

Evolutionary loss of complexity in animal signals: cause and consequence

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Abstract

We identified hypotheses for the cause and consequences of the loss of complexity in animal signals and tested these using a genus of visually communicating lizards, the Southeast Asian *Draco* lizards. Males of some species have lost the headbob component from their display, which is otherwise central to the communication of this genus. These males instead display a large, colorful dewlap to defend territories and attract mates. This dewlap initially evolved to augment the headbob component of the display, but has become the exclusive system of communication. We tested whether the loss of headbobs was caused by relaxed selection, habitat-dependent constraints, or size-specific energetic constraints on display movement. We then examined whether the consequences of this loss have been mitigated by increased signaling effort or complexity in the color of the dewlap. It appears the increased cost of display movement resulting from the evolution of large body size might have contributed to the loss of headbobs and has been somewhat compensated for by the evolution of greater complexity in dewlap color. However, this evolutionary shift is unlikely to have maintained the complexity previously present in the communication system, resulting in an apparent detrimental loss of information potential.

Keywords: animal signal, color signal, energetic cost, environmental noise, evolutionary loss, ornament

The term “complex” has been used to describe various forms of animal communication, including ornaments made up of many colors, acoustic signals consisting of many notes, stridulations or pulses, or signal systems that are multimodal (e.g., rely on both sound and visual components). In essence, complex signals are explicitly defined (or implicitly assumed) to be those that convey more information than simple signals, through the repetition and the use of different types of components (see Nelson et al., 2022). The origins of such complexity have been a classic focus of research for communication biologists (Freeberg et al., 2012). From this body of work, we know that complex communication can evolve to mediate an increasing number of social interactions among conspecifics (e.g., Freeberg, 2006), as a function of increasingly choosy mates (e.g., Choi et al., 2022), or to mediate aggressive encounters by improving opponent assessment among rivals (e.g., Ord et al., 2001). Less attention has been given to the causes (or consequences) of losses in signal complexity, despite such losses being widespread across many taxonomic groups (Maia et al., 2016; Miles & Fuxjager, 2019; Ödeen & Björklund, 2003; Ord & Stuart-Fox, 2006; Price et al., 2009; Romero-Diaz et al., 2021; Starrett et al., 2022). This presents a problem for our general understanding of signal evolution, as we know a reasonable amount about how communicative complexity evolves but not why complexity is often

subsequently lost (Patricelli & Hebets, 2016). It is therefore difficult to fully account for the variation observed among species in the complexity of their signals, especially when those signals are used in the same context by closely related taxa (e.g., to attract mates or defend territories; Nelson et al., 2022).

Of what we do know, there are several potential scenarios in which we might expect the loss of complexity in animal signals. First, the need to have complex social signals could be reduced in instances where sexual selection on those signals has become relaxed. For example, the evolution of herbivory in iguanian lizards has been attributed to the relaxation of territoriality and the subsequent loss of complex territorial displays (Ord & Blumstein, 2002). Competition for mates and other resources can similarly be reduced with changes in conspecific density, obviating the need for complex, costly signals for mate attraction (Ödeen & Björklund, 2003; Rand & Ryan, 1981) or territorial defense (Price et al. 2009). Second, the ability of conspecifics to detect and assess complex signals can depend on environmental conditions and the distance over which signals are transmitted. For example, acoustic or visual background noise can limit the types of songs or visual displays that can be readily detected by conspecifics (Peters, 2008; Reed et al., 2021). There is also evidence that complex signals are more difficult to perceive with increasing

distance between sender and receiver (Nelson et al., 2022). Finally, size-specific metabolic rate can be expected to render some signal components more costly to produce in larger species than in smaller species. For example, large species across a diverse range of taxonomic groups (insects, amphibians, birds, and mammals) are generally constrained to producing low-frequency calls of long duration and at a reduced rate (Gillooly & Ophir, 2010). A similar physiological mechanism underlies the energetic cost of movement in ectotherms, which has been implicated in constraining the evolution of complexity in the visual displays of large lizard species compared to smaller species (Ord & Blumstein, 2002). The evolutionary loss of signal complexity might therefore result from a relaxation of sexual selection, difficulties in signal detection following the colonization of a new habitat, or evolutionary shifts in body size that change the energetic cost of signal production.

Identifying which of these scenarios might account for the evolutionary loss of signal complexity is important because each will have potentially different consequences for species ecology and evolution. These consequences will range from the benign, if the loss of complexity reflects a relaxed selection on signals, to potentially severe impacts on the capacity for effective communication among conspecifics. For example, changes in the properties of the environment that impact signal reception can have adverse impacts on reproduction (Bent et al., 2021; Reed et al., 2021; Seehausen et al., 1997), survival (McIntyre et al., 2014), and ultimately the ability of species to persist in certain environments (McClure et al., 2013). Alternatively, selection against certain signal elements can be compensated for by adaptive evolution in other signal elements. For example, the replicated evolutionary loss of a color signal used during courtship and territorial signaling in various species of North American Spiny lizard (genus *Sceloporus*) has led to an evolutionary shift to motion-based display and chemical signaling (Martins et al., 2015; Romero-Diaz et al., 2021). The loss of a conspicuous courtship song in Hawaiian crickets historically targeted by a parasitoid fly has been counterbalanced in some populations by the evolution of a new call type with a sound frequency outside the hearing range of the parasite (Tinghitella et al., 2018). That is, the cause(s) of complexity loss in itself can be an initiator of adaptive evolution in other aspects of communication and potentially an important source of signal diversification across closely-related species (Nelson et al., 2022).

With this in mind, we investigated the potential cause and the subsequent consequence of a dramatic loss of signal complexity in a clade of territorial lizards, the Southeast Asian *Draco* lizards. Like most Old World agamid and New World iguanid lizards, male *Draco* perform an elaborate display centered on a core component of a stereotypical sequence of headbobbing movements, which is used in courtship and advertising territorial ownership (Hairston, 1957; Mori & Hikida, 1994). *Draco* are remarkable, however, in being one of the few groups that have evolved a second or augmenting component in the form of a large, conspicuously colored throat fan or dewlap, which supplements the headbob component of the display (the Caribbean *Anolis* lizards and south Asian *Sitana* lizards being two other iconic examples of the independent evolution of a dewlap; Hagman & Ord, 2016). These ornaments appear to have initially evolved as colorful static throat appendages to facilitate the detection of male territorial displays in forested habitats (Ord et al., 2015), which

then evolved into a dynamic structure used directly in the display within the *Draco* genus (Ord et al., 2021). We have discovered a small number of *Draco* species that have either entirely lost the headbob component from their signal repertoire or otherwise rarely use headbob movements for communication. Instead, these species rely entirely or predominantly on signaling using the dewlap.

We began our investigation by reconstructing the evolutionary history of display behavior across *Draco* and other agamids. This revealed the absence of the headbob component from the display within some *Draco* as an extraordinary loss of complexity in what is otherwise a central component of iguanian territorial communication. We then tested three hypotheses for the potential causes of this evolutionary loss: (i) relaxed selection for signal complexity; (ii) habitat-dependent constraints on signal efficacy; and (iii) size-dependent energetic constraints on display movement. Finally, we evaluated the extent to which the loss of the headbob has been compensated for by maintaining signal effort using solely the dewlap or by increasing the information potential of the dewlap by increasing its color complexity (or both).

Material and methods

Data

We began by compiling an initial data set on the presence and absence of headbob displays for 15 *Draco* taxa from an earlier field study (11 species, including two geographically separated populations for four species; Ord et al., 2021). An additional four *Draco* species supplemented this data set using species descriptions of display behavior reported by Humraskar (2008), McGuire and Alcalá (2000), and McGuire et al. (2007). The presence of headbob movements used in the display for other agamid lizards outside of the *Draco* genus was verified for 38 species using a combination of reviews summarizing literature descriptions of display behavior for individual species (Ord et al., 2001; Ramos & Peters, 2016), opportunistically recorded videos by TJO or other researchers of species performing displays in the wild, personal observation by TJO in the field or through personal communication with researchers who have made detailed observations of species in the wild. Details on sources for each species included in our study are provided in [Supplementary Table S1](#). These data were used to reconstruct the evolutionary history of display behavior across *Draco* and other agamid lizard species.

To test the relaxed selection and habitat-dependent constraint hypotheses as potential causes of headbob loss within the *Draco* lineage, we focused on the 15 taxa for which we had extensive field observation and data on the social and physical environment of the taxa. These taxa were found at locations in Peninsular Malaysia, Borneo, and the Philippines (see Ord et al., 2021 for location details). The behavior of free-living male lizards on their territories (median per taxon: 14 males, range: 2–32) was video recorded for 10–30 min. The backgrounds of videos were isolated and analyzed using the matlab-based program “Analysis of Image Motion” (Peters et al., 2002; details given in Ord et al., 2021) to estimate the level of visual noise from windblown vegetation occurring at the time males performed displays (headbob and/or dewlap displays). These data were averaged across display bouts for a given male and then averaged again across males for a given taxon to provide a mean estimate of habitat visual noise for each taxon. During video observations, all

conspecific males and females within the line of sight of the subject male were noted. These data were tallied and averaged across males for a given taxon to provide a mean estimate of the density of male neighbors and females. Male and female densities have been previously linked to the intensity of competition experienced by males for territories and mates within populations of other lizards (e.g., Charles & Ord, 2012). At the completion of video observations, ambient light was measured at the location where the male lizard was first observed to display using an LI-190SA Quantum Sensor connected to an LI-250A light meter. To obtain a mean estimate of ambient habitat light for each taxon, data were averaged across males for that taxon. Both visual noise and ambient light are variables known to impact the detection of lizard visual displays (Ord & Stamps, 2008; Peters, 2008). Full details on collection protocols are provided in the supplementary information of Ord et al. (2021).

To test the size-dependent energetic constraint hypothesis, body size data were taken from the repository of Ord et al. (2020) and consisted of measures of maximum snout-vent length (SVL in mm) for 34 *Draco* species (all currently described species). These data were combined with the presence and absence of headbob displays in *Draco* obtained from the evolutionary reconstructions in the first part of our study.

To evaluate the consequences of headbob loss on signal effort, video records of free-living territorial males of the 15 *Draco* taxa were viewed in real-time to score the frequency of headbob and dewlap displays used by a male for social display. The total number of headbob and dewlap bouts performed by a male was counted and then divided by the length of time the male was recorded to provide an estimate of the number of bouts performed per minute. These data were averaged across males for a given taxon to obtain a mean estimate of headbob and dewlap display rate for that taxon in order to provide a measure of the amount of signal-effort males devoted to performing these components during territorial display.

To estimate dewlap color complexity, we used a combination of photographs of live-caught territorial males taken for an earlier study (15 taxa: Klomp et al., 2016), video stills extracted from video records of each male observed in the field used for another study (2 taxa: Summers & Ord, 2022) and color photographs of male *Draco* from field guides (3 taxa: Grismer, 2011), published papers (6 and 1 taxa, respectively: McGuire et al., 2007; Reilly et al., 2021) and a publicly available unpublished thesis (1 taxa: Humraskar, 2008). In all cases, only unobstructed images of a male with the dewlap at full extension and with the dewlap perpendicular to the camcorder or camera were used to obtain estimates. In the case of photographs of live-caught males and video stills, representative photographs and stills for each male were used, and estimates of complexity were averaged across males for a given taxon. In the case of other sources, estimates were taken for the single best representative image of an identified male for that species. Details on sources for each species included in our study are provided in Table S2. Complexity was computed as the proportional area of each color exhibited on the dewlap using ImageJ version 1.53a (imagej.nih.gov/ij). Dewlap color was quantified by a single observer (TJO) and could be easily delineated into general color categories (e.g., yellow, white, black, red, etc.; although the specific color was not particularly relevant, rather the number of different colors and their proportional area). These proportional areas were then used to calculate complexity based on the modified

Shannon Index, H , developed by Nelson et al. (2022). This measure provides an estimate of the amount of potential information that can be encoded by the color morphology of the dewlap and provides a more robust estimate of complexity than simply tallying the number of different colors seen on the dewlap (Nelson et al., 2022). Estimates of dewlap color complexity were obtained for 28 *Draco* taxa (24 species, including two geographically separated populations for four species).

Statistical analyses

All analyses were implemented in R version 4.0.5 (R Development Core Team, The R Foundation for Statistical Computing, Vienna, Austria) and used the time-calibrated phylogeny developed for the agamid family by Ord et al. (2020). Paired populations within *Draco* species were positioned assuming the minimum intra-island population divergence estimated by McGuire and Heang (2001).

A preliminary test was conducted to evaluate the extent to which the likelihood of observing *Draco* lizards using headbob movements in their display was dependent on sampling effort. A phylogenetic Ornstein–Uhlenbeck (OU) regression was applied using the “phylom” package version 2.6.2 (Ho & Ane, 2014) to the proportion of male lizards observed performing headbob movements as a function of the total number of lizards surveyed for that taxon (sampling effort). There was no credible relationship between observing headbobs and sampling effort (Supplementary Figure S1; Supplementary Table S3), indicating that the absence of headbobs for taxa was unlikely to be the result of inadequate sampling of those taxa.

We then reconstructed the evolutionary history of the presence and absence (or rare use) of headbob movements for social display using stochastic character mapping implemented in the “phytools” package version 0.7-80 (Revell, 2012). This was done by using the default settings of the “make.simmap” function to recover the historic presence and absence of headbobs based on 1,000 stochastic character maps. These character maps were also used to infer probable present-day behavior for *Draco* species that lacked observational data on display (NB: reconstructions were repeated using only species with available data and historic assignments of behavior remained qualitatively unchanged). Previous studies have implicated the origin of headbobs for social display likely occurred at or below the basal node shared by the Iguanidae and Agamidae families (Ord et al., 2001; Ord & Blumstein, 2002), which also corresponds to the likely evolution of territoriality in iguanian lizards more generally (Martins, 1994). These previous inferences were consistent with our own historical reconstructions, and we used TimeTree.org to provide a gross date on the probable origin of headbob displays, assuming its evolution occurred at (or near) the basal node shared by the Iguanidae and Agamidae. However, the primary objective for the evolutionary reconstruction of the headbob display was to identify the distribution of its loss across the Agamidae and the relationship of these losses to the previously determined origin of the dewlap at the base of the *Draco* radiation (Hagman & Ord, 2016; Ord et al., 2015). The evolution of a dewlap in itself was not unique to *Draco* and has convergently evolved in at least one other Agamidae group, represented in our dataset by *Sitana ponticeriana* (see Ord et al., 2015; Figure 1). As far as we are aware, species within this second Agamidae group use both the headbob and dewlap

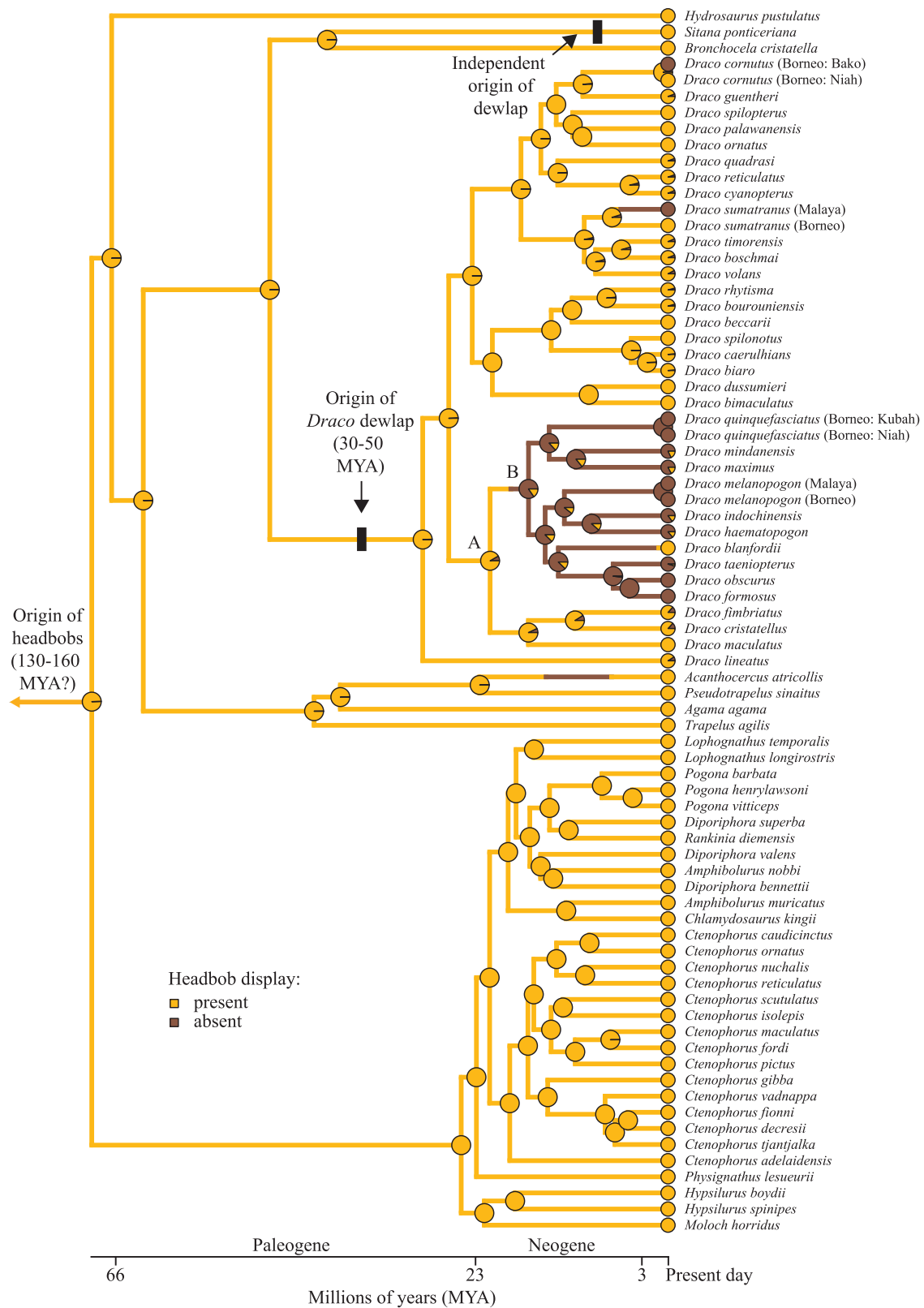


Figure 1. The evolutionary history of the visual displays of agamid lizards illustrating the unusual loss of headbob movements from displays in certain *Draco* species. Dates on the origin of headbobs for territorial visual displays probably originated in the common ancestor of the Iguanidae and Agamidae families approximately 130–160 million years ago based on estimates from TimeTree.org. Dewlaps likely evolved to augment headbob displays in *Draco* sometime between 30 and 50 million years ago. The independent origin of a dewlap has also occurred in *Sitana*, which seems to use both the dewlap and headbob components in display (Ord et al., 2015). Ancestor state reconstructions are based on stochastic character mapping and highlight a large monophyletic clade of *Draco* taxa that have lost the headbob component from their territorial displays, in addition to several others outside of this group. Taxa for which the presence or absence of the headbob has been inferred from stochastic mapping are those with proportional estimates depicted at the phylogenetic tips (e.g., *D. guentheri*, *D. mindanensis*). In all instances, inferences of display type could be unambiguously assigned as either headbob present (e.g., *D. guentheri*) or absent (e.g., *D. mindanensis*). Key nodes for body size evolution and associated loss of the headbob are highlighted with A and B labels (see Figure 2C).

in their territorial advertisement displays. For example, this has been confirmed for *S. ponticeriana* (see the supplementary video in Ord et al. (2015) recorded by A. Kamath), although we acknowledge the group, in general, is poorly studied.

The relaxed selection, habitat-dependent constraint, and size-specific energetic constraint hypotheses were each tested using a phylogenetic logistic regression of the presence versus absence of headbobs (coded 1 and 0, respectively) as a function of conspecific density, habitat properties, or body size using the “*phylolm*” package. The 95% confidence range of coefficients was estimated via 1,000 bootstrap replicates. Coefficients and their confidence ranges were subject to an exponent transform to present effects as odds and odds ratios. We primarily used the confidence range of effects to identify those likely to be statistically different from even odds, but also report z and p values as additional benchmarks. In the case of the size-specific energetic constraint hypothesis, we also reconstructed the body size of evolutionary ancestors to help resolve a trend implied by the logistic regression and visual inspection of taxon data (see Results). This second analysis was used to determine the putative size of the ancestral species from which descendent taxa had subsequently lost the headbob from displays, with the prediction being that this ancestor should be larger in body size than the evolutionary ancestors of lineages in which the headbob had ultimately been retained. These reconstructions were made using maximum likelihood implemented with the “*fastAnc*” function available in the “*phytools*” package. Frequency distributions were used to illustrate the sizes of ancestor species for lineages that ultimately retained or subsequently lost the headbob (based on the stochastic character maps described in the previous paragraph). Two ancestors were of special relevance because these ultimately lead to descendent taxa that had lost the headbob in the largest clade of *Draco* (nodes A and B in Figure 1, from which the Malay radiation of *Draco* are descendent).

Finally, we evaluated the consequences of the loss of headbobs on signal effort by testing the evolutionary correlation between the rate of dewlap display and the rate of headbob display using a phylogenetic OU regression analysis in “*phylolm*.” As applied here, this OU model explicitly models evolutionary change towards a continually shifting adaptive optima. This scenario is an implicit assumption underlying how changes in one aspect of the visual display (the headbob) are expected to be progressively compensated for with increased signal effort in another aspect of the display (the dewlap). The prediction was a negative relationship between dewlap and headbob display rates, such that the intercept of this analysis (corresponding to species that lack the headbob display) should roughly correspond to the maximum display rate of species using both the headbob and dewlap in the display. The extent to which the evolutionary loss of headbobs has corresponded with evolutionary increases in the color complexity of the dewlap was tested by fitting four alternative models of color complexity evolution. This evaluated the extent to which the evolutionary loss of headbob displays (as inferred from the 1,000 stochastic character maps described above) has been disproportionately associated with the evolution of greater dewlap color complexity. This was done using the “*OUwie*” package version 2.6 (Beaulieu et al., 2012) and the application of: (i) a Brownian Motion (BM) null model in which color complexity has evolved stochastically and unrelated to the evolutionary loss of headbobs; (ii) a Brownian Motion model in which stochastic fluctuations (σ^2) in color

complexity evolution has differed in lineages that have lost headbobs compared to lineages retaining headbobs (BM $_{\sigma^2}$); (iii) an OU model in which the adaptive optima of dewlap color complexity (θ) has increased in lineages that have lost headbobs compared to those retaining headbobs (OU $_{\theta}$); and (iv) an OU model in which the adaptive optima (θ), degree of stochastic fluctuation (σ^2), and rate of adaptation (α) in color complexity have differed between lineages with and without headbobs (OU $_{\theta, \alpha, \sigma^2}$). The credibility of each of these models in accounting for the evolutionary relationship between the loss of headbobs and changes in dewlap color complexity was evaluated using a comparison of Akaike information criterion values calculated with a modification for sample size and the number of parameters estimated by a model (AIC $_c$). These values were benchmarked against the BM null model (Δ AIC $_c$), with the model found to have the consistently lowest values considered to be the best-supported model of dewlap complexity evolution.

Results

Evolutionary history of display behavior

The evolutionary loss of headbob movements, or its rarity in social display, appears to have occurred three times in *Draco*, with one instance of a potential secondary gain (in *D. blanfordii*; Figure 1). However, the key result of our ancestor reconstructions was revealing the loss of the headbob component from the display repertoire of lizards belonging to the Malay radiation of *Draco*. All other agamid species examined have retained the headbob as a central component of their display repertoire, with a likely date of origin of somewhere between 160 and 130 million years ago (i.e., in the shared evolutionary ancestor of both the Agamidae and Iguanidae). It has only been following the evolutionary innovation of the dewlap approximately 50–30 million years ago that headbob movements have become lost (or effectively so) from the display repertoire of lizards.

Causes of headbob loss

There was little evidence that the evolutionary loss of headbobs from *Draco* display repertoires has been associated with a relaxation of sexual selection or habitat-dependent constraints on signal detection. Specifically, the odds of taxa concentrating exclusively or predominantly on the dewlap for social display was unrelated to changes in conspecific density (Supplementary Table S4a; Figure 2A)—likely to be associated with the level of competition for territory and mates—or transitions into visually difficult environments (Supplementary Table S4b; Figure 2b)—reflected by reductions in ambient light or increased visual noise from wind-blown vegetation.

There was some evidence for size-specific energetic constraints on display behavior predicting the loss of headbobs in larger species of *Draco*, although results were contingent on the bootstrapped 95% confidence range of odds rather than probability values (Supplementary Table S4c). In general, there appears to have been a considerably greater than even odds of retaining the headbob in displays (odds = 3.10e¹¹; confidence range = 1.98e¹¹, 4.99e¹³), conversely implying that the loss of the headbob has been extremely rare. Of those that have lost the headbob, these taxa seem to have been generally larger in body size than those that have ultimately retained the headbob (odds ratio = 0.005; confidence range

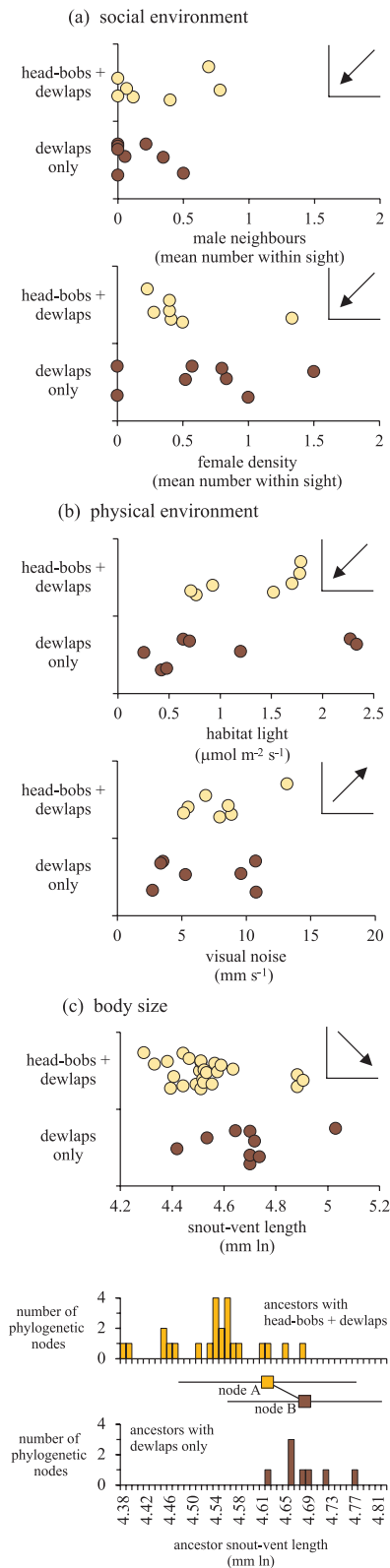


Figure 2. The potential causes for the loss of headbob movements from territorial visual displays of male *Draco* lizards. Each datum represents a single *Draco* taxon jittered on the y-axis within each group (i.e., taxa using displays with headbobs + dewlaps versus those relying on dewlaps only). The inset illustrates the predicted relationship between groups of taxa that use both the headbob and dewlap components versus those that use only the dewlap in display, under the scenario that headbobs had been lost in the latter group because of (A) relaxed

= 0.002–0.007; Supplementary Table S4c; Figure 2C, upper panel). However, the probability values of these effects were modest ($p = 0.11$ – 0.12) suggesting inadequate statistical power for properly resolving trends. The maximum likelihood reconstruction of historic body size similarly suggested that the evolutionary ancestor of the Malay radiation—specifically node B—was at the larger end of the historic body size range of ancestral taxa (Figure 2C, lower panels). To some extent, then, there does appear to be potential support for the hypothesis that energetic costs associated with display might have been greater in larger species compared to smaller species, prompting a shift to predominantly using the dewlap for display.

Consequences of headbob loss

There was a strong positive association between headbob and dewlap display rates, indicating increases in overall signal effort were the product of more frequent use of both headbob and dewlap components in display (Supplementary Table S5; Figure 3A). That is, *Draco* taxa lacking (or rarely using) headbob movements in social display have not compensated for this loss by increasing signal effort through the dewlap display. Instead, species concentrating on the dewlap for display have significantly increased the color complexity of their dewlaps, compared to species using both headbob and dewlap movements in display (Figure 3B). The OU_{θ} model was clearly the best-supported model of color complexity, with complexity being considerably higher in the color morphology of the dewlap in *Draco* taxa lacking headbobs.

Discussion

At some point in the Neogene (Figure 1), the radiation of *Draco* throughout the Malay region coincided with a dramatic change in signal behavior. The headbob display, once a central component of communication, was effectively lost from the signal repertoire. This loss seems to have also occurred on rare occasions in select populations of other *Draco* species from the Philippine radiation (*D. cornutus* and *D. sumatranus*), but the loss in the Malay radiation is clearly the most phylogenetically widespread. Any absence of the headbob is unusual given its ancient origin and near-universal retention in both the agamid and iguanid families (Ord et al., 2001; see also Figure 1). We were unable to confidently resolve why this evolutionary loss might have occurred, but it was unlikely to have been caused by relaxed selection or habitat-dependent constraints on signal design (Supplementary Table S4; Figure 2A and B). Instead, *Draco* lineages that lacked (or greatly reduced) the headbob in social communication were often those with a large body size (Figure 2C). This implies increased energetic costs of display movement associated with increases in body size might have contributed to the evolutionary shift in signal complexity

selection from reduced competition from other males for territories or access to females, (B) constraints on the detection of headbob movements when communicating in visually difficult environments, or (C) the potential cost of physically strenuous body movements in large-bodied species. Also shown in the lower panel (C) are histograms of the inferred historic body sizes reconstructed using maximum likelihood and the phylogeny shown in Figure 1. Highlighted are the size of the evolutionary ancestors just prior to the loss of the headbob from displays (nodes A and B; see Figure 1). Error bars are the 95% confidence intervals associated with the reconstructed body sizes.

from the headbob to exclusively the dewlap. Certainly, lineages that now rely only (or predominantly) on the dewlap for social communication are those that generally exhibit greater color complexity in their dewlaps compared to species that rely on both headbob and dewlap movements for communication (Figure 3B).

While referred to as “headbob” displays, those species of *Draco* that retain this component in their signal repertoire use movements that are typical of other agamid and iguanid lizards in which the body is physically displaced through a combination of head nods and push-ups (e.g., see Mori & Hikida, 1994; Ord et al., 2021). Given the greater mass of the body relative to the dewlap, the energetic cost of headbob movements is presumably greater than the repeated extension and retraction of the dewlap. The Caribbean anole lizards are another group that has independently evolved a dewlap and this difference in energetic cost has been previously used to explain the evolutionary shift in some Caribbean anoles from an energetically costly headbob-centered display to one concentrated more on the dewlap (Ord et al., 2013). The loss of the headbob component from the display of *Draco* could reflect an extreme example of this same evolutionary shift (see Ord et al., 2021). Unlike the Caribbean anoles, however, there are important trade-offs associated with body size evolution in Southeast Asian *Draco* beyond just signal behavior. This makes the potential impacts of body size on signal behavior more challenging to interpret in *Draco*.

Draco are iconic not only for the evolutionary innovation of the dewlap (Ord et al., 2015) but also because modifications to their rib cage allow these arboreal lizards to glide between the trees over considerable distances (Khandelwal & Hedrick, 2020; McGuire & Dudley, 2005). Body size evolution in *Draco* has been subject to severe stabilizing selection in order to maintain the small body sizes required for optimal gliding performance (specifically a snout-to-vent length less than 4.6 mm ln; Ord et al., 2020). Those lineages that have lost headbob movements from their signal repertoire seem to have been those few species that have been pushed off the adaptive optima for gliding performance to larger body sizes (SVL > 4.6 mm ln; Figure 2c). This shift to large size seems to reflect character displacement resulting from historic resource competition among sympatric species (Ord & Klomp, 2014; Ord et al., 2020). The consequence of this size increase has been a large reduction in gliding performance, which has led larger species to switch to other behaviors to compensate for this reduced motility (Ord et al., 2020). It appears, then, that the loss of headbobs from the signal repertoire is potentially another compromise associated with the evolution of large size.

We have proposed an adaptive explanation associated with the increased energetic cost of display behavior in larger species. However, the loss of the headbob could reflect other factors associated with changes in diet or the sensory system resulting from ecological character displacement rather than body size per se. For example, the evolution of a larger body might have similarly increased the size of the eye and its visual acuity, allowing taxa to better resolve the complexity of colors in the dewlap. Communication using the dewlap then superseded the need for the headbob in displays, prompting the loss of the headbob from signal repertoires. It is also possible the loss of the headbob has had little to do with body size (NB: statistical support was tentative). In which case, it remains unclear what has actually caused *Draco* to have lost the headbob from their displays.

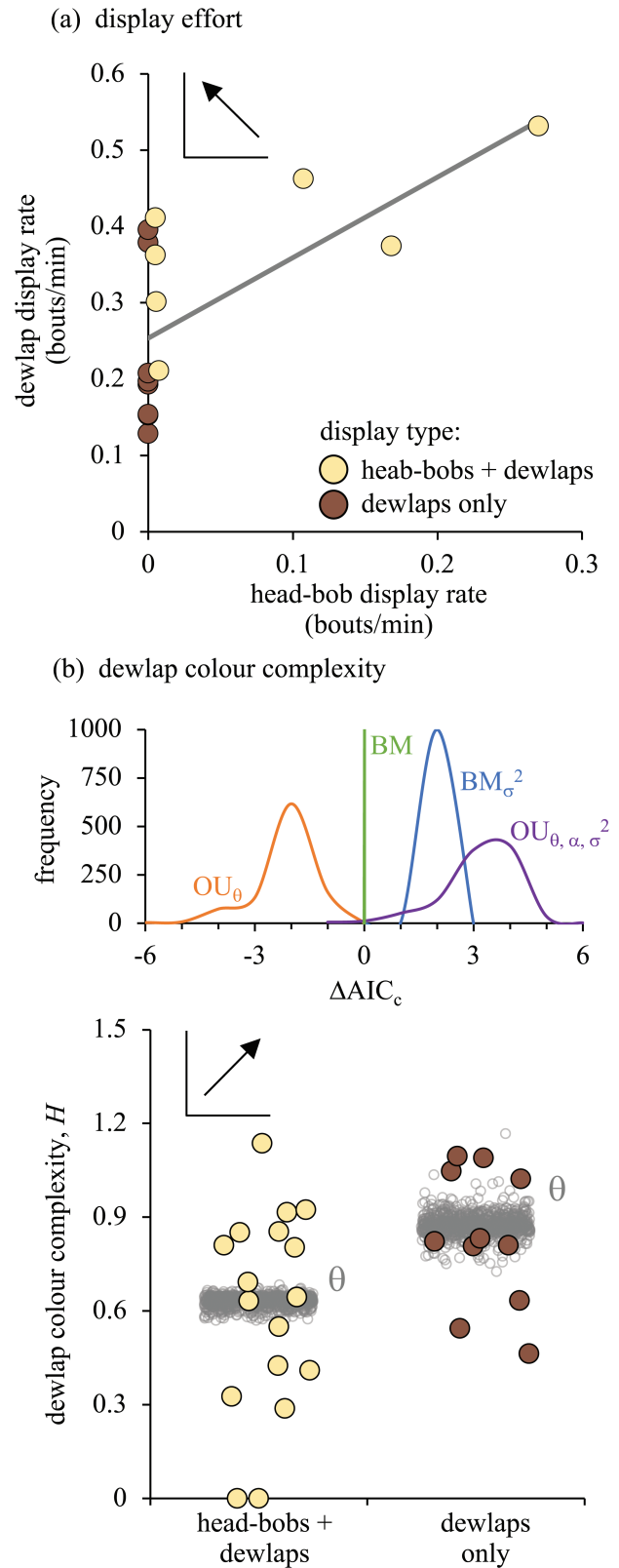


Figure 3. The potential consequences of the loss of headbob movements from territorial visual displays for male *Draco* lizards. Each datum represents a single *Draco* taxon. The inset illustrates the predicted relationship between groups of taxa that use both the headbob and dewlap components versus those that use only the dewlap in display if taxa that have lost headbobs have compensated by increasing (A) signaling effort in the remaining dewlap component or (B) the complexity of color of the dewlap itself. Also shown in (B) is the level of support for alternative models of evolutionary change in dewlap color complexity as a function of the presence or absence of the headbob.

In a variety of animal groups, the loss of one signal component is often compensated for through the elaboration of another signal component. For example, the reduction of a color signal in butterflies and spiny lizards has resulted in communication shifting to chemical signals (Romero-Diaz et al., 2021; Zambre et al., 2022). In *Draco* lizards, it is unlikely that the reduction in information potential from the loss of the headbob display has been fully mitigated by changes in the color morphology of the dewlap, irrespective of whether differences in visual acuity exist between species (see previous paragraph). The color complexity of Malay *Draco* dewlaps ($H \sim 0.9$) is generally comparable to those of Caribbean anoles (median $H = 0.7$; Nelson et al., 2022). The *Anolis* lizards belong to a separate family to the agamids and are far better studied than other dewlapped groups such as *Sitana* (see Figure 1). *Draco* and *Anolis* lizards are morphologically, ecologically, and behaviorally convergent in multiple ways (Ord & Klomp, 2014; Ord et al., 2021), so a comparison of signal complexity between the two groups is likely biologically relevant as well. The complexity of headbob movements used by Caribbean anoles is considerably higher than their dewlap color (median $H = 1.5$; Nelson et al., 2022), and the headbob movements of *Draco* are arguably comparable to those of most anoles (e.g., Ord et al., 2021). That is, even with the increased information potential resulting from the evolution of greater color complexity in the dewlap of Malay *Draco* (and the potential for greater visual acuity in these generally larger species), these species are unlikely to have retained signal complexity by simply shifting information potential exclusively to the dewlap. The consequence, then, is a loss of information that has presumably impacted the capacity for effective social communication in many of these species.

In insects (Hebets & Papaj, 2005), fish (Basolo & Alcaraz, 2003), birds (Petrie & Halliday, 1994), and other lizards (Charles & Ord, 2012), ornaments have often evolved to amplify or elaborate an existing behavioral display. The evolution of the dewlap in *Draco* lizards from a colorful static throat appendage that accompanied the central component of the headbob in displays (Ord et al., 2015) would seem to be typical of this general evolutionary trend. The subsequent loss of complex phenotypes has been an enigma in evolutionary biology (Porter & Crandall, 2003), especially in the context of the widespread loss of elaborate sexually selected characteristics (Wiens, 2001). The loss of signal complexity in Southeast Asian *Draco* lizards is clearly another example of this phenomenon. Yet there are several reasons to highlight this loss as unusual. First, it represents the loss of the core component used for social communication. Second, it has been superseded by a secondary component that initially evolved to augment this core component of communication (Ord et al., 2015). Finally, the information potential of this secondary component is unlikely to have maintained the level of complexity previously present in the communication system. Given that selection for effective communication seems to remain in these lizards—i.e., there appears to be little difference in the level of competition for territories and mates between taxa with and without the headbob—the implications of this loss of signal complexity would seem detrimental. Future research using (for example) robot playback experiments (Klomp et al., 2017; Ord & Stamps, 2009) will need to be done in order to determine how this apparent loss of information potential has impacted the communication and social behavior of these animals in the wild.

Supplementary material

Supplementary material is available online at *Evolution* (<https://academic.oup.com/evolut/qpac057>)

Author contributions

T.J.O. conceived the study, collected and analyzed the data, and wrote the article; A.D., N.A., and I.D. obtained local permissions to conduct fieldwork, provided logistical support, and contributed to manuscript editing.

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