

Repeated evolution of exaggerated dewlaps and other throat morphology in lizards

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Keywords:

aggressive competition;
 animal communication;
 morphological cues;
 sexually selected;
 signal detection.

Abstract

The existence of elaborate ornamental structures in males is often assumed to reflect the outcome of female mate choice for showy males. However, female mate choice appears weak in many iguanian lizards, but males still exhibit an array of ornament-like structures around the throat. We performed a phylogenetic comparative study to assess whether these structures have originated in response to male–male competition or the need for improved signal efficiency in visually difficult environments. We found little evidence for the influence of male–male competition. Instead, forest species were more likely to exhibit colourful throat appendages than species living in open habitats, suggesting selection for signal efficiency. On at least three independent occasions, throat ornamentation has become further elaborated into a large, conspicuously coloured moving dewlap. Although the function of the dewlap is convergent, the underlying hyoid apparatus has evolved very differently, revealing the same adaptive outcome has been achieved through multiple evolutionary trajectories. More generally, our findings highlight that extravagant, ornament-like morphology can evolve in males without the direct influence of female mate choice and that failure to consider alternative hypotheses for the evolution of these structures can obscure the true origins of signal diversity among closely related taxa.

Introduction

Spectacular ornamentation is a hallmark of many social animals. Ornaments are often sexually dimorphic – for example expressed predominately or exclusively in males (Andersson, 1994; Fairbairn, 2013) – and classically believed to function as male sexual advertisements of ‘quality’ to potential mates (Darwin, 1874). Indeed, there is an extensive body of work demonstrating the role of male ornamentation in female mate choice decisions [reviewed by Andersson (1994) and Bradbury & Vehrencamp (2011)]. Yet there are an increasing number of examples in which the presence of exaggerated morphological structures in males seems to have little direct influence on female mating decisions, and

instead function to facilitate the detection of displaying males in visually complex environments [reviewed by Candolin (2003) and Hebets & Papaj (2005)]. Moreover, elaborate ornament-like structures can provide cues for opponent assessment by rival males during aggressive contests (Ord *et al.*, 2001; Lailvaux & Irschick, 2007; Hamilton *et al.*, 2013) or to improve the detection of territorial advertisement displays (Ord & Stamps, 2008; Charles & Ord, 2012), but again have little or nothing to do with courtship.

Despite these alternative functions, there seems to be a prevailing view that the origin of elaborate, sexually dimorphic morphologies (that are not obviously weapons: e.g. Emlen *et al.*, 2005) must reflect the outcome of female mate choice. This implicit assumption can persist for a given study system (e.g. Sullivan & Kwiatkowski, 2007; Gartner *et al.*, 2013; Lambert *et al.*, 2013; Macedonia *et al.*, 2014) despite empirical and experimental tests that fail to support any female discrimination among males on the basis of male ornamentation (Tokarz, 1995, 1998; Jenssen *et al.*, 2001; Tokarz *et al.*,

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2005; Lailvaux & Irschick, 2006). The unfortunate consequence of this bias is that viable alternative hypotheses for the evolution of male extravagant structures – such as signals used in opponent assessment during aggressive interactions or to enhance the detection of displaying males – are rarely tested. This in turn reinforces the notion that factors other than female mate choice are unimportant in driving the evolution of complex, dimorphic morphological structures in males.

Studies of elaborate male ornamentation have often focussed on birds, fish or other taxa in which female mate choice typically plays a dominant role in dictating male reproductive success (e.g. Moller & Pomiankowski, 1993; Jennions *et al.*, 2001; Badyaev & Hill, 2003; Prokop *et al.*, 2012). In these cases, the assumption that sexually dimorphic structures in males have originated through female preference for ornamented males is perhaps reasonable (if not always experimentally confirmed). Nevertheless, even in these cases, extensive variation can still exist among these species in the expression of ornaments that do not necessarily reflect how females discriminate among males within taxa (Marchetti, 1993; Gomez & Théry, 2004; Cummings, 2007; Seehausen *et al.*, 2008). But there are also many taxa in which the reproductive success of males is determined primarily by the ability of males to defend exclusive territories that overlap the home ranges of females, which function to allow males to monopolize matings with resident females (e.g. Jenssen *et al.*, 2001). The presence of elaborate male morphological structures in these systems is unlikely to conform to the classical explanation of ornament evolution via female mate choice.

Obvious examples of such conspicuous ornament-like structures in territorial males are found in two closely related families of iguanian lizard: the Iguanidae and Agamidae. These two families are ecologically diverse and have an extensive global representation of species in both the New and Old Worlds (the Americas, Caribbean, Africa, Asia and Australia). Ornament-like structures are primarily expressed by males, often concentrated around the throat, and are diverse in form (see Ord & Stuart-Fox, 2006). These structures range from coloured throat patches in North American fence lizards (genus *Sceloporus*; Wiens, 1999) and Australian dragons (e.g. *Ctenophorus*; McLean *et al.*, 2014) to the spectacular moving dewlaps of the Caribbean anoles (*Anolis*; Losos, 2009) and South-East Asian gliding lizards (*Draco*; McGuire & Alcalá, 2000), as well as the iconic frills of the Australian frilled-neck lizard and bearded dragon (Hamilton *et al.*, 2013).

There is little evidence of female mate choice in either lizard family, despite considerable research effort to find it (e.g. Tokarz, 1995; Jenssen *et al.*, 2001; LeBas & Marshall, 2001; Lailvaux & Irschick, 2006; Kelso & Martins, 2008). There are some exceptions (e.g. Bleay

& Sinervo, 2007), and it is possible that female mate choice might ultimately be documented in more species, but it is plainly not a dominant selection pressure underlying the reproductive behaviour of the group as a whole. In contrast, adult males of most iguanian lizards vigorously defend territories from rival males (Jenssen *et al.*, 2001; Ord, 2008) and perform a head-bob or push-up display to advertise territory ownership and to convey information on potential fighting ability (e.g. Brandt, 2003; Ord & Evans, 2003). Male territoriality is almost certainly ancestral in both families as well (Martins, 1994). The present-day function of ornamental-like structures in iguanian lizards remains unclear, but the available empirical data suggest exaggerated throat morphologies might have initially originated to enhance the efficacy of displays in visually difficult environments (e.g. in low light or cluttered environments: Ord & Stamps, 2008; Fleishman *et al.*, 2009; Ng *et al.*, 2013) or to provide additional cues for opponent assessment (Ord *et al.*, 2001; Brandt, 2003; Vanhooydonck *et al.*, 2005).

There is recent theoretical support for the notion that exaggerated ornamentation evolves because the increased size and conspicuousness of the ornamental structure facilitate the detection of a male, rather than functioning solely as an indicator of male quality in itself (Tazzyman *et al.*, 2014a,b). An obvious amplifier to a head-bob or push-up display in lizards – or perhaps even the cues conveyed by a colourful throat patch in itself – would be the addition of a large hanging throat appendage or dewlap that draws the attention of receivers to the displaying male (e.g. Ord & Stamps, 2008). Alternatively, or in addition, the size of the structure could in itself provide important information on condition and subsequent fighting ability (e.g. the size of the *Anolis* dewlap has been found to correlate with bite force: Vanhooydonck *et al.*, 2005; Lailvaux & Irschick, 2007) or function to increase the apparent size of a displaying rival. For example, several classic examples of large sexual ornaments in males used by females in mate choice initially evolved to exploit a female bias for large male size, rather than for a preference for the ornament itself (e.g. the elongated tail fin or sword in male swordtails: Rosenthal & Evans, 1998; or the enlarged dorsal fin in sailfin mollies: Kozak *et al.*, 2008). In a similar way, any structure that increases the apparent size of an aggressive rival should also be advantageous because opponent size is an important cue of potential fighting ability (Lopez & Martin, 2001; Umbers *et al.*, 2012; Hamilton *et al.*, 2013).

Given the diversity in throat morphology exhibited by iguanid and agamid lizards, and the general lack of female mate choice governing the evolution of these structures, our goal was to test whether selection for enhanced signal efficacy in visually complex environments, the need for improved opponent assessment among territorial males, or both, explained the origin

and subsequent variation in the exaggeration of throat morphologies among present-day lineages. To this end, our study was conducted in two parts. First, we focussed on the agamid family to leverage its extensive variation in throat morphology among lineages (e.g. throat patches, large fleshy appendages, beards, and highly specialized moving dewlaps or frills) and the large body of existing data on habitat use and body sexual dichromatism for this group that provides a broad index of the intensity of aggressive competition experienced within species (Stuart-Fox & Ord, 2004; Chen *et al.*, 2013; see also Pérez I de Lanuza *et al.*, 2013; NB; sexual size dimorphism (SSD) has also been used as an index of aggressive competition, but there are problems with this measure for some agamid species – see ‘Materials and methods’). Specifically, we tested whether different types of throat ornamentation were associated with increasingly forested environments or male-biased sexual dichromatism (the degree to which males were more conspicuously coloured over their body than females, not including the throat). If throat structures primarily function to enhance the efficacy of territorial head-bob or push-up displays, then they should be associated with genera that typically occupy forest environments in which low ambient light (Ord & Stamps, 2008), increased likelihood of visual obstructions from habitat clutter (Johnson *et al.*, 2010) and greater heterogeneity in visual backgrounds (Ord *et al.*, 2007) should culminate in reduced visibility for displays directed at territorial neighbours. If throat ornamentation functions to improve the assessment of territorial displays (e.g. by providing cues on potential fighting ability or increasing the apparent size of the displaying lizard), then it should be associated with genera that are increasingly more sexually dichromatic (Chen *et al.*, 2013). Following these correlational tests, we reconstructed the evolutionary history of throat ornamentation to evaluate the probable sequence of evolutionary events underlying associations.

Second, we broadened our investigation to include both the agamid and iguanid families to examine the evolution of the most specialized form of throat ornamentation: a large, often conspicuously coloured dewlap that can be rapidly extended and retracted as part of the territorial display (Ord *et al.*, 2013a). The evolution of the dewlap has been described as one of two key innovations that likely promoted the extensive radiation of the iguanid *Anolis* lizards into diverse environments throughout the Caribbean and Americas (the evolution of toepads being the other key innovation; Losos, 2009). The independent evolution of a moveable dewlap to that of anoles has also occurred in agamid *Draco* lizards, which are also notable in the range of habitat types occupied and the size of their radiation throughout Asia (McGuire & Alcalá, 2000). At least one other iguanid and two other agamid lineages have also been reported to extend a dewlap as part of their terri-

torial displays (the iguanid *Polychrus* and the agamids *Otocryptis* and *Sitana*; reviewed by Losos, 2009). The external appearance of the dewlap seems to be remarkably similar between the dewlap of *Anolis* and some agamids (e.g. *Sitana*), implying the structural anatomy of the dewlap has also evolved convergently. However, in other agamids – specifically *Draco* – the outward morphology of the dewlap is unusual compared to *Anolis*, suggesting the hyoid (which controls the dewlap extension) may have evolved quite differently.

Importantly, the morphology of the hyoid has been investigated extensively in *Anolis* (Bels, 1990; Font & Rome, 1990), which provides a functional model for comparison. In particular, the key attributes of the hyoid that dictate the performance of the *Anolis* dewlap have been identified (Ord *et al.*, 2013b), which provides a critical benchmark to compare the anatomy of the hyoid among lineages with and without a moving dewlap. We therefore evaluated (i) how the structural anatomy of the hyoid has evolved in iguanid and agamid lizards; (ii) whether the previously reported examples of a moveable dewlap in these families are in fact consistent with the functional morphology of the hyoid in those species; (iii) how often the dewlap has evolved independently across the two families; and (iv) whether dewlap evolution has likely occurred in response to selection for the enhanced detection of territorial displays in visually difficult environments or selection for improved opponent assessment in the context of intense competition for territories.

Materials and methods

Agamid database

An extensive survey using a variety of sources was made to classify the presence or absence of various types of throat morphology for as many agamid species as possible. Details on the protocols used for this survey are provided in the Supporting information that accompanies this article. Throat morphology for all species could be easily assigned to one of four categories: no visible throat ornamentation, a conspicuously coloured throat, an obvious throat appendage such as a gular pouch, frill or dewlap that was not conspicuously coloured (e.g. was the same drab colour as the rest of the body), or an obvious throat appendage that was conspicuously coloured. Information on sexual dichromatism (not including throat coloration) and habitat was obtained from an existing archive that was the basis of Stuart-Fox & Ord (2004). Sexual dichromatism was measured as the number of body regions for which the sexes were dichromatic and ranged from 0 to 10 (see Stuart-Fox & Ord, 2004 for details).

An alternative index for the magnitude of aggressive competition frequently used is SSD (e.g. see Ord *et al.*, 2001; Stuart-Fox & Ord, 2004; Chen *et al.*, 2013). SSD

was problematic for our study because body size in the gliding genus *Draco* – which is a key agamid group exhibiting dewlaps and prominent throat coloration – is subject to strong negative selection as a result of their gliding lifestyle (Shine *et al.*, 1998; McGuire, 2003; Husak & McGuire, 2014). The potential magnitude of dimorphism that can be exhibited by *Draco*, irrespective of the probable level of male–male competition experienced within species, will therefore be lower than other agamid lizards. We know, however, that SSD and dichromatism are tightly correlated with one another in nongliding agamids (Chen *et al.*, 2013) and that conspicuous coloration is used in opponent assessment by agamids as well (e.g. Stuart-Fox & Johnston, 2005; Whiting *et al.*, 2006; Baird *et al.*, 2013). We therefore used dichromatism rather than SSD as our index of aggressive competition as dichromatism provides a more broadly comparable measure for all taxa included in our study.

Habitat type was scored based on descriptions of the environment for which species were typically found living in: open rocky outcrops, deserts, savannahs, heath or sand dunes were classified as predominantly ‘open’ species; arid acacia woodland or open woodland as predominantly ‘woodland’ species; forest, montane cloud forest or rainforest as predominantly ‘forest’ species.

Species categorizations and sources used to verify those categorizations are described in the data archive associated with this paper deposited in the Dryad Digital Repository (<http://www.dx.doi.org/10.5061/dryad.f01t1>). Our final data set of throat morphology included 274 species (62% of recognized species) from 48 agamid genera (86% of recognized genera; Uetz & Hošek, 2013), with additional information on sexual dichromatism and habitat for 100 and 119 species, respectively (22–27% of recognized species across 86% of recognized genera).

Hyoid morphology

Details of the hyoid apparatus for iguanid and agamid genera were obtained primarily from computed tomography (CT) scans of specimens made in the Biological Resources Imaging Laboratory at the University of New South Wales or that were available online at the National Science Foundation Digital Library at the University of Texas, Austin (www.digimorph.org). These were supplemented with digital photographs of cleared and stained specimens obtained from the collections of the Chicago Field Museum and the Museum of Comparative Zoology at Harvard University (e.g. Ord *et al.*, 2013b). These cleared and stained specimens were also used to confirm that images taken from CT scans provided full and accurate representation of the hyoid, parts of which consisted of cartilage that can be difficult to fully resolve in CT scans of low resolution (M. Hagman & T.J. Ord, personal observation). For

three species, we used published drawings of the hyoid made from dissections: *Chlamydosaurus kingii* (Beddard, 1905), *Pogona barbata* and *Amphibolurus muricatus* (Throckmorton *et al.*, 1985). Ventral images of the throat region exported from CT scans, or shown in photographs of cleared and stained specimens, or in figures of published papers (Beddard, 1905; Throckmorton *et al.*, 1985), were imported into Adobe Illustrator and traced at high magnification using the segmented pen tool to obtain detailed line drawings of the hyoid and its positioning relative to the lower jaw.

We initially thought to include a third iguanian family – the chameleons – that are generally considered to be basal to the agamids in most recent phylogenies (Townsend *et al.*, 2011; Wiens *et al.*, 2012; Pyron & Burbrink, 2014). However, an early review of CT scans of the hyoid and head morphology of a range of species showed chameleons to be highly derived and specialized in form, so much so that any comparison with the agamid and iguanid families was virtually meaningless (e.g. the hyoid is vastly different in chameleons, which made direct comparison impossible for key components of the hyoid relevant for the moving dewlap in agamids and iguanids; see below). The chameleons were therefore not considered further by our study.

Based on previous biomechanical modelling (Ord *et al.*, 2013b) and detailed investigations of the action of the hyoid as the dewlap is extended by adult male *Anolis* lizards (Font & Rome, 1990), there are several key components that govern the performance of the dewlap mechanism that also clearly delineate the overall appearance of the hyoid in *Anolis* (a genus with a notable moving dewlap) from most other iguanid lizards (genera that do not possess an extendible dewlap; this study).

Briefly, the hyoid in *Anolis* functions as a first-order lever system in which the hypohyal acts as the in-lever (with force being applied to the hypohyal from the movement of the ceratohyal as the ceratohyoideus muscles straddling the ceratohyal and first ceratobranchials contract – Bels, 1990; Font & Rome, 1990) and the second ceratobranchials as the out-lever (which in turn pushes out the envelope of the dewlap from the throat). The efficiency of this lever, or more broadly the ability to extend a morphological appendage out from the throat, is dependent on a number of aspects of the hyoid (Ord *et al.*, 2013b), but in particular the relative length of the hypohyal to the second ceratobranchials, or the fulcrum ratio (F_{ratio}). For example, among *Anolis* species, the speed at which the dewlap can be extended during territorial displays increases with F_{ratio} , which seems to be primarily achieved by elongating the second ceratobranchials relative to the hypohyals (Ord *et al.*, 2013b). At a more basic level, this suggests that to power a moving dewlap, there must be an evolutionary change in the length of the hypohyals or second ceratobranchials that greatly increases the F_{ratio} .

In addition to the F_{ratio} , the transfer of force through the lever system and how rapidly a throat appendage can be extended is also dependent on the angle of orientation of the hypohyal to the second ceratobranchials (HH°). The most efficient transfer of force generally occurs if the hypohyals and second ceratobranchials are roughly 180° to one another, which is typical for *Anolis* (this study). Other aspects of the hyoid that likely dictate whether a throat appendage can be extended as a movement display are specific to the ceratohyoideus muscles powering the lever system (Ord *et al.*, 2013b). Obtaining data on the ceratohyoideus muscles would require a detailed study of muscle physiology, and issues still remain on what aspects of the muscle are likely to be biologically relevant (see Ord *et al.*, 2013b for discussion).

Measuring F_{ratio} and HH° is more tractable and the biomechanical basis of these variables more clearly defined (Ord *et al.*, 2013b). The type of information that can be obtained for these variables from CT scans and other visualizations of the hyoid are approximations that should be suitable for the goals of the current study (see Supporting information for discussion). To obtain estimates of F_{ratio} and HH° , the original digital images extracted from CT scans or taken of cleared and stained specimens (or the diagrams of the hyoid taken from published papers – Beddard, 1905; Throckmorton *et al.*, 1985) were imported into IMAGEJ VER 1.42Q (W. Rasband 1997–2009 NIH), and the relative lengths of the hypohyal and second ceratobranchial on the right side of the lizard were measured to compute F_{ratio} , in addition to the angle of orientation of the hypohyal to the second ceratobranchial to provide an estimate of HH° .

Our subsequent evaluation of the hyoid relied on highlighting obvious differences in the values of the F_{ratio} and HH° that might typify genera with a moving dewlap. Although this evaluation was made with explicit reference to the phylogenetic relationships among genera, no attempt was made to formally reconstruct evolutionary changes in the hyoid across the phylogeny. To do so would require detailed information on all aspects of the hyoid and their probable biomechanical relationship to one another, which was beyond the scope of the current study. Instead, our goal was to corroborate (or refute) previous reports of species with putative moving dewlaps, as well as potentially identify new species not previously known to possess a moving dewlap, and to then assess the number of times a moving dewlap has likely evolved and what social or ecological conditions might have promoted the evolution of such a highly specialized ornament.

Statistical analyses

Our analyses focussed primarily on assessing variation in throat ornamentation among genera (see Supporting

information for discussion). Variation among species within genera for throat morphology was taken into account by estimating the proportion of species for a genus that exhibited a given ornament type [these proportional data were handled in our analyses using a logit transformation following Warton & Hui (2011)]. The median value of sexual dichromatism exhibited among species within a genus was used to characterize the typical level of dichromatism for that genus (medians ranged from 0 to 6), whereas the most common habitat type recorded for species within a genus was used to characterize the typical environment of a genus [scored as either 0 (absent) or 1 (present) for open, woodland and forest environments, respectively].

To confirm that genus-level analyses provided a reasonable assessment of ornament evolution, we also conducted comparable analyses on the available species data (Supporting information), although these analyses were necessarily more limited.

Phylogeny

We first checked and updated species synonyms using the Reptile Database (www.reptile-database.org; Uetz & Hošek, 2013). We then used Pyron & Burbrink (2014)'s time-calibrated phylogeny of squamate reptiles pruned down to the genera of interest using MESQUITE VER 3.01 (Maddison & Maddison, 2010). Eight genera (corresponding to 10 species) were not included in the Pyron & Burbrink phylogeny (*Complicitus*, *Cryptagama*, *Dendragama*, *Harpesaurus*, *Hypsicalotes*, *Lophocalotes*, *Pseudocophotis* and *Thaumatorhynch*). These genera were included in the data presented in Figs 1 and S2, but were otherwise left out of formal phylogenetic analyses.

Three genera were not monophyletic in the Pyron & Burbrink phylogeny and subsequently presented a challenge for collapsing the phylogeny down to genera: species of *Lophognathus* were found basal to the *Diporiphora-Chlamydosaurus* clade or within that clade as a sister taxa to *Amphibolorus*; species of *Japalura* were sister taxa to *Ptyctolaemus* and *Gonocephalus* and basal to *Salea* and *Pseudocalotes*; species of *Gonocephalus* in themselves were basal to the *Coryphophylax-Pseudocalotes* clade (with some species of *Japalura*) or within that clade as sister taxa to *Bronchocela* (see Fig. S3). To resolve these, we created 12 alternative genera trees that covered all possible topologies for these three genera and repeated our analyses across all of these alternative phylogenies.

Hypothesis testing

Four evolutionary predictor models were applied using a generalized least squares (PGLS) analysis implemented with Blomberg's K statistic (Blomberg *et al.*, 2003) in R software ver 3.1.1 (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria) and the package 'APE' VER 3.1-4 (Paradis *et al.*, 2004). (NB: the logit transformation of the ornament

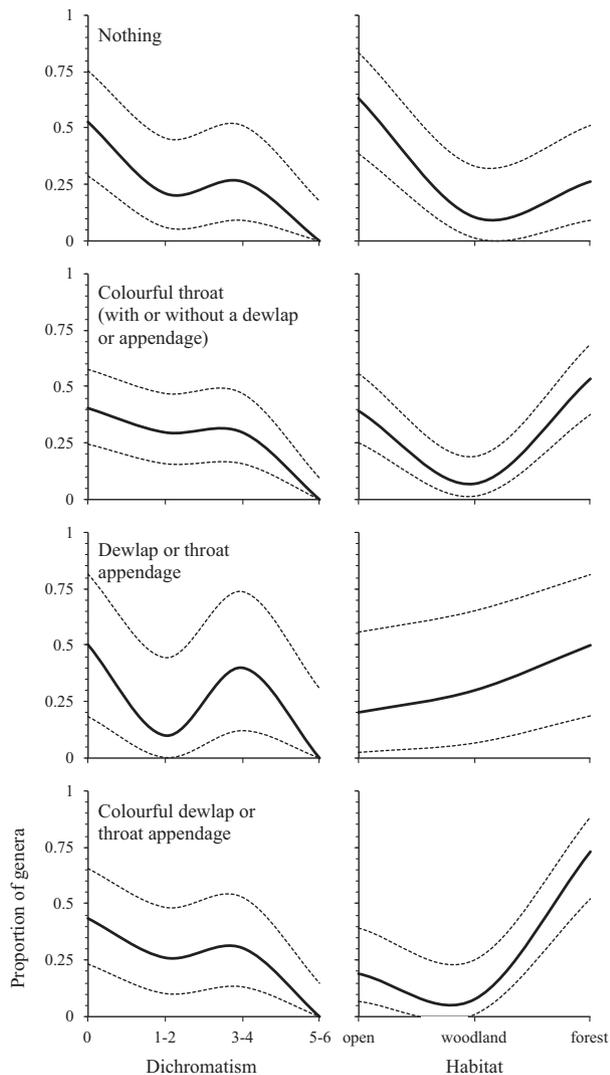


Fig. 1 The proportion of agamid genera that exhibit different types of throat morphology as a function of the median sexual dichromatism and type of habitat in which species within those genera are most often found. Dashed lines correspond to 95% confidence intervals (see Fig. S2 for species-level patterns).

data effectively applied a log-link function version of this analysis; see Martins & Hansen, 1997.) The first model was a phylogenetic null model that assumed that ornament evolution was not associated with any predictor variable. The second model included the median level of sexual dichromatism for genera as a predictor and assumed that the likelihood of evolving a given ornament type increased with increasing sexual dichromatism. The third model included habitat type as a predictor variable and assumed that the likelihood of evolving a given ornament type was associated with the need for effective communication in complex forest environments. The fourth model included both median

dichromatism and habitat type and assumed that both of these have been influential in increasing the likelihood of evolving a given ornament type.

The level of support for each model was evaluated using a second-order variant of Akaike's information criterion (Akaike, 1973) that compensates for differences in the number of model parameters relative to sample size (AIC_c ; Burnham & Anderson, 2002). The model receiving the lowest AIC_c value is considered to be the best model explaining patterns in the data, but by convention any model within two units of this lowest value ($\Delta AIC_c \leq 2.0$) is considered equally compelling. We also computed model weights, AIC_w , using formula presented in Burnham & Anderson (2002) to provide an index of the relative weight of evidence for a given model compared to the other three models applied to the data. AIC_w ranges from 0.0, or virtually no evidence for a given model relative to the others applied, to 1.0, in which a model receives exclusive support over all others. The computed t values associated with a given predictor variable were used to assess the magnitude and direction of the effect. The set of four models was applied to each of the 12 alternative phylogenies.

Although an additional goal of our study was to identify the potential evolutionary origins of a moving dewlap in relation to dichromatism and habitat more specifically – with genera classified as having a moving dewlap corroborated by the morphology of their hyoid – it became clear that a formal phylogenetic analysis was not warranted to achieve this goal (see 'Results').

Historical reconstructions

We examined the probable evolutionary history of colourful throat patches, and colourful dewlaps and appendages, using ancestor state reconstructions of logit-transformed proportions of occurrence for these morphologies within genera. We focussed on these two throat morphologies specifically because PGLS regression analyses suggested strong associations between these ornaments and forest habitats. Reconstructions were made with the 'ace' function in the R package 'APE' and a Brownian motion model of character evolution fitted using restricted maximum likelihood (which provides an unbiased estimate of the variance associated with the Brownian motion process; for details see 'ace' help documentation in R). To visualize reconstructions on the phylogeny, estimated node values and associated 95% confidence intervals were back-transformed from their logit values to proportions. We also assessed the sensitivity of these reconstructions to changes in the topology of the phylogeny by implementing reconstructions across a range of phylogenies in which the positions of *Lophognathus*, *Japalura* and *Gonocephalus* varied. All reconstructions were qualitatively similar, and the choice of phylogeny was subsequently negligible for the final interpretation of

evolutionary patterns. These evolutionary patterns were also consistent with reconstructions based on the restricted species-level reconstruction (Supporting information).

Results

Predictors of extravagant throat morphology

We began our analyses by first comparing the variation in the expression of different types of throat morphology among different agamid genera in relation to male-biased sexual dichromatism and habitat type. The only compelling trend in the data was a marked increase in the number of genera exhibiting a colourful throat appendage in forest environments (Fig. 1), whereas genera with no ornamentation tended to be more common in open environments (Fig. 1; see also Fig. S2). In comparison, there was no obvious increase in the presence of any type of throat ornament with increasing male-biased sexual dichromatism.

These patterns were confirmed with PGLS regressions fitting four alternative evolution models across 12 alternative phylogenies. The forest habitat model was consistently the best-supported model accounting for variation among genera in the possession of a colourful dewlap or throat appendage (Table 1). The more general characteristic of exhibiting a colourful throat with or without some form of throat appendage was also associated with forest environments, but this relation-

ship was driven entirely by forest genera that had a large appendage (i.e. genera with colourful throats but no appendage were more common in open habitats). The phylogenetic null model was the only compelling model for variation in the expression of drab throat appendages (dewlaps or appendages that were not conspicuously coloured). In no instance was male-biased sexual dichromatism a compelling evolutionary model accounting for the presence of throat ornamentation (e.g. effect sizes for dichromatism ranged from $t = 0.53$ to 1.91). Restricted species-level analyses corroborated these results (Tables S1 and S2).

Evolutionary history of extravagant throat morphology

Regardless of how the data were examined (genus or species), ancestor state reconstructions inferred a single, ancient origin of a colourful throat (≥ 110 MYA; Figs 2 and S4). Subsequent change in ornamentation has followed one of two evolutionary trajectories: an additional elaboration with the evolution of a large appendage (e.g. a gular pouch or dewlap), or a reversal to a nonornamented state following the loss of a colourful throat (Figs 2 and S4). Most evolutionary losses of colourful ornamentation appear to have been concentrated in the Australian and African radiations, and potentially because of historical transitions into increasingly more open habitats (see previous section). In contrast, throat ornamentation appears to have

Table 1 PGLS regressions implemented with Blomberg's K statistic and a log-link function [$n = 34$ genera; of the original 48 genera, six did not have information on dichromatism and eight were not included in the Pyron & Burbrink (2014) phylogeny]. Model support was evaluated across 12 alternative phylogenetic hypotheses. Shown are the minimum and maximum support values and effect sizes, with the best-supported model across all trees highlighted in bold. See Tables S1 and S2 for comparable species-level analyses.

Type of ornamentation Model	ΔAIC_c	AIC_w	Effect size (t)
Colourful throat, with or without dewlap or appendage $K = 0.1-0.4$			
Null	7.3-7.3	0.02-0.02	na
Dichromatism	10.6-11.1	0.00-0.00	1.25-1.91
Mainly forest	0.0-0.0	0.82-0.84	3.59-3.61
Dichromatism + mainly forest	3.4-3.7	0.14-0.15	1.50-1.59, 3.72-3.72
Noncoloured dewlap or appendage $K = 0.1$			
Null	0.00-0.00	0.76-0.77	na
Dichromatism	5.34-5.35	0.05-0.05	0.56-0.57
Mainly forest	2.97-3.07	0.17-0.17	-0.96 to -0.91
Dichromatism + mainly forest	8.50-8.59	0.01-0.01	0.53-0.54, -0.88 to -0.93
Colourful dewlap or appendage $K = 0.1-0.5$			
Null	16.39-17.03	0.00-0.00	na
Dichromatism	19.69-20.34	0.00-0.00	1.04-1.43
Mainly forest	0.00-0.00	0.90-0.90	5.52-5.60
Dichromatism + mainly forest	4.31-4.47	0.10-0.10	0.95-1.03, 5.54-5.63

PGLS, phylogenetic generalized least squares.

reached its most elaborate form in the forest genera of the South-East Asian radiation, with the evolution of large throat appendages to enhance an already conspicuously coloured throat (≥ 70 MYA; Figs 2 and S4). This includes the spectacularly dewlapped lineages of *Draco*, *Otocryptis* and *Sitana* (NB: although present-day *Sitana* occupy open habitats (e.g. see Movie S3), they have almost certainly originated from a forest ancestor and one that already possessed a moveable dewlap).

Hyoid morphology and the evolution of the dewlap

Most iguanid genera exhibit the same, conserved hyoid morphology (Fig. 3). For example, *Sceloporus* possess a hyoid that is typical of most iguanid lizards (Fig. 5). In contrast, the *Anolis* are a genus known for their large moving dewlaps and their hyoid is highly specialized for this purpose. This includes reduced hypohyals and greatly elongate second ceratobranchials (Figs 3 and 5a) that culminate in a large F_{ratio} (Fig. 4). The orientation of the hypohyal relative to the second ceratobranchials, HH° , has also converged on 180° from the more typical $\leq 150^\circ$ of other iguanids (Figs 4 and 5a).

Corytophane are another notable exception in the iguanids. Although the changes in the hypohyals and second ceratobranchials are not as accentuated as in *Anolis*, the *Corytophane* do nevertheless exhibit a hyoid

that is arguably more similar to *Anolis* than other iguanids. Externally, the genus appears to have a large throat appendage (Fig. 5a), and the morphology of the hyoid suggests that *Corytophane* might be capable of moving this appendage in a similar fashion to an *Anolis* dewlap. The horned lizards, *Phrynosoma*, were also unusual in their hyoid morphology. In this genus, however, there have been major reductions in the length of both the hypohyals and second ceratobranchials, as well as in several other aspects of their hyoid morphology (Fig. 3). Externally, *Phrynosoma* do not exhibit any form of throat appendage (T.J. Ord, personal observation), which is consistent with their hyoid morphology.

Polychrus has been reported to possess a moveable dewlap similar to that of *Anolis* (see Losos, 2009). However, the hyoid of *Polychrus* is unremarkable and appears very similar to other iguanids that do not have a dewlap or any type of throat appendage for that matter (e.g. compare *Polychrus* and *Sceloporus*; Fig. 5a). Based on the morphology of the hyoid, there is no evidence for a moveable dewlap in this genus, at least based on the species examined so far (see Fig. S1).

In stark contrast to the iguanids, there was extensive variation in hyoid morphology among agamid genera (Fig. 3). Although there are several agamid genera with hyoids similar to the conserved hyoid of most iguanids

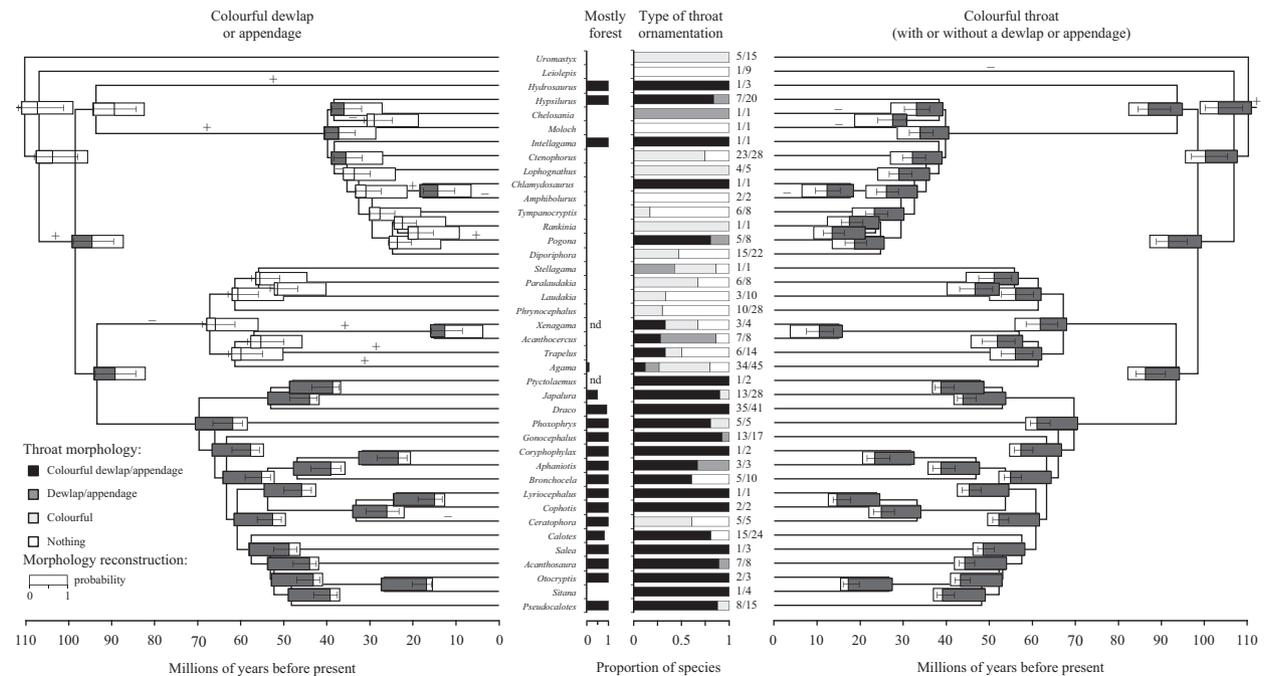


Fig. 2 Maximum likelihood ancestor state reconstructions of the proportion of species within agamid genera (back-transformed from logit reconstructions) exhibiting different types of throat ornamentation. Error bars correspond to 95% confidence intervals (CIs). Nodes with 95% CIs that do not overlap zero are highlighted in grey. At the tips of the phylogeny are the proportion of species found in predominantly forest habitats. The inferred earliest likely gains (+) or losses (–) of an ornament type are indicated alongside corresponding lineages (see Fig. S4 for species-level reconstructions).

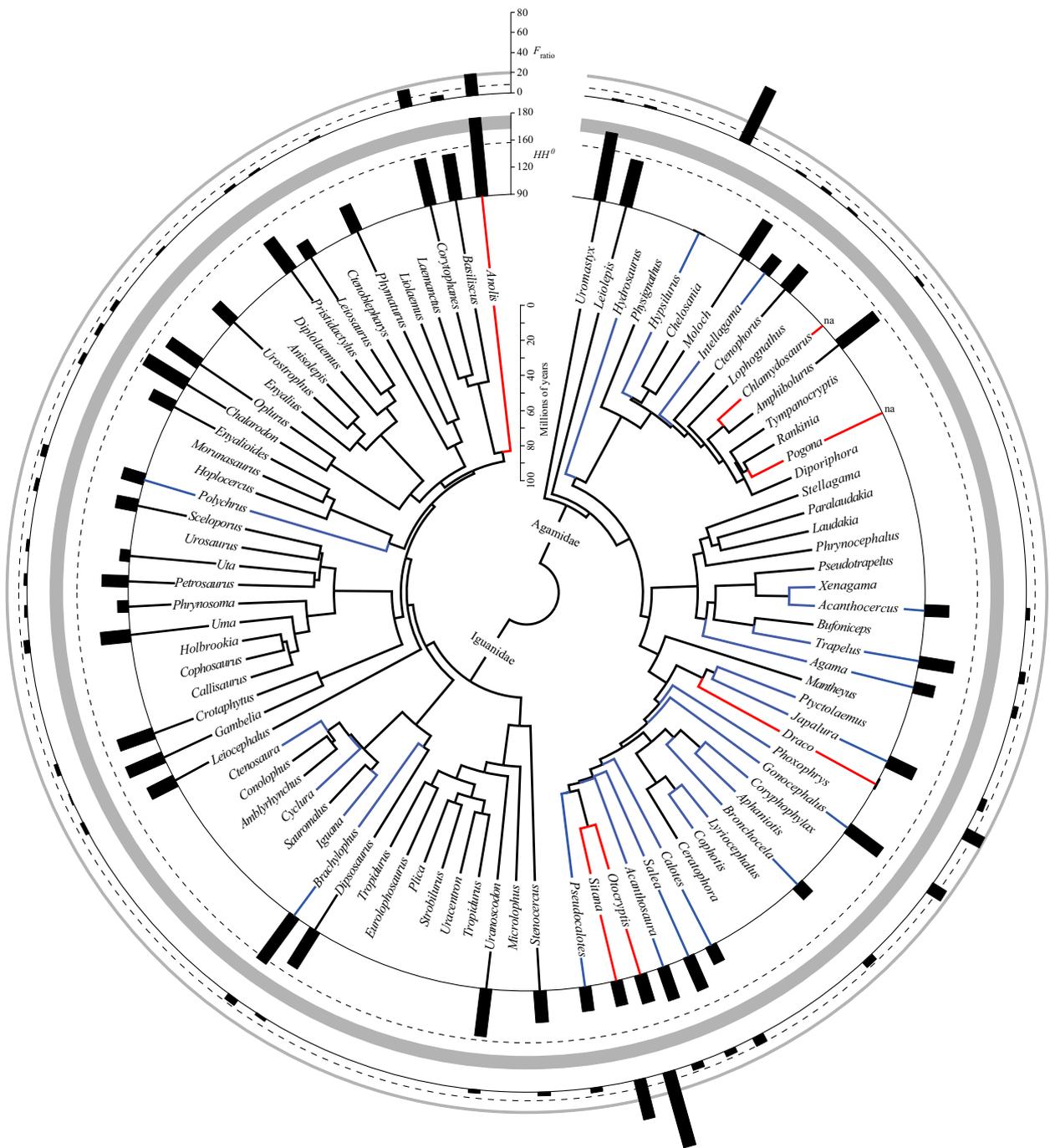


Fig. 4 Variation in two key components of the hyoid expected to affect the performance of a dynamic dewlap display: the length of the second ceratobranchials relative to the length of the hypohyals, or F_{ratio} , and the angle of orientation of the second ceratobranchials to the hypohyals, HH° . Those genera indicated by ‘na’ (not applicable) are those possessing an elaborate frill display where the mechanism of ornament extension is not comparable to that of an extendible dewlap and where F_{ratio} and HH° are not relevant variables. The shaded region provides a benchmark of the minimum and maximum values of F_{ratio} and HH° for 11 *Anolis* taxa from Puerto Rico and Jamaica (Ord *et al.*, 2013b). The dashed line corresponds to the hyoid of *A. poncensis*, which is an anole lizard that lacks a dewlap display (Ord *et al.*, 2013a). Note that the HH° for *Draco*, *Sitana* and *Otocryptis* is questionable because the hypohyal has become so reduced that its angle to the ceratobranchials is unlikely to be functional in the same capacity as *Anolis*. See Fig. 3 for other details.

Finally, *Draco*, *Otocryptis* and *Sitana* – all genera known for their large moveable dewlaps – have noticeable differences in their hyoid that separate them from most other agamids. Furthermore, the morphology of the hyoid in these three genera was quite different to that of the dewlapped *Anolis* in Iguanidae. In contrast to *Anolis*, the hypohyal has become so reduced in *Draco*, *Otocryptis* and *Sitana* that it is almost absent from the hyoid altogether. Nevertheless, *Anolis*, *Draco*, *Otocryptis* and *Sitana* all share highly elongated second ceratobranchials, which appear to be the key (and only) unifying characteristic of a moveable dewlap for these genera. In addition, the changes to the hypohyal and second ceratobranchials in the dewlapped agamids place them on par or beyond the F_{ratio} of the dewlapped *Anolis*. Interpretation of HH° in *Draco*, *Otocryptis* and *Sitana* was difficult given that the hypohyal was so reduced in these genera that its measurement was difficult. This in itself suggests that the biomechanical relevance of HH° is probably questionable for these genera. Another obvious difference between the dewlapped agamid genera and *Anolis* was the large reduction in the ceratohyals, and in the case of *Draco*, a major increase in the size of first ceratobranchials (Fig. 5b).

One other agamid genus, *Hypsilurus*, exhibits a hyoid remarkably similar in morphology to that of *Draco*, *Otocryptis* and *Sitana* (Figs 3–5). This genus has a number of species with large throat appendages, but has not previously been reported to have a moveable dewlap. The morphology of the hyoid in *Hypsilurus* strongly suggests that it could be capable of rapidly extending and retracting its appendage in a comparable way to that of dewlapped agamids (*Draco*, *Otocryptis* and *Sitana*).

Taken together, the morphology of the hyoid implies only one clear origin of a moveable dewlap in iguanids – that of *Anolis* (Figs 3 and 4) – and at least two independent origins of a moveable dewlap in agamid – in *Draco* and in the monophyletic clade of *Otocryptis* and *Sitana* (Figs 3 and 4) – with a potential third independent origin in *Hypsilurus* based on its hyoid morphology. In addition to these genera, a very different moveable throat ornament – the frill or beard – has originated in some Australian lizards through other modifications to the hyoid (Figs 3 and 5).

There was little in the territoriality or ecology distinguishing these dewlapped or frilled genera from other iguanids and agamids. Genera with a moveable dewlap were predominantly arboreal, tropical forest lizards (*Anolis*, *Draco*, *Hypsilurus* and *Otocryptis*; or likely originated from ancestors that were in the case of *Sitana*; Fig. 2), whereas the frilled genera were typical semi-arboreal Australian agamids commonly found in woodland arid environments (*Chlamydosaurus* and *Pogona*). The dewlapped and frilled agamids were also unremarkable in their sexual dichromatism (range: 0–2; compare with the range across all agamids in Fig. 1),

which is generally true for *Anolis* as well (T.J. Ord, personal observation).

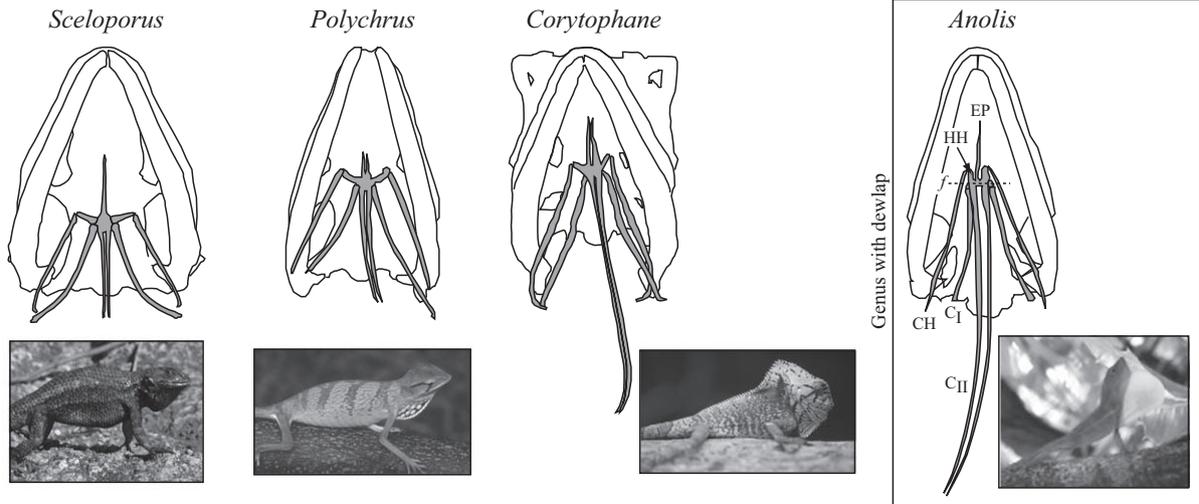
Discussion

There has been much research effort attempting to link variation in female mate choice decisions to the elaboration of male signals such as ornaments [reviewed by Andersson (1994) and Bradbury & Vehrencamp (2011)]. Similar research – be it notably less common – has focussed on the consequences of male–male competition over access to females (e.g. territoriality) and the elaboration of male signals that might be useful in opponent assessment (Ord *et al.*, 2001; Lappin *et al.*, 2006; Lailvaux & Irschick, 2007; Pérez I de Lanuza *et al.*, 2013). When males are observed to use signals to attract mates or defend territories, a focus on sexual selection as the cause of elaboration in male signals seems reasonable. However, our results emphasize that an exclusive focus on sexual selection can obscure the details behind the true origins of a male signal.

In iguanian lizards, those species that have a colourful dewlap or other exaggerated throat appendage typically display it prominently during territorial advertisements and aggressive encounters with male rivals (T.J. Ord, personal observation). This intuitively implies some role in opponent assessment. Furthermore, a positive correlation between dewlap size and bite force among *Anolis* males has been documented within several species (Vanhooydonck *et al.*, 2005; Lailvaux & Irschick, 2007), and a positive correlation between mean dewlap size and the likely intensity of competition experienced by males has been found across populations in at least one *Anolis* species (Vanhooydonck *et al.*, 2009). Given that combat in lizards is centred on inflicting injury through biting (Lappin *et al.*, 2006), these data would suggest the size of the extended dewlap in *Anolis* signals potential fighting ability (Vanhooydonck *et al.*, 2005, 2009; Lailvaux & Irschick, 2007). Similarly, in agamids, the colour of the large, extendible frill in male frillneck lizards determines contest outcome between size-matched territorial males without the need to resort to physical combat, probably because frill colour conveys reliable information on physical condition (not bite force *per se*; Hamilton *et al.*, 2013). These examples imply that elaborate throat appendages should be useful in conveying threat and that the initial evolution of such appendages occurred because of the need for improved opponent assessment during aggressive competition.

Yet we found the origin of these structures was not predicted by male-biased sexual dichromatism, which is an index of the probable intensity of male–male competition experienced within species (Stuart-Fox & Ord, 2004; Chen *et al.*, 2013). In fact, genera that were sexually monomorphic in body colour were equally likely to possess a colourful dewlap or throat appendage as

(a) Iguanidae



(b) Agamidae

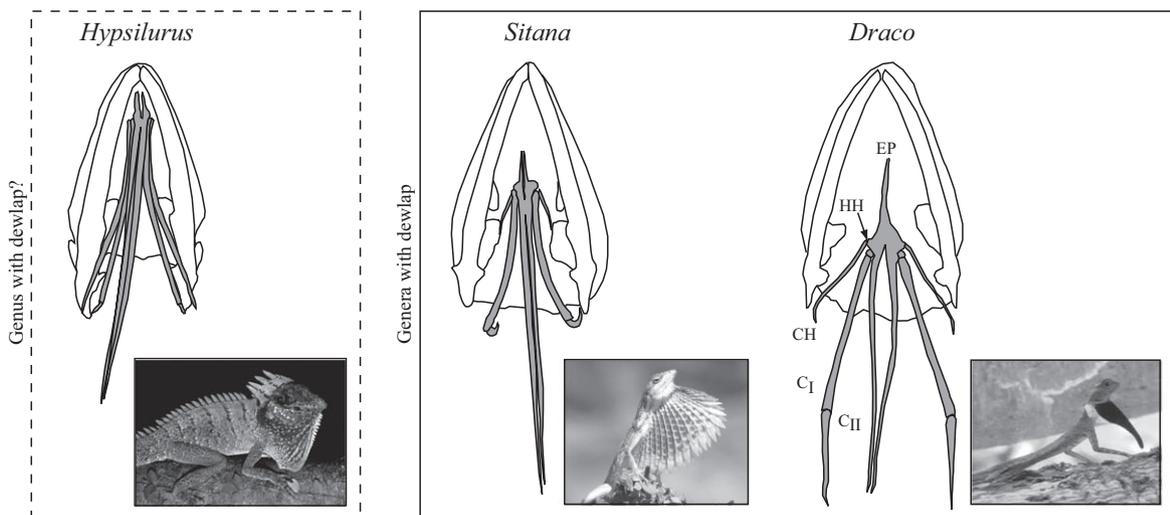
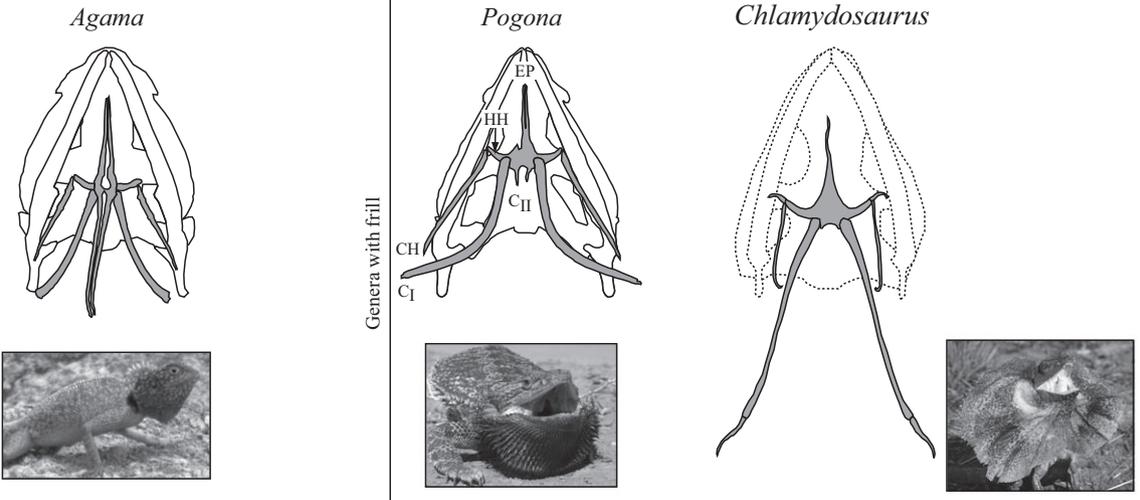


Fig. 5 The hyoid detailed in representative (a) iguanid and (b) agamid genera with photographs of throat structures in life. Labelled are the entoglossal process (EP), hypohyal (HH), ceratohyal (CH), first ceratobranchial (C_1), second ceratobranchial (C_{II}) and the fulcrum (if known, *f*). Photograph credits: *Sceloporus occidentalis* (Yoni Brandt), *Polychrus gutturosus* (Jonathan Losos), *Corytophane cristatellus* (Stanley Rand and the Smithsonian Tropical Institute), *Anolis lineatopus* (Terry Ord), *Agama lanzai* (Phillip Wagner), *Hypsilurus dilophus* and *Pogona barbata* (Devi Stuart-Fox), *Chlamydosaurus kingii* (Mattias Hagman), *Sitana ponticeriana* (Ambika Kamath), and *Draco melanopogon* (Terry Ord). Videos of the dewlap being used in territorial advertisement displays for *Anolis*, *Draco* and *Sitana* (courtesy of Ambika Kamath) are found in electronic supporting information.

lack throat ornament altogether. It is possible that sexual dichromatism fails to capture the full variation in aggressive competition among species. However, male-biased sexual dichromatism in lizards is strongly correlated with other indices of male–male competition (Stuart-Fox & Ord, 2004; Pérez I de Lanuza *et al.*, 2013) and has been implicated in the evolution of increasing colour complexity in visual signalling more broadly (Chen *et al.*, 2013). It seems reasonable to assume, then, that sexual dichromatism does provide at least a rough index of competitive intensity within species. Our results therefore imply that selection from aggressive competition might not have been the primary evolutionary force initially generating large changes in throat morphology, but it could still play a role in the subsequent elaboration of appendages once they originate (e.g. size, colour; see previous paragraph).

The vast majority of dewlapped and appendaged species were those that lived in closed environments such as forests. This infers selection for improved signal efficacy has been the likely factor driving the evolutionary origin of large, conspicuously coloured throat appendages (in at least agamids). In particular, a large throat appendage would improve the detection of a head-bob or push-up display used to advertise territorial ownership in visually complex environments (Ord & Stamps, 2008; see also Charles & Ord, 2012) or to accentuate an existing colour badge on the throat (Hamilton *et al.*, 2013). Although throat appendages are clearly part of the aggressive display, and may even convey cues on potential fighting ability in some species today (e.g. Lailvaux & Irschick, 2007; Hamilton *et al.*, 2013), habitat-dependent selection appears to have been the instigating factor that initially prompted the evolution of conspicuous throat appendages in most lineages. Visual signals are often linked to the type of environment in which signals are produced. For example, natural selection dictates the range of colours used in visual signals because some colours are inherently more conspicuous in certain light environments than others (lizards: Fleishman, 2000; fish: Seehausen *et al.*, 2008; birds: Marchetti, 1993; Gomez & Théry, 2004). The same is also true for the manner in which movement-based displays are performed, such as their speed or duration (Peters & Evans, 2003; Peters *et al.*, 2007; Ord *et al.*, 2010). Sexual selection might invariably act on the finer details of signals [e.g. females might prefer particular combinations or intensity of colours (Endler & Houde, 1995; Williams & Mendelson, 2011), or male

rivals might be intimidated by certain combinations or repetitions of display movement (Ord *et al.*, 2001; Ord & Evans, 2003)], but the gross structure of signals has been naturally selected by the environment (Endler, 1992).

Our results are broadly consistent with recent theoretical evidence showing that the evolution of large, conspicuous structures in males can be enforced by improvements in signal efficiency (natural selection), but less so by increases in information content that might occur through the elaboration of a structure (sexual selection; Tazzyman *et al.*, 2014a,b). Other empirical examples exist as well. In addition to the dewlap, territorial males of several *Anolis* species have another prominent ornament-like structure in the form of a large tail crest. This structure appears to have initially evolved to improve the detection of displaying males to distant receivers, but has been subsequently co-opted as an aggressive signal in its own right (Charles & Ord, 2012). The evolution of an elongated sword in male swordtails seems to have originated to exploit a more general bias in females of preferring large males, either because large body size effectively stimulates the visual system or because it indicates a male of superior quality (Rosenthal & Evans, 1998). That is, the elongated sword serves as an energetically inexpensive means of appearing large. In both cases, the function of a male ornamental structure based on how it appears to be used within a species is quite different to the evolutionary process that actually generated the structure.

In some iguanian lineages, the extravagant throat appendage has undergone an extraordinary elaboration in form to produce a moveable dewlap or frill that can be displayed or retracted at will. Why this innovation has occurred remains unclear. There was little to distinguish these genera from taxa exhibiting static throat appendages. For example, dewlapped and frilled genera were unremarkable in their sexual dichromatism, suggesting little influence from sexual selection. However, there are other potential adaptive reasons why a static throat ornament might become elaborated into a moving structure. For example, improved signal detection might still play a role if conspecific receivers in dewlapped taxa are often quite distant. Receiver distance can vary among species independently of the structural environment (Ord, 2012), and a large rapidly moving dewlap has been experimentally confirmed in *Anolis* to be highly effective at facilitating signal detection by distant territorial neighbours in forest habitats (Ord &

Stamps, 2008). The dewlap has also been argued to play an important role in species recognition in *Anolis* (Rand & Williams, 1970; Vanhooydonck *et al.*, 2009; see Macedonia *et al.*, 2013 for an experimental test), largely because its colour and pattern vary so widely among closely related species (Nicholson *et al.*, 2007). However, the benefits conveyed by improved species recognition would presumably be similar regardless of whether species identity cues were conveyed through a static morphological structure or as part of a moving appendage.

Conspicuous coloration and ornamentation can attract the attention of unintended receivers such as predators (Endler, 1982; Huhta *et al.*, 2003; Stuart-Fox *et al.*, 2003; Husak *et al.*, 2006). Lizards with a colourful throat patch or large throat appendage have a signal that is on permanent display to both conspecifics and potential predators alike. The subsequent modification of that signal into a moveable dewlap (in particular) would allow lizards to not only to increase the conspicuousness of the signal to distant (intended) receivers in visually difficult environments, but also provide a means of 'turning off' the signal when not actively communicating to conspecifics. This would be especially beneficial for arboreal lizards, which often exhibit colourful throat appendages and dewlaps, because the throat would presumably be more visible to predators given its elevated angle of view with an arboreal lifestyle. For example, the presence of the dewlap and its colour are virtually invisible when the dewlap is retracted in *Anolis* and *Draco* (T.J. Ord, personal observation).

Although the adaptive origins of the dewlap remain unknown, its evolution has clearly not been a unique event but occurred independently on at least three occasions (and possibly a fourth in *Hypsilurus*). It is also functionally convergent – in all taxa possessing a dewlap, it is deployed as a prominent, moving signal during territorial advertisements and aggressive encounters with rival males, and often as part of a head-bob and push-up display (e.g. see videos for *Anolis*, *Draco* and *Sitana* in Supporting information; the behaviour of *Otocryptis* has been poorly studied, but is likely to be similar to that of other dewlapped genera – Bahir & Silva, 2005; the signal behaviour of *Hypsilurus* is unknown). Nevertheless, the underlying morphology of the hyoid has evolved quite differently on each occasion. In fact, the only similarity in hyoid morphology among dewlapped lizards seems to be the extensive elongation of the second ceratobranchials, which physically pushes out the dewlap envelope. Beyond that, the hyoid seems to have evolved very differently in almost all other aspects of the hyoid. That is, the same adaptive function – a rapidly moving dewlap for social communication – has been achieved in iguanian lizards through multiple evolutionary trajectories.

Functional redundancy through divergent phenotypes is not surprising considering the length of evolutionary

time separating dewlapped genera (140–70 MYA): the more distantly related taxa are from one another, the more likely those taxa will respond in different ways to similar selection pressures (Ord & Summers, 2015). However, the components of the hyoid are interdependent with one another in such a way that change in one component would presumably impact the articulation of other aspects of the hyoid (Ord *et al.*, 2013b). Nevertheless, this interdependency appears not to have resulted in any constraint on the number of ways the dewlap (or frill) has evolved in disparate taxa.

Taken together, our findings show that elaborate, colourful ornament-like structures in males can evolve largely independently of sexual selection, certainly in the absence of selection from female mate choice, but also seemingly without direct selection from male–male aggressive competition. Instead, the prevailing trend appears to be the evolution of large throat appendages and dewlaps to improve signal efficiency when lizards communicate to one another in closed environments; that is, as an alerting structure or amplifier that facilitates receiver orientation to a head-bob or push-up display (Ord & Stamps, 2008) or the colour of the throat more generally (Hamilton *et al.*, 2013). Although it might seem reasonable to infer that an extravagant morphological structure exhibited predominantly (or exclusively) in males is the sole product of sexual selection, our study highlights this assumption can be misleading. If the motivation is to understand the factors that promote the evolution of complex male signals, or why diversity in male morphology evolves across closely related taxa, then processes other than sexual selection must be considered as well.

Acknowledgments

We thank A. Resetar and the Field Museum in Chicago for access to specimens, Yoni Brandt, Ambika Kamath, Jonathan Losos, the Smithsonian Tropical Institute, Devi Stuart-Fox and Phillip Wagner for sharing photographs of key species and observations of lizard behaviour in the field, and Nicola Nadeau and several anonymous reviewers who provided constructive comments on an earlier version of the manuscript. We are especially grateful to Ambika Kamath for allowing us to reproduce her video of *Sitana ponticeriana* display as part of this article. Holly Pickett helped produce the detailed hyoid sketches in Fig. 3. B. Lee from the Biological Resource Imaging Laboratory at The University of New South Wales helped us perform CT scans. This work was partly supported by funds from a UNSW SFRGP grant to M. Hagman. The authors declare no conflict of interest.

References

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. In: *Second International Sympo-*

- sium on *Information Theory* (B.N. Petrov, F. Csaki, eds), pp. 267–281. Akademiai Kiado, Budapest.
- Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton, NJ.
- Badyaev, A.V. & Hill, G.E. 2003. Avian sexual dichromatism in relation to phylogeny and ecology. *Annu. Rev. Ecol. Evol. Syst.* **34**: 27–49.
- Bahir, M.M. & Silva, A. 2005. *Otocryptis nigristigma*, a new species of agamid lizard from Sri Lanka. *Raffles Bull. Zool.* **12**: 393–406.
- Baird, T.A., Baird, T.D. & Shine, R. 2013. Showing red: male coloration signals same-sex rivals in an Australian water dragon. *Herpetologica* **69**: 436–444.
- Beddard, F.E. 1905. A contribution to the anatomy of the frilled lizard (*Chlamydosaurus kingi*) and some other Agamidae. *Proc. Zool. Soc. Lond.* **1905**: 9–22.
- Bels, V.L. 1990. The mechanism of dewlap extension in *Anolis carolinensis* (Reptilia: Iguanidae) with histological analysis of the hyoid apparatus. *J. Morphol.* **206**: 225–244.
- Bleay, C. & Sinervo, B. 2007. Discrete genetic variation in mate choice and a condition-dependent preference function in the side-blotched lizard: implications for the formation and maintenance of coadapted gene complexes. *Behav. Ecol.* **18**: 204–310.
- Blomberg, S.P., Garland, T. Jr & Ives, A.R. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**: 717–745.
- Bradbury, J.W. & Vehrencamp, S.L. 2011. *Principles of Animal Communication*, 2nd edn. Sinauer Associates, Sunderland, MA.
- Brandt, J.M. 2003. Lizard threat display handicaps endurance. *Proc. R. Soc. Lond. B* **270**: 1061–1068.
- Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer, New York.
- Candolin, U. 2003. The use of multiple cues in mate choice. *Biol. Rev.* **78**: 575–595.
- Charles, G.K. & Ord, T.J. 2012. Factors leading to the evolution and maintenance of a male ornament in territorial species. *Behav. Ecol. Sociobiol.* **66**: 231–239.
- Chen, I.-P., Stuart-Fox, D., Hugall, A.F. & Symonds, M.R.E. 2013. Sexual selection and the evolution of complex color pattern in dragon lizards. *Evolution* **66**: 3605–3616.
- Cummings, M.E. 2007. Sensory trade-offs predict signal divergence in surfperch. *Evolution* **61**: 530–545.
- Darwin, C. 1874. *The Descent of Man*, 2nd edn. Prometheus Books, New York.
- Emlen, D.J., Marangelo, J., Ball, B. & Cunningham, C.W. 2005. Diversity in the weapons of sexual selection: horn evolution in the beetle genus *Onthophagus* (Coleoptera: Scarabaeidae). *Evolution* **59**: 1060–1084.
- Endler, J.A. 1982. Convergent and divergent effects of natural selection on color patterns in two fish faunas. *Evolution* **36**: 178–188.
- Endler, J.A. 1992. Signals, signal conditions, and the direction of evolution. *Am. Nat.* **139**: S125–S153.
- Endler, J.A. & Houde, A.E. 1995. Geographic variation in female preferences for male traits in *Poecilia reticulata*. *Evolution* **49**: 456–468.
- Fairbairn, D.J. 2013. *Odd Couples: Extraordinary Differences Between the Sexes in the Animal Kingdom*. Princeton University Press, Princeton, NJ.
- Fleishman, L.J. 2000. Signal function, signal efficiency and the evolution of anoline lizard dewlap color. In: *Animal Signals: Signalling and Signal Design in Animal Communication* (Y. Espmark, T. Amundsen, G. Rosenqvist, eds), pp. 209–236. Tapir Academic Press, Trondheim, Norway.
- Fleishman, L.J., Leal, M. & Persons, M.H. 2009. Habitat light and dewlap color diversity in four species of Puerto Rican anoline lizards. *J. Comp. Physiol. A* **195**: 1043–1060.
- Font, E. & Rome, L.C. 1990. Functional morphology of dewlap extension in the lizard *Anolis equestris* (Iguanidae). *J. Morphol.* **206**: 245–258.
- Gartner, G.E., Gamble, T., Jaffe, A.L., Harrison, A.S. & Losos, J.B. 2013. Left-right dewlap asymmetry and phylogeography of *Anolis lineatus* on Aruba and Curacao. *Biol. J. Linn. Soc.* **110**: 409–426.
- Gomez, D. & Théry, M. 2004. Influence of ambient light on the evolution of colour signals: comparative analysis of a neotropical rainforest bird community. *Ecol. Lett.* **7**: 279–284.
- Hamilton, D.G., Whiting, M.J. & Pryke, S.R. 2013. Fiery frills: carotenoid-based coloration predicts contest success in frill-neck lizards. *Behav. Ecol.* **24**: 1138–1149.
- Hebets, E.A. & Papaj, D.R. 2005. Complex signal function: developing a framework of testable hypotheses. *Behav. Ecol. Sociobiol.* **57**: 197–214.
- Huhta, E., Rytönen, S. & Solonen, T. 2003. Plumage brightness of prey increases predation risk: an among species comparison. *Ecology* **84**: 1793–1799.
- Husak, J.F. & McGuire, J.A. 2014. Does ‘gliding while gravid’ explain Rensch’s rule in flying lizards? *Biol. J. Linn. Soc.* **113**: 270–282.
- Husak, J.F., Macedonia, J.M., Fox, S.F. & Saucedo, R.C. 2006. Predation cost of conspicuous male coloration in collared lizards (*Crotaphytus collaris*): an experimental test using clay-covered model lizards. *Ethology* **112**: 572–580.
- Jennions, M.D., Moller, A.P. & Petrie, M. 2001. Sexually selected traits and adult survival: a meta-analysis. *Q. Rev. Biol.* **76**: 3–36.
- Jenssen, T.A., Lovorn, M.B. & Congdon, J.D. 2001. Field-testing the protandry-based mating system for the lizard, *Anolis carolinensis*: does the model organism have the right model? *Behav. Ecol. Sociobiol.* **50**: 162–172.
- Johnson, M.A., Revell, L.J. & Losos, J.B. 2010. Behavioral convergence and adaptive radiation: effects of habitat use on territorial behavior in *Anolis* lizards. *Evolution* **64**: 1151–1159.
- Kelso, E.C. & Martins, E.P. 2008. Effects of two courtship display components on female reproductive behaviour and physiology in the sagebrush lizard. *Anim. Behav.* **75**: 639–646.
- Kozak, K.H., Cirino, L.A. & Ptacek, M.B. 2008. Female mating preferences for male morphological traits used in species and mate recognition in the Mexican sailfin mollies, *Poecilia velifera* and *Poecilia petenensis*. *Behav. Ecol.* **19**: 463–474.
- Lailvaux, S.P. & Irschick, D.J. 2006. No evidence for female association with high-performance males in the green anole lizard, *Anolis carolinensis*. *Ethology* **112**: 707–715.
- Lailvaux, S.P. & Irschick, D.J. 2007. The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. *Am. Nat.* **170**: 573–586.
- Lambert, S.M., Geneva, A.J., Mahler, D.L. & Glor, R.E. 2013. Using genomic data to revisit an early example of reproductive character displacement in Haitian *Anolis* lizards. *Mol. Ecol.* **22**: 3981–3995.

- Lappin, A.K., Brandt, Y., Husak, J.F., Macedonia, J.M. & Kemp, D.J. 2006. Gaping displays reveal and amplify a mechanically based index of weapon performance. *Am. Nat.* **168**: 100–113.
- LeBas, N.R. & Marshall, N.J. 2001. No evidence of female choice for a condition-dependent trait in the agamid lizard, *Ctenophorus ornatus*. *Behaviour* **138**: 965–980.
- Lopez, P. & Martin, J. 2001. Fighting rules and rival recognition reduce costs of aggression in male lizards, *Podarcis hispanica*. *Behav. Ecol. Sociobiol.* **49**: 111–116.
- Losos, J.B. 2009. *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. University of California Press, Berkeley, CA.
- Macedonia, J.M., Clark, D.L., Riley, R.G. & Kemp, D.J. 2013. Species recognition of color and motion signals in *Anolis grahami*: evidence from response to lizard robots. *Behav. Ecol.* **24**: 846–852.
- Macedonia, J.M., Clark, D.L. & Tamasi, A.L. 2014. Does selection favor dewlap colors that maximize detectability? A test with five species of Jamaican *Anolis* lizards. *Herpetologica* **70**: 157–170.
- Maddison, W.P. & Maddison, D.R. 2010. Mesquite: a modular system for evolutionary analysis. <http://mesquiteproject.org>.
- Marchetti, K. 1993. Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature* **362**: 149–152.
- Martins, E.P. 1994. Phylogenetic perspectives on the evolution of lizard territoriality. In: *Lizard Ecology: Historical and Experimental Perspectives* (L.J. Vitt, E.R. Pianka, eds), pp. 117–144. Princeton University Press, Princeton, NJ.
- Martins, E.P. & Hansen, T.F. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *Am. Nat.* **149**: 646–667.
- McGuire, J.A. 2003. Allometric prediction of locomotor performance: an example from southeast Asian flying lizards. *Am. Nat.* **161**: 337–349.
- McGuire, J.A. & Alcala, A.C. 2000. A taxonomic revision of the flying lizards (Iguania: Agamidae: *Draco*) of the Philippine Islands, with a description of a new species. *Herpetol. Monogr.* **14**: 81–138.
- McLean, C.A., Moussall, A. & Stuart-Fox, D. 2014. Local adaptation and divergence in colour signal conspicuousness between monomorphic and polymorphic lineages in a lizard. *J. Evol. Biol.* **27**: 2654–2664.
- Moller, A.P. & Pomiankowski, A. 1993. Why have birds got multiple sexual ornaments. *Behav. Ecol. Sociobiol.* **32**: 167–176.
- Ng, J., Landeen, E.L., Logsdon, R.M. & Glor, R.E. 2013. Correlation between *Anolis* lizard dewlap phenotype and environmental variation indicates adaptive divergence of a signal important to sexual selection and species recognition. *Evolution* **67**: 573–582.
- Nicholson, K.E., Harmon, L.J. & Losos, J.B. 2007. Evolution of *Anolis* lizard dewlap diversity. *PLoS One* **2**: e274.
- Ord, T.J. 2008. Dawn and dusk ‘chorus’ in visually communicating Jamaican anole lizards. *Am. Nat.* **172**: 585–592.
- Ord, T.J. 2012. Receiver perception predicts species divergence in long-range communication. *Anim. Behav.* **83**: 3–10.
- Ord, T.J. & Evans, C.S. 2003. Display rate and opponent assessment in the Jacky dragon (*Amphibolurus muricatus*): an experimental analysis. *Behaviour* **140**: 1495–1508.
- Ord, T.J. & Stamps, J.A. 2008. Alert signals enhance animal communication in ‘noisy’ environments. *Proc. Natl. Acad. Sci. USA* **105**: 18830–18835.
- Ord, T.J. & Stuart-Fox, D. 2006. Ornament evolution in dragon lizards: multiple gains and widespread losses reveal a complex history of evolutionary change. *J. Evol. Biol.* **19**: 797–808.
- Ord, T.J. & Summers, T.C. 2015. Repeated evolution and the impact of evolutionary history on adaptation. *BMC Evol. Biol.* **15**: 137.
- Ord, T.J., Blumstein, D.T. & Evans, C.S. 2001. Intrasexual selection predicts the evolution of signal complexity in lizards. *Proc. R. Soc. Lond. B* **268**: 737–744.
- Ord, T.J., Peters, R.A., Clucas, B. & Stamps, J.A. 2007. Lizards speed up visual displays in noisy motion habitats. *Proc. R. Soc. Lond. B* **274**: 1057–1062.
- Ord, T.J., Stamps, J.A. & Losos, J.B. 2010. Adaptation and plasticity of animal communication in fluctuating environments. *Evolution* **64**: 3134–3148.
- Ord, T.J., Stamps, J.A. & Losos, J.B. 2013a. Convergent evolution in the territorial communication of a classic adaptive radiation: Caribbean *Anolis* lizards. *Anim. Behav.* **85**: 1415–1426.
- Ord, T.J., Collar, D.C. & Sanger, T.J. 2013b. The biomechanical basis of evolutionary change in a territorial display. *Funct. Ecol.* **27**: 1186–1200.
- Paradis, E., Claude, J. & Strimmer, K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**: 289–290.
- Pérez I de Lanuza, G., Font, E. & Monterde, J.L. 2013. Using visual modelling to study the evolution of lizard coloration: sexual selection drives the evolution of sexual dichromatism in lacertids. *J. Evol. Biol.* **26**: 1826–1835.
- Peters, R.A. & Evans, C.S. 2003. Introductory tail-flick of the Jacky dragon visual display: signal efficacy depends upon duration. *J. Exp. Biol.* **206**: 4293–4307.
- Peters, R.A., Hemmi, J.M. & Zeil, J. 2007. Signaling against the wind: modifying motion-signal structure in response to increased noise. *Curr. Biol.* **17**: 1231–1234.
- Prokop, Z.M., Michalczyk, L., Drobnik, S.M., Herdegen, M. & Radwan, J. 2012. Meta-analysis suggests choosy females get sexy sons more than “good genes”. *Evolution* **66**: 2665–2673.
- Pyron, R.A. & Burbrink, F.T. 2014. Early origin of viviparity and multiple reversions to oviparity in squamate reptiles. *Ecol. Lett.* **17**: 13–21.
- Rand, A.S. & Williams, E.E. 1970. An estimation of redundancy and information content of anole dewlaps. *Am. Nat.* **104**: 99–103.
- Rosenthal, G.G. & Evans, C.S. 1998. Female preference for swords in *Xiphophorus helleri* reflects a bias for large apparent size. *Proc. Natl. Acad. Sci. USA* **95**: 4431–4436.
- Seehausen, O., Terai, Y., Magalhaes, I.S., Carleton, K.L., Mrosso, H.D.J., Miyagi, R. et al. 2008. Speciation through sensory drive in cichlid fish. *Nature* **455**: 620–626.
- Shine, R., Keogh, S., Doughty, P. & Giragossyan, H. 1998. Costs of reproduction and the evolution of sexual dimorphism in a ‘flying lizard’ *Draco melanopogon* (Agamidae). *J. Zool.* **246**: 203–213.
- Stuart-Fox, D. & Johnston, G.R. 2005. Experience overrides colour in lizard contests. *Behaviour* **142**: 329–350.
- Stuart-Fox, D. & Ord, T.J. 2004. Sexual selection, natural selection and the evolution of dimorphic coloration and

- ornamentation in agamid lizards. *Proc. R. Soc. Lond. B* **271**: 2249–2255.
- Stuart-Fox, D., Moussalli, A., Marshall, N.J. & Owens, I.P.F. 2003. Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. *Anim. Behav.* **66**: 541–550.
- Sullivan, B.K. & Kwiatkowski, M.A. 2007. Courtship displays in anurans and lizards: theoretical and empirical contributions to our understanding of costs and selection on males due to female choice. *Funct. Ecol.* **21**: 666–675.
- Tazzyman, S.J., Iwasa, Y. & Pomiankowski, A. 2014a. Signaling efficacy drives the evolution of larger sexual ornaments by sexual selection. *Evolution* **68**: 216–229.
- Tazzyman, S.J., Iwasa, Y. & Pomiankowski, A. 2014b. The handicap process favors exaggerated, rather than reduced, sexual ornaments. *Evolution* **68**: 2534–2549.
- Throckmorton, G.S., de Bavay, J., Chaffey, W., Merrotsy, B., Noske, S. & Noske, R. 1985. The mechanism of frill erection in the bearded dragon *Amphibolurus barbatus* with comments on the Jacky lizard *A. muricatus* Agamidae. *J. Morphol.* **183**: 285–292.
- Tokarz, R.R. 1995. Mate choice in lizards: a review. *Herpetol. Monogr.* **9**: 17–40.
- Tokarz, R.R. 1998. Mating pattern in the lizard *Anolis sagrei*: implications for mate choice and sperm competition. *Herpetologica* **54**: 388–394.
- Tokarz, R., Paterson, A.V. & McMann, S. 2005. Importance of dewlap display in male mating success in free-ranging brown anoles (*Anolis sagrei*). *J. Herpetol.* **39**: 174–177.
- Townsend, T.M., Mulcahy, D.G., Noonan, B.P., Sites, J.W. Jr, Kuczynski, C.A., Wiens, J.J. *et al.* 2011. Phylogeny of iguanian lizards inferred from 29 nuclear loci, and a comparison of concatenated and species-tree approaches for an ancient, rapid radiation. *Mol. Phylogenet. Evol.* **61**: 363–380.
- Uetz, P. & Hošek, J. 2013. The reptile database. <http://www.reptile-database.org>.
- Umbers, K.D.L., Osborne, L. & Keogh, J.S. 2012. The effects of residency and body size on contest initiation and outcome in the territorial dragon, *Ctenophorus decresii*. *PLoS One* **7**: e47143.
- Vanhooydonck, B., Herrel, A.Y., Van Damme, R. & Irschick, D.J. 2005. Does dewlap size predict male bite performance in Jamaican *Anolis* lizards? *Funct. Ecol.* **19**: 38–42.
- Vanhooydonck, B., Herrel, A., Meyers, J.J. & Irschick, D.J. 2009. What determines dewlap diversity in *Anolis* lizards? An among-island comparison. *J. Evol. Biol.* **22**: 293–305.
- Warton, D.I. & Hui, F.K.C. 2011. The arcsine is asinine: the analysis of proportions in ecology. *Ecology* **92**: 3–10.
- Whiting, M.J., Stuart-Fox, D.M., O'Connor, D., Firth, D., Bennett, N.C. & Blomberg, S.P. 2006. Ultraviolet signals ultra-aggression in a lizard. *Anim. Behav.* **72**: 353–363.
- Wiens, J.J. 1999. Phylogenetic evidence for multiple losses of a sexually selected character in phrynosomatid lizards. *Proc. R. Soc. Lond. B* **266**: 1529–1535.
- Wiens, J.J., Hutter, C.R., Mulcahy, D.G., Noonan, B.P., Townsend, T.M., Sites, J.W. Jr *et al.* 2012. Resolving the phylogeny of lizards and snakes (Squamata) with extensive sampling of genes and species. *Biol. Lett.* **8**: 1043–1046.
- Williams, T.H. & Mendelson, T.C. 2011. Female preference for male coloration may explain behavioural isolation in sympatric darters. *Anim. Behav.* **82**: 683–689.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Additional methods and results.

Table S1 Species-level phylogenetic logistic regressions ($n = 100$ species).

Table S2 Species-level phylogenetic correlations ($n = 119$ species) using Pagel's (1994) test in which habitat was coded as either exclusively forest (*a*) or more generally 'closed' environments of woodland and forest (*b*).

Figure S1 The hyoid of different species within representative genera show the morphology of the hyoid is largely conserved within genera.

Figure S2 The proportion of agamid species that exhibit different types of throat morphology as a function of the median sexual dichromatism and type of habitat in which species within those genera are most often found.

Figure S3 Genus-level phylogeny showing polyphyletic genera highlighted as dashed branches.

Figure S4 Maximum likelihood ancestor state reconstructions of different types of throat ornamentation at the level of species.

Movie S1 The use of the dewlap during the territorial advertisement display of an adult male *Anolis lineatopus* lizard recorded at Discovery Bay, Jamaica by Terry Ord.

Movie S2 The use of the dewlap during the territorial advertisement display of an adult male *Draco melanopogon* lizard recorded at Ulu Gombak, Malaysia by Terry Ord.

Movie S3 The use of the dewlap during the territorial advertisement display of an adult male *Sitana ponticerian* lizard recorded at Maharashtra, India by Ambika Kamath.

Data deposited at Dryad: 10.5061/dryad.f01t1

Received 17 June 2015; revised 15 July 2015; accepted 29 July 2015