* again had the most complex combinations of motifs, 6.69 bits/display, although *A. stratulus* performed the least complex motif combinations, 2.34 bits/display. Finally, the number of distinct colors on the dewlap ranged from 1 to 4, with the Cambalache population of *A. cristatellus* exhibiting the most complex dewlap coloration (1.02 bits/dewlap).

Correlations in the magnitude of complexity among signal characteristics were large between dewlap movements, dewlap color, and motif combinations ($r = 0.29$ – 0.56), although the complexity of headbob movements seemed to vary largely independently of these characteristics ($r = 0.03$ – 0.22 ; Table 2).

Variation in signal complexity among *Anolis* taxa

The complexity of headbob movements and motif combinations have been largely free to vary among taxa independently of phylogeny (Figure 1c), and evolutionary regressions implied this variation was likely the product of adaptive evolution (see below). In contrast, estimates of phylogenetic signal (K) for the complexity of dewlap movements and color were high and statistically distinguishable from 0, with computed values (1.09 and 1.18, respectively) consistent with incremental changes accumulating over evolutionary time through a Brownian motion-like process (Figure 1c).

In the case of both headbob movements and motif combinations, complexity varied among taxa as a function of the typical distance over which territorial advertisement displays were likely to have been viewed by male neighbors (Tables S3b, S3c, and S5a). This was the case irrespective of whether the complexity measure controlled for the number of characteristics making up the display (V , Tables S4b, S4c, and S5b). Those taxa advertising territory ownership to neighbors typically within 3 to 4 meters exhibited

greater complexity in headbob movements compared with taxa advertising to more distant neighbors (H : $t = -2.43$, Figure 1d; V : $t = -2.68$, Figure S1). Those taxa displaying to more distant neighbors instead performed displays with greater complexity in motifs than taxa displaying to nearby neighbors (H : $t = 2.34$, Figure 1d; V : $t = 2.30$, Figure S1).

There was also some evidence that taxa living in communities with several congeners tended to perform advertisement displays with more complex headbob movements (Tables S3c and S5a; Figure 1d), although this was dependent on one complexity measure (H : $t = 2.19$; note too the influential outlier in Figure 1d and compare with Figure S1) and sympatry being treated as a categorical variable (Table S3c; see also Table S4c). We examined a multivariable model inclusive of both neighbor distance and sympatry that showed both variables had effects that were statistically distinguishable from zero (i.e., 95% confidence intervals did not overlap zero; Table S6), although the magnitude of the effect of sympatry was unconvincing ($t < 1.96$). There appeared to be a positive association between the complexity of dewlap movements included in display and sex ratio, but only when complexity accounted for the number of movement types included (V : $t = 6.28$; Figure S1; Tables S4d and S5b). Given sympatry and sex ratio were dependent on the type of complexity measure considered, and in the case of sympatry the way in which the predictor was treated (categorical), we consider these effects with caution.

DISCUSSION

Overall, the complexity of signals used by male *Anolis* lizards was high (6.54–15.40 bits/display) when compared with the handful of other taxonomic groups where the Shannon–Wiener index has also been used to measure signal complexity: the territorial visual displays of sagebrush lizards (*Sceloporus graciosus*: 4.26 bits/display, Martins 1994), the songs of black-capped and Carolina chickadees (*Poecile atricapillus* and *P. carolinensis*: 4.64 and 5.79 bits/song, respectively; Hailman et al. 1985; Freeberg and Lucas 2012) and the multimodal honey bee waggle dance (*Apis mellifera*: 7.43 bits/dance; Schurch and Ratnieks 2015). In fact, it appears the information potential of the visual signals of these Puerto Rican *Anolis* lizards exceeds these other communication systems. However, our method of applying the Shannon–Wiener index was able to leverage all aspects of the territorial display by utilizing a conversion standard applied in physics and engineering (see Methods). Communication biologists do not seem to have been aware of this conversion standard and have probably not measured the full information potential encoded in these other animal groups. Regardless, our study does provide a robust comparison of signal complexity among these particular Puerto Rican lizards, and the factors leading to the observed variation in complexity among these taxa.

Initially, *Anolis* lizards might have evolved highly complex visual signals to convey messages in various contexts, such as species recognition, opponent assessment, and mate attraction. Today, although all *Anolis* lizards perform headbob and dewlap displays to advertise territorial ownership and resolve territorial disputes, the complexity of how these displays were put together varied widely among species, and even among populations of the same species (Figure 1b). Previous investigations of signal complexity in this system, but also other animals more generally, have been limited. There is some evidence that variation in complex signaling behaviors among closely related species might reflect differences in the social or environmental pressures experienced by signaling animals (in lizards: Ord et al.

2001; Ord and Martins 2006; Chen et al. 2013; and various other taxa: Ord and Garcia-Porta 2012). In the context of the putative role sexual selection might have in promoting complexity in animal signals (Freeberg et al. 2012; Ord and Garcia-Porta 2012), our study found little to support the view that variation in the intensity of territorial competition among closely related *Anolis* taxa accounts for differences in territorial display complexity. Although the complexity of dewlap movements might have varied among taxa as a function of the number of males to females within a population (Figure S1), the finding was linked to a specific measure (V) that arguably removed an important aspect of complexity (i.e., the number of different types of movements included in the dewlap display).

Classically, the *Anolis* dewlap has been considered to be an important cue of species identity (Rand and Williams 1970; Echelle et al. 1971) and, through its putative role in species recognition, a key innovation that opened the door to the extensive radiation of species within the genus as a whole (Streelman and Danley 2003). As a diagnostic of species identity, the complexity of dewlap color and movement is potentially a useful one because it closely tracks the underlying phylogenetic relationships of taxa. It has also not, in general, seemed to have adaptively differentiated across environments (rather variation appears to have been largely the cumulative product of stochastic evolutionary changes). Whether or not male lizards rely on the cues conveyed by the dewlap for species recognition is unclear. Robot playback experiments suggest *Anolis* lizards assess multiple cues of species identity across the entirety of the territorial advertisement display (Ord and Stamps 2009; Dufour et al. 2020). Regardless, our findings indicate that the complexity of the dewlap signal has followed a different evolutionary process of differentiation than headbob movements and motifs.

The complexity of headbob movements and combinations of motifs employed in territorial advertisement displays have been largely free to vary independently of phylogeny (Figure 1c), and apparently in response to changes in the required transmission distance of displays (Figure 1d). Regardless of the measure used (H or V), the complexity of headbob movements has decreased as the average distance to territorial neighbors has increased, with displays instead being augmented with increased motif complexity (Figure 1d). This seems to reflect a constraint on the information potential of headbob movements that can be reliably transmitted to distant receivers. Previous study of these Puerto Rican *Anolis* lizards has shown the capacity of males to detect subtle changes in display motion is dependent on the visual resolving power of these lizards (Ord 2012), and this progressively decreases at greater transmission distances (Ord and Stamps 2008). This seems to have resulted in selection against complex movements being included in the headbob performance when advertising territory ownership to distant neighbors. This seems to have been compensated by the addition of increasingly complex combinations of different display components or motifs. For example, the addition of an exaggerated 4-legged push-up to a display has been shown to improve display detection in *Anolis* (Ord and Stamps 2008), although the presentation of a large tail crest through exaggerated tail arching has also been linked to neighbor distance, and as an explicit strategy for improving display detection (Charles and Ord 2012). Given headbob movements and motifs make up the bulk of the complexity of *Anolis* territorial advertisement displays (Figure 1b), the variation observed among taxa in signal complexity appears to have been driven in part by taxon differences in receiver distance, and specifically the differences in information potential that can be reliably conveyed by these two display components (headbobs and motifs).

This apparent trade-off between the complexity of headbob movements and motif combinations does not adequately explain why the complexity of the entire signal varied so widely among taxa. Differences in cognition among species might have resulted in some species being better able to perceive and process complex signals than other species. To some extent, differences in cognition can be indexed by the size of the brain. For example, regions of the brain associated with reproductive behavior in lizards are larger in those species experiencing greater sexual selection (Hoops et al. 2017). For six of the 11 Puerto Rican *Anolis* taxa studied, Powell and Leal (2014) have reported differences in the size of brain regions associated with sensory integration (the dorsal ventricular ridge) and general cognitive ability (the dorsal cortex). Using their data, we were unable to find any statistical relationship between the complexity of the territorial signal and the size of either of these brain regions (phylogenetic regressions with body size as a covariate: $t = -0.85$ to -0.41 , $P = 0.46$ – 0.78), or total brain size ($t = -0.92$, $P = 0.43$), across the six species. Some of this variation in signal complexity potentially reflects, at least in part, the number of coexisting congeners a species might encounter in the environment (Echelle et al. 1971; Figure 1d), and the extent to which complex displays have been needed to reduce recognition errors among those congeners (e.g., Table S5; NB: this result should be considered with some level of caution as it was dependent on the metric of sympatry used).

There remains the general question of what has driven the evolution of complex territorial advertisement displays in *Anolis* in the first place. It is typically assumed that signal complexity reflects social complexity. That is, taxa with more complex social systems require more complex signals to regulate interactions among conspecifics, such as assessing and managing the behavior of group members (Freeberg and Lucas 2012; Pollard and Blumstein 2012). Social complexity has been measured in a number of different ways, but the two major methods involve group size (e.g., Freeberg 2006) and the number of social relationships within groups (e.g., Blumstein and Armitage 1997; Freeberg and Lucas 2012; reviewed by Pollard and Blumstein 2012). Neither measure adequately reflects the social dynamics of territorial animals. For example, the reproductive success of male *Anolis* lizards is determined primarily by their ability to establish and defend territories against rival males with the ultimate goal of monopolizing access to females (Jenssen et al. 2001; Bush and Simberloff 2018). In this context, males must keep track of their neighboring rivals, but also frequently engage with some of those rivals on a daily basis (Freeberg et al. 2012). Therefore, social complexity in *Anolis* lizards is perhaps better described by the frequency of these territorial interactions, or more specifically the extent to which the outcome of those interactions has an impact on a male's likelihood of reproducing. Measuring this in the wild would be challenging, but possible through prolonged observation of individually marked males or paternity analysis of juveniles.

Although group size and the diversity of relationships within groups are traditionally thought to drive communicative complexity, for territorial animals it is more likely to be the increasing competition among males for access to mates that selects for increasingly more complex displays (Kareklas et al. 2019). For example, the intensity of male-male competition has often been found to be positively associated with the evolution of multi-colored ornamentation or large display repertoires in lizards (Ord et al. 2001; Stuart-Fox and Ord 2004; Ord and Garcia-Porta 2012; Chen et al.

2013; Pérez i de Lanuza et al. 2013, 2017). Although some of our results implied competition (indexed by population sex ratio) might promote an increase in some characteristics of display complexity among Puerto Rican *Anolis* taxa (Table S4d; Figure S1), the evidence was limited. However, an investigation is perhaps more appropriate at a broader scale where factors might be identified that initially drove the evolution of complexity in *Anolis* (such as sexual selection): for example, a comparative investigation inclusive of sister genera such as *Sceloporus* (Martins 1993), *Uta* (Ferguson 1970), *Cyclura* (Martins and Lamont 1998) and *Liolaemus* (Martins et al. 2004) where the social system of territoriality is broadly similar but where variation likely exists in the competitive pressure for territories as well as the types of habitats occupied.

It has also been suggested that signal complexity has evolved to allow signalers to convey various types of information in a single display; for example to facilitate species recognition, opponent assessment, and mate choice together (“multiple messages”: Johnstone 1996). Rather than a single factor driving signal complexity (e.g., sexual selection), it is a combination of pressures that elaborate a signal to incorporate multiple functions. The visual signals of *Anolis* have been suggested to convey information on species identity (Rand and Williams 1970; Losos 1985; Macedonia and Stamps 1994) and opponent assessment (Driessens et al. 2014), as well as the addition of “alerting” or amplifying components to help facilitate detection (Fleishman 1988; Ord and Stamps 2008; which likely accounts for variation in motif combinations in this study as well, which are discussed above). Testing the “multiple messages” hypothesis as the origin of display complexity in *Anolis* lizards is difficult using comparative analysis and is probably better investigated through experiments with select taxa (e.g., using robot playback techniques: Martins et al. 2005; Ord and Stamps 2009; Dufour et al. 2020).

More broadly, signal complexity has been commonly quantified by counting the number of distinct display repertoires (Seyfarth et al. 1980; Blumstein and Armitage 1997; Templeton et al. 2005) or the number of modifiers added to a signal (Jenssen 1977, 1978; Ord et al. 2001), but it is impossible to determine whether a large repertoire in lizards is comparable in complexity to a large repertoire in birds (as an example). These methods do not provide an objective comparison of complexity that can be used to compare among diverse taxonomic groups that are often using a host of different methods and modalities to communicate with one another. In contrast, information theory provides an especially useful tool for describing the information potential and coding efficiency of animal communication systems and, critically, can be used to compare the signal systems of different species at any taxonomic scale (e.g., Rand and Williams 1970; Martins 1994; this study). Unfortunately, we cannot make a robust comparison yet because the few cases where the Shannon–Wiener index has been used to measure complexity have been limited to a subset of signal features that naturally fit a proportional measure. We illustrate a standard scaling conversion that allows most features of animal signals to be included in estimates of complexity, regardless of taxonomic group and irrespective of signal modality. We should also emphasize that, with any measure of signal complexity, values will remain estimates of “information potential” until experimentation confirms animals perceive and act on the various putative cues being conveyed by different signal features (i.e., what might be referred to as “fundamental” versus “realized” signal complexity).

More generally, the use of information theory for objectively quantifying complexity by researchers of animal communication has been vastly underutilized. Although a more labor-intensive method than simply counting repertoire size, applying information theory to animal signals provides an objective, continuous, and (now) comprehensive index of complexity (McShea 1991). In doing so, it offers a powerful tool to understand the evolution of complex signals through phylogenetic analyses across closely related taxa, although also providing a means of comparing the complexity of communication systems of distantly related taxa. For example, we have shown that differences in the complexity of functionally equivalent signals among closely related taxa (including populations of the same species) can be accounted for in part by the stochastic nature of the evolution process and adaptive trade-offs resulting from long range communication. With greater taxonomic sampling that expands phylogenetic analyses of signal complexity across many closely related species, it should become possible to infer the historic origins of complexity in communication systems as well (*sensu* Chen and Wiens 2020; Garcia et al. 2020).

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

We thank Richard Peters, Matthew Symonds, Amanda Ridley, and three anonymous reviewers for comments that helped improve this paper.

Data availability: Analyses reported in this article can be reproduced using the data provided by Nelson et al. (2022).

Handling Editor: Amanda Ridley

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