

Ornament size and colour as alternative strategies for effective communication in gliding lizards

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Abstract

Sexual ornamentation needs to be conspicuous to be effective in attracting potential mates and defending territories and indeed, a multitude of ways exists to achieve this. Two principal mechanisms for increasing conspicuousness are to increase the ornament's colour or brightness contrast against the background and to increase the size of the ornament. We assessed the relationship between the colour and size of the dewlap, a large extendible throat-fan, across a range of species of gliding lizards (Agamidae; genus *Draco*) from Malaysia and the Philippines. We found a negative relationship across species between colour contrast against the background and dewlap size in males, but not in females, suggesting that males of different species use increasing colour contrast and dewlap size as alternative strategies for effective communication. Male dewlap size also increases with increasing sexual size dimorphism, and dewlap colour and brightness contrast increase with increasing sexual dichromatism in colour and brightness, respectively, suggesting that sexual selection may act on both dewlap size and colour. We further found evidence that relative predation intensity, as measured from predator attacks on models placed in the field, may play a role in the choice of strategy (high chromatic contrast or large dewlap area) a species employs. More broadly, these results highlight that each component in a signal (such as colour or size) may be influenced by different selection pressures and that by assessing components individually, we can gain a greater understanding of the evolution of signal diversity.

Introduction

The ability to communicate effectively influences a range of conspecific and interspecific interactions, and failure to communicate may result in the loss of resources or reproductive opportunity (Hauser, 1996; Bradbury & Vehrencamp, 1998; Epsmark & Amundsen, 2000); thus, effective communication ultimately affects

individual fitness. Species that rely on visual display for social communication must maintain signals that are conspicuous enough to be readily detected by conspecifics (Bradbury & Vehrencamp, 1998). As detection depends on many situational or environmental variables, species occupying different habitats potentially experience very different selection pressures on signal design, which may ultimately generate much of the signal diversity that characterizes some groups of closely related species (Endler, 1992; Leal & Fleishman, 2004; Nicholson *et al.*, 2007).

Even phylogenetically closely related species may optimize signal conspicuousness through alternative means. For instance, species that use a similar ornament in display may evolve different but equally

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effective solutions for increasing conspicuousness – for example, by increasing ornament size, its contrast against the background in colour or brightness, or by increasing the speed or amplitude of movement in display (Endler, 1993a; Dawkins & Guilford, 1997; Ord *et al.*, 2007). Costs associated with particular strategies for conspicuousness (energetic, or increased risk of predation) may reduce the efficacy of one or more of the strategies under a given set of conditions (Godin & McDonough, 2003; Hill & McGraw, 2006; Simon, 2007; Woods *et al.*, 2007). The resultant strategy, or combination of strategies, depends on the social requirements of the signal, its evolutionary history and the environment occupied by the species (Boughman, 2001; Ord & Martins, 2006; Chen *et al.*, 2012). Additionally, just as multiple signals within a species can be evolutionarily coupled (e.g. under correlational selection), so too can multiple aspects of the same ornament (e.g. size and colour) such that changes to one aspect of the ornament may influence change in some other aspect of that ornament (Hebets & Papaj, 2005).

Environmental factors determine the effectiveness of different signalling strategies in many ways. For example, ambient light influences the conspicuousness of different colours by limiting the availability of light at different wavelengths (Endler, 1993b), and in very low light conditions, the signal-to-noise ratio may decrease to a point where colour vision becomes unreliable and individuals instead rely on achromatic information (Vorobyev, 1997; Cronin *et al.*, 2014). Thus, signals that generate high colour contrast against the background might be effective in a well-lit habitat but harder to detect in full shade forests (Endler & Thery, 1996). Similarly, visual acuity also decreases with decreasing habitat light such that colour patches may need to be larger to be detected (Endler, 1992). For example, some species of birds of the genus *Phylloscopus* that live in darkly shaded habitats signal with colour patches that are larger than those of species in better lit habitats and also have greater brightness contrast (targeting the achromatic channel – Marchetti, 1993).

Habitats also vary in predator community and abundance, both of which play a role in determining the most effective strategies for communication. Animals living in habitats with relatively high predation intensity may have signals with reduced conspicuousness or may limit conspicuousness to the behaviourally controlled aspects of the signal (Zuk & Kolluru, 1998; Stuart-Fox *et al.*, 2003; Husak *et al.*, 2006). For example, Martins *et al.* (2015) found independent evolutionary losses of the ancestral blue ventral colour patch in some species of spiny lizards (genus *Sceloporus*) which are less active overall, consistent with the hypothesis that the colour was lost due to increased predation pressure. Instead, these species compensate with more frequent head-bobbing displays of longer duration, thereby limiting conspicuous display to occasions when predators

are apparently absent. Although similar examples of alternative strategies for effective communication appear to exist in several taxa (Podos, 1997; Cardoso & Hu, 2011; Ord *et al.*, 2011; Ossip-Klein *et al.*, 2013), few studies have systematically assessed the relationships between aspects of a single ornament and how social and environmental factors may influence those relationships.

Gliding lizards belonging to the genus *Draco* are appropriate for addressing questions regarding selection on different signal components and the relationship between them as *Draco* possess dewlaps, a large extendable throat-fan, used in display for social communication, and dewlaps vary among species in multiple aspects such as size, colour and brightness. There are over 40 described species found throughout Asia (McGuire & Heang, 2001), and although they are all arboreal, they live in diverse habitats (open full sun environments through to deep shade forests). The dewlap of *Draco* lizards is solely used for communicating in territory defence and mate attraction (Mori & Hikida, 1993). During display, the dewlap is extended and retracted at varying speeds and motion patterns, and in some species, the dewlap display is accompanied by ‘push-ups’. Given these uses and that, more broadly, ornaments are often important in both aggressive competition and mate choice (Andersson, 1994; Wong & Candolin, 2005; Hunt *et al.*, 2009), we expect that the elaboration of the dewlap to be influenced by sexual selection. Species vary markedly in the colour of their dewlaps (Fig. 1) which are mostly conspicuous in males (although only visible during display). In most *Draco* species, males appear to signal more frequently than females and possess larger, more conspicuously coloured dewlaps, although this does vary and in some species males and females have very different but equally conspicuous dewlap colours (Mori & Hikida, 1994). The colours of the bodies and gliding membranes are cryptic for both males and females of most species and vary between species and sexes (Klomp *et al.*, 2014).

We tested whether *Draco* species have evolved alternative ways to increase dewlap conspicuousness by examining the relationship between colour and brightness contrast of the dewlap against the background and its area relative to body size, for both males and females. Both dewlap size and colour traits are likely to be important for territorial defence (or mate choice) and so may increase together in response to stronger selection for signal conspicuousness. Conversely, if *Draco* are using dewlap size and colour as alternative strategies to increase dewlap conspicuousness, we would predict a negative relationship between these traits. As we expect these traits to be under sexual selection for elaboration, we tested whether they were associated with potential indicators of sexual selection: sexual size dimorphism, sexual dichromatism in dewlap colour and brightness and dimorphism in relative

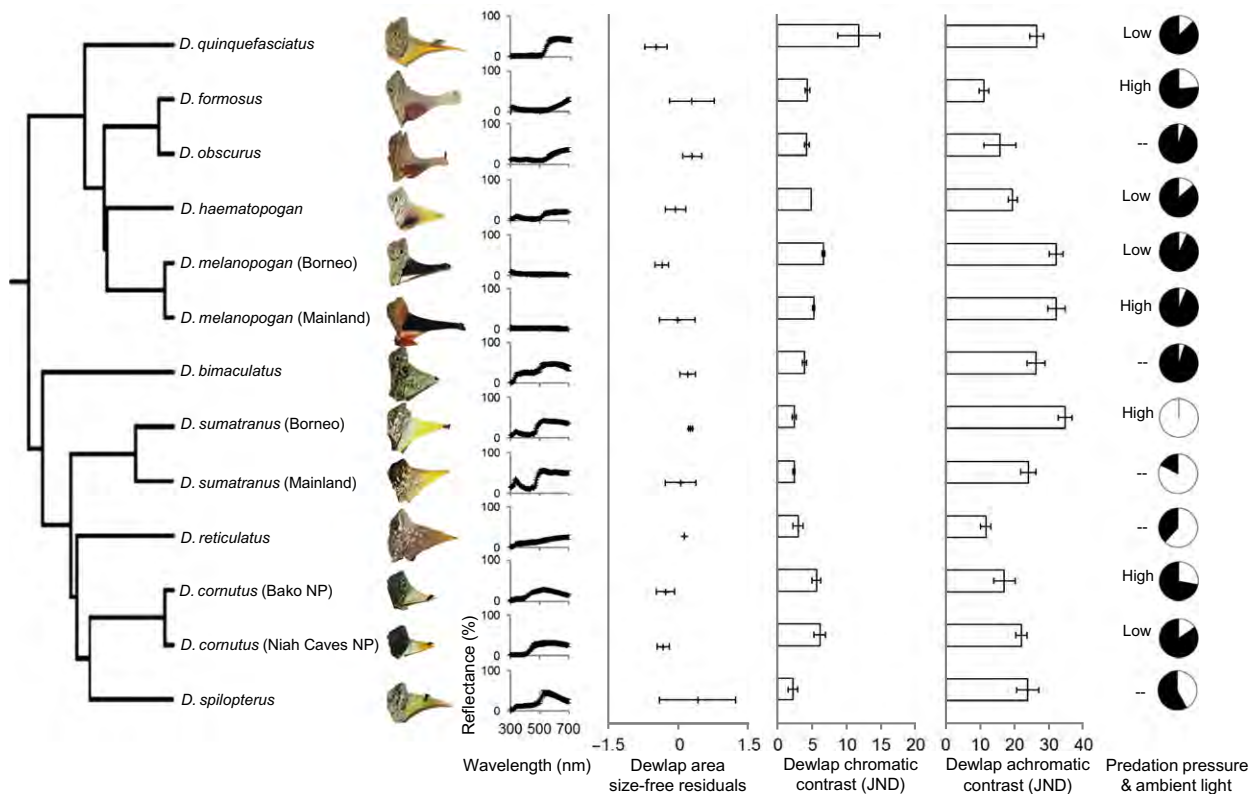


Fig. 1 Phylogeny of *Draco* species sampled, images of the male dewlaps and spectral reflectance of the primary dewlap colour (with standard errors), male dewlap area size-free residuals (with 95% confidence intervals), male dewlap conspicuousness in terms of chromatic and achromatic contrast (species means and 95% confidence intervals), and relative predation pressure and ambient light level (relative to the brightest habitat sampled), for each species.

dewlap area. Finally, to understand how the relationships between dewlap traits may be influenced by environmental factors, we tested whether dewlap conspicuousness is predicted by habitat light or potential predation intensity, estimated from experimental data of relative predation on plasticine models across different habitats.

Materials and methods

Data collection

Between April 2011 and June 2012, we captured 122 individuals of 13 *Draco* taxa (Fig. 1), from locations on Borneo, Peninsula Malaysia, and the islands of Luzon and Bohol in the Philippines. Although males are the more elaborately ornamented sex for most species, female *Draco* lizards also use the dewlap in display, and so in this study, we included both males and females. Lizards were caught using a small fishing-line noose at the end of a 6 m extendable pole. The colours of the lizard's dewlap were measured with a JAZ EL-200 spectrometer with inbuilt Jaz PX pulsed xenon light source,

calibrated using a diffuse white reflectance standard (Ocean Optics). Measurements were taken at a 45° angle relative to the surface, and spectra were smoothed over 5-nm intervals between 300 and 700 nm, the approximate visual spectrum of diurnal lizards (Loew *et al.*, 2002). Photographs were also taken of each lizard with the dewlap extended (using a Canon PowerShot SX1-IS digital camera, saving in RAW format), and the proportions of each colour in the dewlap were measured using the same 1 cm² grid. The photographs included a scale and were also used to measure the area of individual dewlaps using the 'free-hand selection' tool in ImageJ (Abramoff *et al.*, 2004). The snout-vent length (SVL) of each lizards caught in the field was measured to the nearest mm, with a ruler.

The predominant background colours of leaves, bark and lichen (green, brown, dark brown/black and white/pale green) were also measured with a spectrometer and used in visual modelling. In order to quantify the proportions in which these colours are present in the background to the lizard's dewlap display, we took digital photographs using the same camera, framing the

lizard's perch to the side and capturing representative background vegetation colour and density. The proportions of each colour in these photographs were estimated using a 1 cm² grid overlaid on the background photographs.

Side-welling absolute irradiance (90° from the ground) was measured at the time of capture, with a Jaz-ULM-200 spectrometer and cosine corrected irradiance probe (Ocean Optics) from the position of capture facing away from the sun, as described in Stuart-Fox *et al.* (2007) and Klomp *et al.* (2014). Only those irradiance measurements that were taken between 0830 and 1030 h (a period of heightened activity for the diurnal lizards) were used in analysis to standardize light conditions across habitats. These were smoothed over 5-nm intervals and were used as a measure of habitat light level (area under the spectral curve for absolute irradiance, between 300 and 700 nm, denoted by 'AUC') as well as being normalized to a maximum of one for use in visual modelling (irradiance spectrum shape).

Visual modelling

To measure the chromatic and achromatic contrast of the dewlap against the background, from the perspective of *Draco* conspecifics, we applied the model of Vorobyev and Osorio (1998), which estimates how well the receiver can discriminate between two colours in units of 'just noticeable differences' (JNDs). One JND is the threshold of discrimination – i.e. the minimum difference, given photoreceptor noise – for a visual system to be able to distinguish two colours. We estimated chromatic contrast based on the four single cones (UVS, SWS, MWS and LWS), and achromatic (luminance) contrast based on the double cone, which is probably used to detect luminance variation in most diurnal lizards (Loew *et al.*, 2002; Osorio & Vorobyev, 2005; Fleishman *et al.*, 2011). As the visual sensitivities of *Draco* species are not known, we used information on the only related agamid lizard for which the spectral sensitivities have been quantified, *Ctenophorus ornatus* (Barbour *et al.*, 2002), as detailed in Klomp *et al.* (2014), Teasdale *et al.* (2013) McLean *et al.* (2010) and detailed in Appendix S1.

We calculated the chromatic and achromatic contrasts of each dewlap colour, for each species, when viewed against each of the predominant colours in their local habitats. An overall contrast was then calculated, based on the sum of contrasts for each colour in the dewlap against each colour in the background weighted by the relative area each colour occupied. In the absence of behavioural data for agamid lizards, we assume that JNDs (i.e. discrimination thresholds) are linearly related to the perceptual distance between any two colours, although this assumption requires testing (Kemp *et al.*, 2015).

Sexual dimorphism

We calculated both sexual size dimorphism (SSD) and trait-specific dimorphism (i.e. sexual dichromatism in colour and brightness, and sexual dimorphism in dewlap area), as these are both potential indicators of sexual selection. Sexual dimorphism and dichromatism are well supported indices of the intensity of intrasexual competition in a variety of taxa (Shine, 1978; Bisazza, 1993; Mitani *et al.*, 1996; McElligott *et al.*, 2001; Serrano-Meneses *et al.*, 2007), especially in lizards (Stamps *et al.*, 1997; Butler *et al.*, 2000; McBrayer & Anderson, 2007; Pérez i de Lanuza *et al.*, 2013). SSD was calculated as the average male SVL divided by the average female SVL for a species, so species with female-biased SSD had values less than one, and those with male-biased SSD had values >1 (Smith, 1999; Fairbairn *et al.*, 2007). Sexual dichromatism was calculated as the chromatic and achromatic contrast of the primary male dewlap colour (i.e. the colour patch occupying the majority of the dewlap area) against the primary female dewlap colour, using the model of colour discrimination described above. Sexual dimorphism in dewlap area was calculated as the average male relative dewlap area divided by the average female relative dewlap area for each species.

Predation experiment

To test the relative difference in predation between habitats, we deployed plasticine *Draco* models in six different habitats (encompassing capture sites for eight different species) for 48 h and recorded signs of probable predation upon collection. This technique has been used successfully in a number of other studies (e.g. Stuart-Fox *et al.*, 2003; Husak *et al.*, 2006; McLean *et al.*, 2010; Morgans & Ord, 2013). We made realistic casts of a *Draco* lizard (species: *D. haematopogon*) with liquid silicone rubber and used the casts to construct each model from 10 g of plasticine (Fig. S1).

Draco lizards of different species vary in their dorsal colours (light to dark grey, brown and green). In order to create standard predation models, we chose to make the models plain grey, which blends-in with most bark colours. Half the models were light grey and half were dark grey, which functioned to reduce the likelihood of the model being more conspicuous in any given habitat due to that habitat possessing predominately dark or light coloured bark (see Fig. S2 for model and bark reflectance spectra). Each model was affixed to the tree at a height of 2–3 m, using clear fishing line. In each habitat, a total of 52 models were placed at a minimum distance of 5 m from each other, with equal numbers of each model facing in different directions (12 o'clock, 3 o'clock, 6 o'clock, 9 o'clock) relative to the direction of the limb of the tree. We collected models after 48 h and took detailed notes of all markings present.

Upon collection, the state of each model was characterized as follows: (1) no marks; (2) single or multiple small nicks; (3) large punctures or nicks; or (4) entire portions missing, following Morgans & Ord (2013). As categories 3 and 4 are the mostly likely instances of true predation attempts, we used only those in our analyses. Relative predation intensity was calculated as the percentage of all models recovered in a given habitat that had category 3 or 4 markings. The relative predation intensity across habitats was bimodally distributed (Fig. S3) so we divided the habitats into either 'high predation' or 'low predation' and analysed predation as a binary variable.

Statistical methods

All statistical analyses were conducted in R version 3.0.3 (R Development Core Team, R Foundation for Statistical Computing, Vienna). We first used the 'phyl-resid' method implemented with the lambda option in 'phytools' version 0.4-31 (Revell, 2012) on species mean dewlap area against species mean SVL to calculate 'size-free' residuals of dewlap area for males and females. We then assessed how relative dewlap area, chromatic contrast and achromatic contrast against the background were related to each other by computing Pearson product moment correlation coefficients. This was done by taking the average of two phylogenetic generalized least squares (PGLS) regressions in which the y and x variables were swapped, which provides an equivalent estimate of Pearson's r (e.g. Ord & Martins, 2006; see also Smith, 2009).

To confirm that dewlap characteristics vary among taxa with the probable strength of sexual selection experienced within those taxa, we ran a PGLS regression of each characteristic against SSD and trait-specific measures of sexual dimorphism – dewlap size dimorphism, chromatic and achromatic dichromatism. To assess the possibility that female ornament evolution is a correlated response to that of males, we ran phylogenetic regressions of female dewlap traits against male dewlap traits. To determine whether habitat factors play a role in which dewlap traits increase in elaboration between species, we conducted phylogenetic regressions of dewlap chromatic contrast and dewlap relative area, against habitat light level (AUC) and relative predation intensity (high vs. low). For this, we focussed just on males, because only males showed a relationship between dewlap chromatic contrast and dewlap relative area. All PGLS regressions were applied using Pagel's lambda, a model of phenotypic evolution where lambda values below one indicate that species are more dissimilar than expected based on the phylogeny (Pagel, 1999), in the 'ape' package version 3.2 (Paradis *et al.*, 2004).

Phylogenetic relationships for the species in our study were derived by pruning the agamid phylogeny by

Collar *et al.* (2010), which is based on a BEAST (Drummond *et al.*, 2006; Drummond & Rambaut, 2007) analysis of 1.2 kb mitochondrial protein coding genes. The relationships between the species examined in this paper are well supported (>0.95 Bayesian posterior probability) for all but the sister relationship between *D. haematopogon* and the two populations of *D. melanopogon* (0.71 posterior probability). Weak support for this relationship is reflected in the short branch length (Fig. 1), and our analyses included branch length information. As our analyses included both Malay and Bornean populations of *D. melanopogon* and *D. cornutus*, which were not included in the phylogeny as separate taxa, we added these with branch-lengths based on the minimum divergence estimated for intra-island populations of Philippine *Draco* (from McGuire & Heang, 2001), following Ord & Klomp (2014).

Results

Are there alternative strategies for conspicuousness?

Males of different species showed a strong negative relationship between the chromatic contrast and relative area of the dewlap (Table 1; Fig. 2a), indicating that male dewlaps tend to be conspicuous either in terms of colour contrast or relative area, but not both. This suggests that increasing chromatic contrast against the background and increasing dewlap area relative to body size are alternative signalling strategies. There was no relationship between achromatic contrast and either relative dewlap area or chromatic contrast for males. For females chromatic contrast increased with achromatic contrast (Table 1; Fig. 2b), indicating that females of some species have dewlaps that are conspicuous in terms of both chromatic and achromatic contrast against the background.

Table 1 Phylogenetic analysis of pairwise comparisons among dewlap traits contributing to conspicuousness (relative dewlap area, chromatic contrast and achromatic contrast). Phylogenetic signal (Pagel's lambda, λ), effect size (r) and P values are given from a phylogenetic equivalent of a Pearson correlation.

Dewlap traits	N_{taxa}	λ	r	P
A				
Male dewlaps				
Area vs. chromatic contrast	13	0.93	0.87	<0.0001
Area vs. achromatic contrast	13	1.10	0.14	0.62
Chromatic vs. achromatic contrast	13	0.97	0.13	0.63
B				
Female dewlaps				
Area vs. chromatic contrast	13	0.33	0.02	0.94
Area vs. achromatic contrast	13	0.23	0.06	0.85
Chromatic vs. achromatic contrast	13	0.06	0.70	0.005

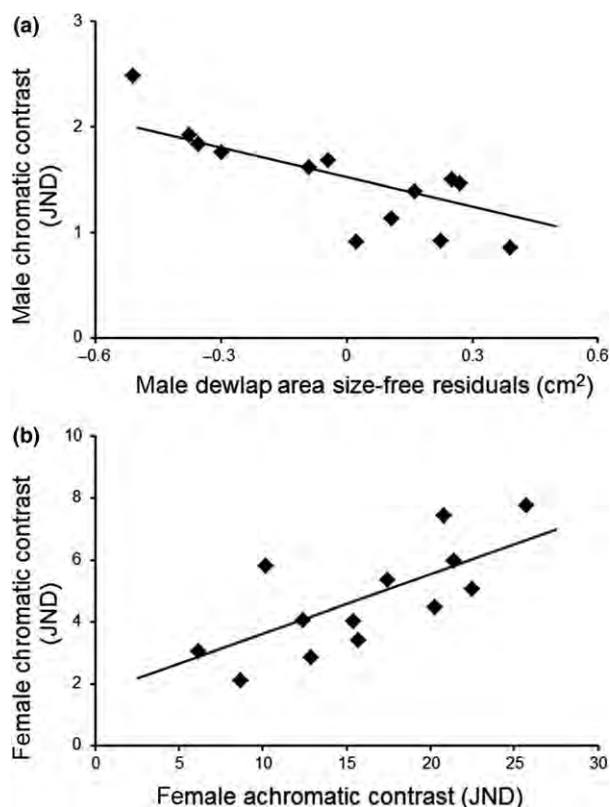


Fig. 2 (a) Male chromatic contrast (log-transformed) against relative dewlap area and (b) female chromatic contrast against achromatic contrast.

Female chromatic and achromatic contrast was uncorrelated with that of males (Fig. S4a,b), but female relative dewlap area increased with male relative dewlap area ($t_{13} = 2.89$, $P = 0.01$; Fig. S4c), raising the possibility that dewlap size is evolutionarily coupled between the sexes.

Dewlap trait relationships with sexual dimorphism

All male dewlap traits (relative area, chromatic and achromatic contrast) and some female dewlap traits were correlated with a measure of sexual dimorphism or dichromatism (Table 2). Male relative dewlap area increased with increasing sexual size dimorphism: as males become increasingly larger than females in body size they invest in larger dewlap areas relative to their size (Fig. 3a). *Draco quinquefasciatus* was excluded from this regression as an obvious model outlier, although removal did not change the conclusions. Neither male dewlap chromatic nor achromatic contrast nor any female dewlap traits were correlated with SSD. However, male chromatic contrast increased with increasing sexual dichromatism (in chromatic contrast between the sexes), whereas female chromatic contrast

decreased with increasing sexual dichromatism (males: Fig. 3c; females: Fig. 3d). This trend for females appeared to be primarily due to a few taxa (circled in the figure) where females have greater chromatic contrast than males, rather than a general pattern across all taxa studied. Thus, sexual dichromatism in chromatic contrast is more likely driven by increasing male chromatic contrast, whereas female chromatic contrast varies inconsistently between species. For males, achromatic contrast against the background also increased with increasing sexual dichromatism (in achromatic contrast between the sexes), but there was no relationship for females, suggesting again that increasing male dewlap brightness contrast against the background is driving the achromatic dichromatism between the sexes (males: Fig. 3e; females: Fig. 3f).

Do habitat factors influence signalling strategy?

As our results suggest that males of different species employ one of two strategies for signalling – larger dewlaps or greater chromatic contrast – we looked at how habitat factors may affect male conspicuousness in these two dewlap traits. Male relative dewlap area showed no relationship with habitat light, but there was a trend for relatively larger dewlaps in high-predation habitats and relatively smaller dewlaps in low-predation habitats (Fig. 4a, Table 3B). Male chromatic contrast was negatively correlated with habitat light (Fig. 4d, Table 3A), and whereas the relationship between chromatic contrast and predation pressure was not statistically significant (Table 3B), there was a trend for chromatic contrast to decrease with predation (Fig. 4b).

Discussion

Males of *Draco* species appear to employ alternative strategies for being conspicuous to conspecifics: either having larger dewlaps relative to their body size or having dewlaps with a greater colour contrast against the background, but not both. We found some evidence to suggest that predation pressure may play a role in determining which strategy males of a species employ (i.e. larger, but less colourful dewlaps in ‘high’-predation areas and smaller, but more colourful dewlaps in ‘low’-predation areas). For females, we found no relationship between dewlap size and colour, but chromatic contrast increased with achromatic contrast. Additionally, conspicuousness in all male dewlap traits was positively correlated with measures of sexual dimorphism and dichromatism, suggesting that elaboration of male traits is sexually selected, but this was not the case for females.

There are many examples where different aspects of visual signals (e.g. size and colour) increase in conspicuousness simultaneously in response to social and

Table 2 Phylogenetic regressions of male and female dewlap traits (dewlap area size-free residuals, chromatic contrast and achromatic contrast against the background) against SSD and trait-specific sexual dimorphisms (dimorphism in dewlap area and sexual dichromatism in chromatic and achromatic contrast). Phylogenetic signal (Pagel's lambda, λ), effect size (t) and P values are given. Outlier species removed – *D. quinquefasciatus* (see Fig. 3a).

Dewlap traits	N_{taxa}	A	t	P
A				
Male dewlaps on SSD				
Chromatic contrast	13	0.98	−0.81	0.44
Achromatic contrast	13	−0.38	−1.12	0.29
Area (outlier removed)	13 (12)	0.77 (−0.13)	2.22 (4.37)	0.05 (0.001)
B				
Female dewlaps on SSD				
Chromatic contrast	13	0.59	0.51	0.62
Achromatic contrast	13	0.28	0.77	0.46
Area	13	−0.12	1.59	0.14
C				
Male dewlaps on trait-specific dimorphism				
Chromatic contrast, chromatic sexual dichromatism	13	−0.39	12.92	<0.0001
Achromatic contrast, achromatic sexual dichromatism	13	0.42	3.46	0.005
Area, sexual dewlap size dimorphism	13	−0.40	1.72	0.11
D				
Female dewlaps on trait-specific dimorphism				
Chromatic contrast, chromatic sexual dichromatism	13	−0.02	−2.45	0.03
Achromatic contrast, achromatic sexual dichromatism	13	0.37	0.34	0.74
Area, sexual dewlap size dimorphism	13	0.04	−0.37	0.71

environmental selective pressures, both at the individual and population level (Hill, 1999; Torok, 2003; Loyau *et al.*, 2005; Hebets *et al.*, 2013), although examples of alternative pathways of elaboration for a single ornament type are rarer. Studies of species that signal in multiple modalities, however, do report the use of alternative signalling strategies, for many reasons, including physiological constraints (Podos, 1997) and the need to signal in diverse or changing environments (Bro-Jørgensen, 2010). These same constraints may also differentially affect the expression of aspects of a single ornament – as results of this study suggest. For male *Draco*, having a dewlap that is both highly chromatically contrasting and large in area may be too costly or is constrained in some way. Signals can be energetically costly to produce and maintain, and conspicuousness can be costly due to increased predation risk (Bradbury & Vehrencamp, 1998).

We did not find the same negative correlation between colour contrast and relative dewlap size for females as for males, potentially because males and females signal in different ecological and/or social circumstances. Although data on the social ecology of *Draco* are sparse, in most *Draco* species, males have the more elaborate dewlap in size and colour and use the dewlap more frequently in broadcast display, suggesting males may experience greater selective pressures for effective signalling than females (Inger, 1983; Mori & Hikida, 1993). It is also possible that the evolution of female relative dewlap area is a correlated response to

that of males, given the significant correlation of male and female relative dewlap size across taxa. Although there was no correlation between the relative size and colour of female dewlaps, we found a positive correlation between colour and brightness contrast, suggesting that for taxa where there is increased pressure for females to signal more effectively, they rely on elaboration in both colour and brightness contrast. Selection for increased signal complexity as well as redundancy in signals has been found in diverse taxa, such as spiders and frogs, and is hypothesized to increase signal reliability and allow species to maintain effective signals in fluctuating social and ecological environments (Bro-Jørgensen, 2010; Akre *et al.*, 2011; Hebets *et al.*, 2013).

Our results also suggest that sexual selection plays a role in driving all aspects of male dewlap conspicuousness, as all dewlap traits were positively correlated with measures of sexual dimorphism or dichromatism. Selection for efficient gliding in *Draco* species has led to constraints on body and head size for males, and the need to balance body and head weight in gravid females (Shine *et al.*, 1998; Husak & McGuire, 2014). Husak & McGuire (2014) found that *Draco* species may exhibit either female or male-biased SSD, but that male-biased SSD was more prevalent in larger species. They suggest a shift away from selection for better gliding ability in males for species with male-biased SSD, as increases in body size increases wing loadings, and a shift towards more intense selection for fighting performance. This

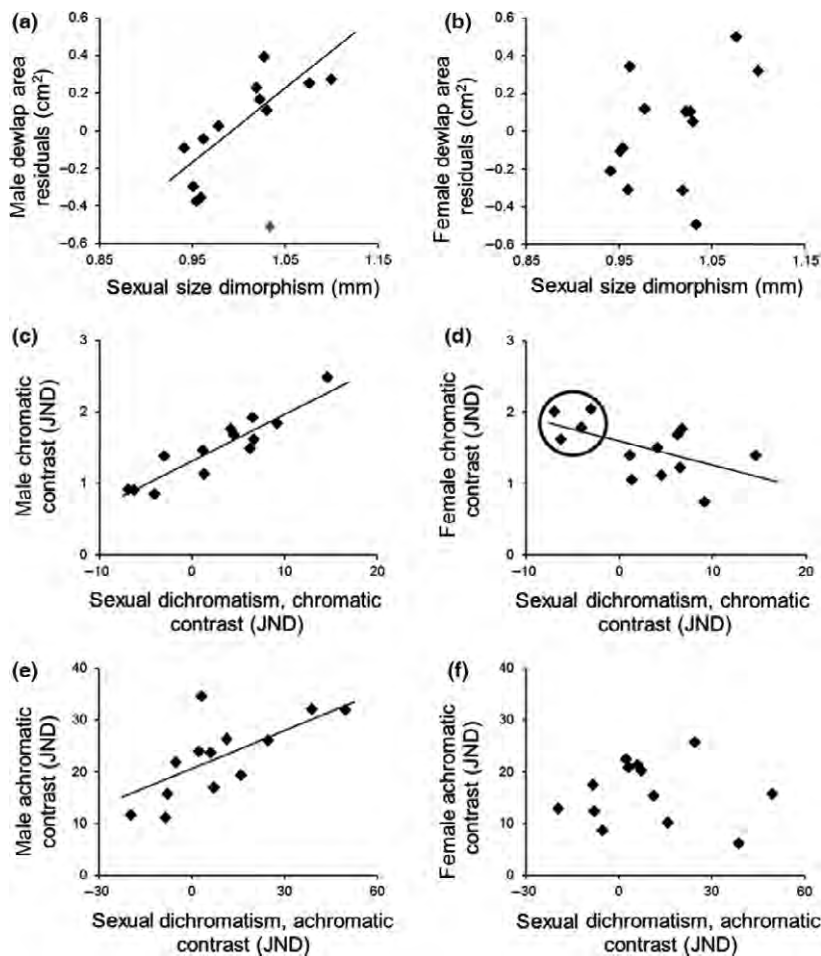


Fig. 3 (a) Male and (b) female relative dewlap area as a function of sexual size dimorphism; (c) male and (d) female chromatic contrast (log-transformed) as a function of sexual dichromatism (JND, chromatic contrast between the primary dewlap colour of the sexes); and (e) male and (f) female achromatic contrast as a function of sexual dichromatism (JND, achromatic contrast between the primary dewlap colour of the sexes). Outlier species (*D. quinquefasciatus*) in grey, panel (a).

hypothesis predicts two strategies for male territory defence (good gliders or good fighters), where the good fighter strategy is associated with male-biased SSD. Our data suggest that male-biased SSD is also associated with larger relative dewlaps, suggesting that assessing the relationship between relative dewlap size and fighting ability may be an interesting avenue for further research.

Although we found evidence to suggest that all three dewlap traits in males – dewlap colour contrast, brightness contrast and relative dewlap area – are sexually selected, this was not the case for females. In fact, it appears that the chromatic contrast of female dewlaps decreases with increased sexual dichromatism, but this result is driven by a group of four taxa in which females have greater chromatic contrast than males. Females of these four taxa (*D. sumatranus* on Borneo, *D. sumatranus* on the Malay Peninsula, *D. spiloferus* and *D. bimaculatus*) possibly have different social ecology and thus may be experiencing more similar selection pressures to males than in other species. For example, our observations in the field suggest that

females of these four taxa signal more frequently and vigorously than females of other species and may be defending territories.

Our results indicate that predation pressure may play a role in determining the strategy employed by a species to increase dewlap conspicuousness – larger dewlaps or more chromatically contrasting dewlaps – as taxa in habitats with relatively higher predation intensity tended to have relatively larger dewlaps. Although we found a correlation between relative dewlap size and predation intensity, we did not find the corresponding correlation between predation intensity and chromatic contrast, which we might expect if predation intensity was the primary determinant of signalling strategy (although the relationship was certainly in the right direction, Fig. 4b). It is notoriously difficult to get a realistic measure of predation intensity, but model prey experiments such as we have used here can give us a general indication of the potential variation in predation intensity across habitats (Stuart-Fox *et al.*, 2003; Husak *et al.*, 2006; McLean *et al.*, 2010; Morgans & Ord, 2013). Diurnal birds are perhaps the most common

Fig. 4 (a) Male relative dewlap area for species sampled in high- and low-predation habitats ($N = 8$ taxa), (b) male chromatic contrast (log-transformed) for species sampled in high- and low-predation habitats ($N = 8$ taxa), (c) male relative dewlap area as a function of ambient light level ($N = 13$ taxa; white points are species for which we also have predation data) and (d) male chromatic contrast (log-transformed) as a function of ambient light level ($N = 13$ taxa; white points are species for which we also have predation).

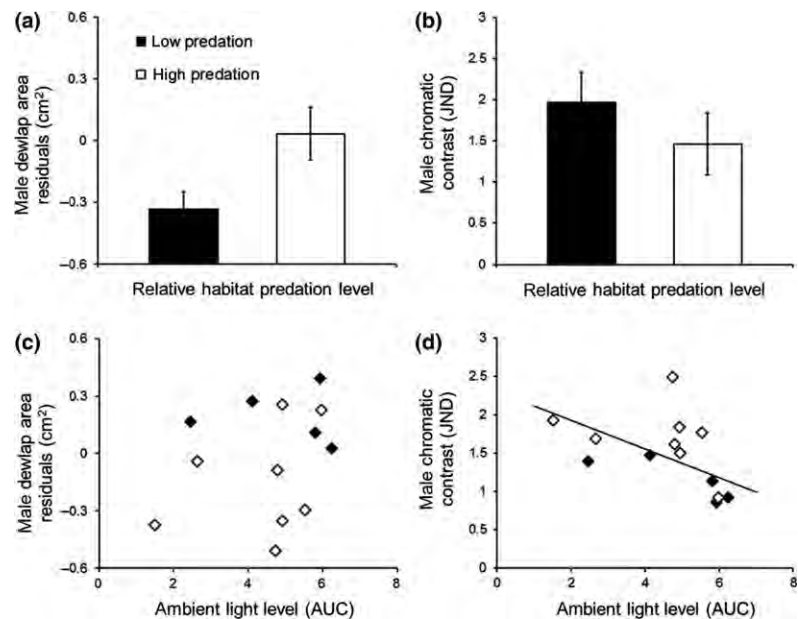


Table 3 Phylogenetic analyses of male chromatic contrast and relative dewlap size against ambient habitat light and relative predation intensity. Phylogenetic signal (Pagel's lambda, λ), effect size (t) and P values are given.

Dewlap traits	W_{taxa}	A	t	P
A Habitat light				
Area	13	1.24	0.25	0.81
Chromatic contrast	13	1.02	-5.98	0.0001
B Relative predation pressure				
Area	8	-0.19	2.27	0.06
Chromatic contrast	8	-2.42	-2.12	0.08

predators of *Draco* lizards (Ouithavon, 1999; Chalsurlyanun, 2011). Predatory birds have high visual acuity allowing them to resolve small colour patches at large distances and are good at detecting movements (Donner, 1951; Lea & Dittrich, 2001; Osorio & Vorobyev, 2008). However, some birds may rely primarily on chromatic information in prey detection (Goldsmith *et al.*, 1981; Kelber *et al.*, 2003; Stuart *et al.*, 2012). Therefore, it is possible that both signalling strategies – increased relative dewlap size and increased chromatic contrast – increase signal conspicuousness to predators. Furthermore, an increased abundance of predators in some habitats is likely to favour reduced overall conspicuousness, or increased antipredator behaviour (Endler, 1987; Slagsvold *et al.*, 1995; Koga *et al.*, 1998; Taylor *et al.*, 2005), rather than select for one form of dewlap conspicuousness over the other.

An alternative explanation for the trend for species with relatively larger dewlaps to occur in higher predation habitats is that larger dewlaps may be more beneficial in close-range predator encounters. Vanhooydonck

et al. (2009) found a species of anole (which also use dewlaps in display and are ecologically analogous to *Draco*) also showed increased relative dewlap size with increasing sexual size dimorphism, and that in populations where a ground-based lizard predator (*Leiocephalus* species) is present, males have larger relative dewlaps than those in populations where that predator is absent. They proposed that the investment in larger dewlaps may be beneficial in pursuit deterrence, in that it more effectively signals to a predator that it has been seen and that the individual is unprofitable prey – perhaps due to hyperaggression or ability to flee (Caro, 1995). However, this hypothesis is problematic where the main predators are birds, as signalling aggression or ability to flee does not seem likely to deter a bird from attacking potential prey, and overall the hypothesis has been somewhat controversial (Caro, 1995).

We also found a negative relationship between chromatic contrast and habitat light that is partially driven by a cluster of four taxa found in most well-lit habitats (Fig. 4d). Species found in open, well-lit habitats are thought to experience greater levels of predation than those in closed habitats (Stuart-Fox & Ord, 2004). For three of these four species, we did not have data on relative predation intensity, and the fourth was found in a relatively high-predation habitat. Therefore, it remains possible that the low chromatic contrast for these four species in the brightest habitat reflects high predation risk in these more open habitats.

To conclude, our study finds evidence for alternate signalling strategies of increased colour contrast or increased dewlap area relative to body size, for males of several *Draco* taxa, and that relative predation intensity between habitats may influence the particular strategy

a species employs. Furthermore, these results highlight how ornaments used in communication are composed of multiple components (e.g. size and colour), and that each of these components may be influenced by different selection pressures. Ideally, the nature of selection acting on dewlap size and coloration should be corroborated by independent measures of sexual selection (e.g. mating system or testis size) and manipulative experiments (e.g. male contest or mate choice experiments). Determining how selection acts on different signal components will enable a fuller understanding of the evolution of signal diversity, which characterizes many of the world's adaptive radiations.

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Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article: **Figure S1** Photograph of plasticine lizard models used in predation experiment.

Figure S2 Mean spectra of predation models (dark grey and light grey plasticine) with standard error, and example bark spectra from all six habitats where relative predation was measured.

Figure S3 Frequency histogram of relative predation levels of all habitats studied, showing bimodal distribution.

Figure S4 (a) Female chromatic contrast as a function of male chromatic contrast (JND, log-transformed); (b) female achromatic contrast as a function of male achromatic contrast (JND); and (c) female relative dewlap area as a function of male relative dewlap area (size-free residuals, cm²).

Appendix S1 Visual modelling methodology.

Data deposited at Dryad: doi: 10.5061/dryad.0g3d5

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