

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

Danielle A. Klomp¹, Terry J. Ord¹, Indraneil Das², Arvin Diesmos³, Norhayati Ahmad⁴ & Devi Stuart-Fox⁵

1. Evolution & Ecology Research Centre, and the School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, Australia
2. Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, Kota Samarahan, Sarawak, Malaysia
3. Herpetology Section, Zoology Division, National Museum of the Philippines, Manila, Philippines
4. Faculty of Science and Technology, School of Environment and Natural Resource Sciences, Universiti Kebangsaan Malaysia, Selangor, Malaysia
5. School of BioSciences, University of Melbourne, Melbourne, Australia

E-mail: d.klomp@unsw.edu.au

Phone: +61 419 418 711

Mail: Room 406, Biological Sciences Building (D26), School of Biological, Earth and Environmental Sciences
The University of New South Wales, Kensington, Sydney
NSW, Australia 2052

Short Title: Strategies for communication in gliding lizards

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/jeb.12908](https://doi.org/10.1111/jeb.12908)

This article is protected by copyright. All rights reserved

1

2 Received Date : 12-Oct-2015

3 Revised Date : 04-May-2016

4 Accepted Date : 17-May-2016

5 Article type : Research Papers

6

7

8 **Abstract**

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

29

1

2

3 **Introduction**

4 The ability to communicate effectively influences a range of conspecific and
5 interspecific interactions, and failure to communicate may result in the loss of
6 resources or reproductive opportunity (Hauser, 1996; Bradbury & Vehrencamp, 1998;
7 Epsmark & Amundsen, 2000; Maynard Smith & Harper, 2003); thus, effective
8 communication ultimately affects individual fitness. Species that rely on visual display
9 for social communication must maintain signals that are conspicuous enough to be
10 readily detected by conspecifics (Bradbury & Vehrencamp, 1998; Maynard Smith &
11 Harper, 2003). As detection depends on many situational or environmental variables,
12 species occupying different habitats potentially experience very different selection
13 pressures on signal design, which may ultimately generate much of the signal
14 diversity that characterises some groups of closely related species (Endler, 1992;
15 Leal & Fleishman, 2004; Nicholson *et al.*, 2007).

16 Even phylogenetically closely related species may optimise signal
17 conspicuousness through alternative means. For instance, species that use a similar
18 ornament in display may evolve different but equally effective solutions for increasing
19 conspicuousness – for example, by increasing ornament size, its contrast against the
20 background in colour or brightness, or by increasing the speed or amplitude of
21 movement in display (Endler, 1993a; Dawkins & Guilford, 1997; Ord *et al.*, 2007).
22 Costs associated with particular strategies for conspicuousness (energetic, or
23 increased risk of predation) may reduce the efficacy of one or more of the strategies
24 under a given set of conditions (Godin & McDonough, 2003; Hill & McGraw, 2006;
25 Simon, 2007; Woods *et al.*, 2007). The resultant strategy, or combination of
26 strategies, depends on the social requirements of the signal, its evolutionary history
27 and the environment occupied by the species (Boughman, 2001; Ord & Martins,
28 2006; Chen *et al.*, 2012). Additionally, just as multiple signals within a species can be
29 evolutionarily coupled (e.g. under correlational selection), so too can multiple aspects
30 of the same ornament (e.g. size and colour) such that changes to one aspect of the

1 ornament may influence change in some other aspect of that ornament (Hebets &
2 Papaj, 2005).

3 Environmental factors determine the effectiveness of different signalling
4 strategies in many ways. For example, ambient light influences the conspicuousness
5 of different colours by limiting the availability of light at different wavelengths (Endler,
6 1993b), and in very low light conditions the signal-to-noise ratio may decrease to a
7 point where colour vision becomes unreliable and individuals instead rely on
8 achromatic information (Vorobyev, 1997; Cronin *et al.*, 2014). Thus, signals that
9 generate high colour contrast against the background might be effective in a well-lit
10 habitat but harder to detect in full shade forests (Endler & Thery, 1996). Similarly,
11 visual acuity also decreases with decreasing habitat light such that colour patches
12 may need to be larger to be detected (Endler, 1992). For example, some species of
13 birds of the genus *Phylloscopus* that live in darkly-shaded habitats signal with colour
14 patches that are larger than those of species in better lit habitats and also have
15 greater brightness contrast (targeting the achromatic channel – Marchetti, 1993).

16 Habitats also vary in predator community and abundance, both of which play a
17 role in determining the most effective strategies for communication. Animals living in
18 habitats with relatively high predation intensity may have signals with reduced
19 conspicuousness, or may limit conspicuousness to the behaviourally controlled
20 aspects of the signal (Zuk & Kolluru, 1998; Stuart-Fox *et al.*, 2003; Husak *et al.*,
21 2006). For example, Martins *et al.* (2015) found independent evolutionary losses of
22 the ancestral blue ventral colour patch in some species of spiny lizards (genus
23 *Sceloporus*) which are less active overall, consistent with the hypothesis that the
24 colour was lost due to increased predation pressure. Instead, these species
25 compensate with more frequent head-bobbing displays of longer duration, thereby
26 limiting conspicuous display to occasions when predators are apparently absent.
27 Although similar examples of alternative strategies for effective communication
28 appear to exist in several taxa (Podos, 1997; Cardoso & Hu, 2011; Ord *et al.*, 2011;
29 Ossip-Klein *et al.*, 2013), few studies have systematically assessed the relationships
30 between aspects of a single ornament and how social and environmental factors may
31 influence those relationships.

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

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

1 traits may be influenced by environmental factors, we tested whether dewlap
2 conspicuousness is predicted by habitat light or potential predation intensity,
3 estimated from experimental data of relative predation on plasticine models across
4 different habitats.

8 **Methods**

9 **Data collection**

10 Between April 2011 and June 2012, we captured 122 individuals of 13 *Draco* taxa
11 (Fig.1), from locations on Borneo, Peninsula Malaysia, and the islands of Luzon and
12 Bohol in the Philippines. Though males are the more elaborately ornamented sex for
13 most species, female *Draco* lizards also use the dewlap in display, and so in this
14 study we included both males and females. Lizards were caught using a small
15 fishing-line noose at the end of a 6 m extendable pole. The colours of the lizard's
16 dewlap were measured with a JAZ EL-200 spectrometer with inbuilt JAZ-PX pulsed
17 xenon light source, calibrated using a diffuse white reflectance standard (Ocean
18 Optics). Measurements were taken at a 45° angle relative to the surface and spectra
19 were smoothed over 5 nm intervals between 300–700 nm, the approximate visual
20 spectrum of diurnal lizards (Loew *et al.*, 2002). Photographs were also taken of each
21 lizard with the dewlap extended (using a Canon PowerShot SX1-IS digital camera,
22 saving in RAW format) and the proportions of each colour in the dewlap were
23 measured using the same 1cm² grid. The photos included a scale and were also
24 used to measure the area of individual dewlaps using the 'freehand selection' tool in
25 ImageJ (Abramoff *et al.*, 2004). The snout-vent length (SVL) of each lizards caught in
26 the field was measured to the nearest mm, with a ruler.

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

1 took digital photographs using the same camera, framing the lizard's perch to the
2 side and capturing representative background vegetation colour and density. The
3 proportions of each colour in these photographs were estimated using a 1 cm² grid
4 overlaid on the background photographs.

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

15 **Visual modelling**

16 To measure the chromatic and achromatic contrast of the dewlap against the
17 background, from the perspective of *Draco* conspecifics, we applied the model of
18 Vorobyev and Osorio (1998), which estimates how well the receiver can discriminate
19 between two colours in units of 'just noticeable differences' (JND). One JND is the
20 threshold of discrimination—i.e. the minimum difference, given photoreceptor noise—
21 for a visual system to be able to distinguish two colours. We estimated chromatic
22 contrast based on the four single cones (UVS, SWS, MWS, and LWS), and
23 achromatic (luminance) contrast based on the double cone, which is probably used
24 to detect luminance variation in most diurnal lizards (Loew *et al.*, 2002, Osorio &
25 Vorobyev, 2005, Fleishman *et al.*, 2011). As the visual sensitivities of *Draco* species
26 are not known, we used information on the only related agamid lizard for which the
27 spectral sensitivities have been quantified, *Ctenophorus ornatus* (Barbour *et al.*,
28 2002), as detailed in Klomp *et al.* (2014), Teasdale *et al.* (2013) McLean *et al.* (2010)
29 and detailed in Supplementary Material S1.

30 We calculated the chromatic and achromatic contrasts of each dewlap colour,
31 for each species, when viewed against each of the predominant colours in their local
32 habitats. An overall contrast was then calculated, based on the sum of contrasts for

1 each colour in the dewlap against each colour in the background weighted by the
2 relative area each colour occupied. In the absence of behavioural data for agamid
3 lizards, we assume that JNDs (i.e. discrimination thresholds) are linearly related to
4 the perceptual distance between any two colours, although this assumption requires
5 testing (Kemp *et al.*, 2015).

6 **Sexual dimorphism**

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

23 **Predation experiment**

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

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

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

20 **Statistical methods**

21 All statistical analyses were conducted in R version 3.0.3 (R Development Core
22 Team, R Foundation for Statistical Computing, Vienna). We first used the 'phyl.resid'
23 method implemented with the lambda option in 'phytools' version 0.4-31 (Revell,
24 2012) on species mean dewlap area against species mean SVL to calculate 'size-
25 free' residuals of dewlap area for males and females. We then assessed how relative
26 dewlap area, chromatic contrast and achromatic contrast against the background
27 were related to each other by computing Pearson product moment correlation
28 coefficients. This was done by taking the average of two phylogenetic generalized
29 least squares (PGLS) regressions in which the y and x variables were swapped,
30 which provides an equivalent estimate of Pearson's r (e.g., Ord & Martins, 2006; see
31 also Smith, 2009).

1 To confirm that dewlap characteristics vary among taxa with the probable
2 strength of sexual selection experienced within those taxa, we ran a PGLS
3 regression of each characteristic against SSD and trait-specific measures of sexual
4 dimorphism – dewlap size dimorphism, chromatic and achromatic dichromatism. To
5 assess the possibility that female ornament evolution is a correlated response to that
6 of males we ran phylogenetic regressions of female dewlap traits against male
7 dewlap traits. In order to determine whether habitat factors play a role in which
8 dewlap traits increase in elaboration between species, we conducted phylogenetic
9 regressions of dewlap chromatic contrast and dewlap relative area, against habitat
10 light level (AUC) and relative predation intensity (high vs low). For this we focussed
11 just on males, because only males showed a relationship between dewlap chromatic
12 contrast and dewlap relative area. All PGLS regressions were applied using Pagel's
13 lambda, a model of phenotypic evolution where lambda values below one indicate
14 that species are more dissimilar than expected based on the phylogeny (Pagel,
15 1999), in the 'ape' package version 3.2 (Paradis *et al.*, 2004).

16 Phylogenetic relationships for the species in our study were derived by
17 pruning the agamid phylogeny by Collar *et al.* (2010), which is based on a BEAST
18 (Drummond *et al.*, 2006; Drummond & Rambaut, 2007) analysis of 1.2 kb
19 mitochondrial protein coding genes. The relationships between the species examined
20 in this paper are well supported (>0.95 Bayesian posterior probability) for all but the
21 sister relationship between *D. haematopogon* and the two populations of *D.*
22 *melanopogon* (0.71 posterior probability). Weak support for this relationship is
23 reflected in the short branch length (Fig. 1) and our analyses included branch length
24 information. As our analyses included both Malay and Bornean populations of *D.*
25 *melanopogon* and *D. cornutus*, which were not included in the phylogeny as separate
26 taxa, we added these with branch-lengths based on the minimum divergence
27 estimated for intra-island populations of Philippine *Draco* (from McGuire & Kiew,
28 2001), following Ord & Klomp (2014).

29

30 **Results**

31 **Are there alternative strategies for conspicuousness?**

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

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

15 **Dewlap trait relationships with sexual dimorphism**

16 All male dewlap traits (relative area, chromatic and achromatic contrast) and some
17 female dewlap traits were correlated with a measure of sexual dimorphism or
18 dichromatism (Table 2). Male relative dewlap area increased with increasing sexual
19 size dimorphism: as males become increasingly larger than females in body size they
20 invest in larger dewlap areas relative to their size (Fig. 3a). *Draco quinquefasciatus*
21 was excluded from this regression as an obvious model outlier, though removal did
22 not change the conclusions. Neither male dewlap chromatic nor achromatic contrast,
23 nor any female dewlap traits were correlated with SSD. However, male chromatic
24 contrast increased with increasing sexual dichromatism (in chromatic contrast
25 between the sexes), while female chromatic contrast decreased with increasing
26 sexual dichromatism (males: Fig. 3c; females: Fig. 3d). This trend for females
27 appeared to be primarily due to a few taxa (circled in the figure) where females have
28 greater chromatic contrast than males, rather than a general pattern across all taxa
29 studied. Thus sexual dichromatism in chromatic contrast is more likely driven by
30 increasing male chromatic contrast, while female chromatic contrast varies
31 inconsistently between species. For males, achromatic contrast against the
32 background also increased with increasing sexual dichromatism (in achromatic

1 contrast between the sexes), but there was no relationship for females, suggesting
2 again that increasing male dewlap brightness contrast against the background is
3 driving the achromatic dichromatism between the sexes (males: Fig. 3e; females:
4 Fig. 3f).

5 **Do habitat factors influence signalling strategy?**

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

15 **Discussion**

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

27 There are many examples where different aspects of visual signals (e.g. size
28 and colour) increase in conspicuousness simultaneously in response to social and
29 environmental selective pressures, both at the individual and population level (Hill,
30 1999; Torok, 2003; Loyau *et al.*, 2005; Hebets *et al.*, 2013), though examples of
31 alternative pathways of elaboration for a single ornament type are rarer. Studies of

1 species that signal in multiple modalities, however, do report the use of alternative
2 signalling strategies, for many reasons, including physiological constraints (Podos,
3 1997) and the need to signal in diverse or changing environments (Bro-Jørgensen,
4 2010). These same constraints may also differentially affect the expression of
5 aspects of a single ornament – as results of this study suggest. For male *Draco*,
6 having a dewlap that is both highly chromatically contrasting and large in area may
7 be too costly or is constrained in some way. Signals can be energetically costly to
8 produce and maintain, and conspicuousness can be costly due to increased
9 predation risk (Bradbury & Vehrencamp, 1998).

10 We did not find the same negative correlation between colour contrast and
11 relative dewlap size for females as for males, potentially because males and females
12 signal in different ecological and/or social circumstances. Though data on the social
13 ecology of *Draco* are sparse, in most *Draco* species males have the more elaborate
14 dewlap in size and colour and use the dewlap more frequently in broadcast display,
15 suggesting males may experience greater selective pressures for effective signalling
16 than females (Inger, 1983; Mori & Hikida, 1993). It is also possible that the evolution
17 of female relative dewlap area is a correlated response to that of males, given the
18 significant correlation of male and female relative dewlap size across taxa. Although
19 there was no correlation between the relative size and colour of female dewlaps, we
20 found a positive correlation between colour and brightness contrast, suggesting that
21 for taxa where there is increased pressure for females to signal more effectively, they
22 rely on elaboration in both colour and brightness contrast. Selection for increased
23 signal complexity as well as redundancy in signals has been found in diverse taxa,
24 such as spiders and frogs, and is hypothesised to increase signal reliability and allow
25 species to maintain effective signals in fluctuating social and ecological environments
26 (Bro-Jørgensen, 2010; Akre *et al.*, 2011; Hebets *et al.*, 2013).

27 Our results also suggest that sexual selection plays a role in driving all
28 aspects of male dewlap conspicuousness, as all dewlap traits were positively
29 correlated with measures of sexual dimorphism or dichromatism. Selection for
30 efficient gliding in *Draco* species has led to constraints on body and head size for
31 males, and the need to balance body and head weight in gravid females (Shine *et al.*,
32 1998; Husak & McGuire, 2014). Husak and McGuire (2014) found that *Draco* species
33 may exhibit either female or male-biased SSD, but that male-biased SSD was more

1 prevalent in larger species. They suggest a shift away from selection for better gliding
2 ability in males for species with male-biased SSD, as increases in body size
3 increases wing loadings, and a shift towards more intense selection for fighting
4 performance. This hypothesis predicts two strategies for male territory defence (good
5 gliders or good fighters), where the good fighter strategy is associated with male-
6 biased SSD. Our data suggest that male-biased SSD is also associated with larger
7 relative dewlaps, suggesting that assessing the relationship between relative dewlap
8 size and fighting ability may be an interesting avenue for further research.

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

20 Our results indicate that predation pressure may play a role in determining the
21 strategy employed by a species to increase dewlap conspicuousness – larger
22 dewlaps or more chromatically contrasting dewlaps – as taxa in habitats with
23 relatively higher predation intensity tended to have relatively larger dewlaps.
24 Although we found a correlation between relative dewlap size and predation intensity,
25 we did not find the corresponding correlation between predation intensity and
26 chromatic contrast, which we might expect if predation intensity was the primary
27 determinant of signalling strategy (though the relationship was certainly in the right
28 direction, figure 4b). It is notoriously difficult to get a realistic measure of predation
29 intensity, but model-prey experiments such as we have used here can give us a
30 general indication of the potential variation in predation intensity across habitats
31 (Stuart-Fox *et al.*, 2003; Husak *et al.*, 2006; McLean *et al.*, 2010; Morgans & Ord,
32 2013). Diurnal birds are perhaps the most common predators of *Draco* lizards
33 (Outhavon, 1999; Chalsurlyanun, 2011). Predatory birds have high visual acuity

1 allowing them to resolve small colour patches at large distances, and are good at
2 detecting movements (Donner, 1951; Lea & Dittrich, 2001; Osorio & Vorobyev,
3 2008). However, some birds may rely primarily on chromatic information in prey
4 detection (Goldsmith *et al.*, 1981; Kelber *et al.*, 2003; Stuart *et al.*, 2012). Therefore,
5 it is possible that both signalling strategies – increased relative dewlap size and
6 increased chromatic contrast – increase signal conspicuousness to predators.
7 Furthermore, an increased abundance of predators in some habitats is likely to
8 favour reduced overall conspicuousness, or increased anti-predator behaviour
9 (Endler, 1987; Slagsvold *et al.*, 1995; Koga *et al.*, 1998; Taylor *et al.*, 2005), rather
10 than select for one form of dewlap conspicuousness over the other.

11 An alternative explanation for the trend for species with relatively larger
12 dewlaps to occur in higher predation habitats is that larger dewlaps may be more
13 beneficial in close-range predator encounters. Vanhooydonck *et al.* (2009) found a
14 species of anole (which also use dewlaps in display and are ecologically analogous
15 to *Draco*) also showed increased relative dewlap size with increasing sexual size
16 dimorphism, and that in populations where a ground-based lizard predator
17 (*Leiocephalus* species) is present, males have larger relative dewlaps than those in
18 populations where that predator is absent. They proposed that the investment in
19 larger dewlaps may be beneficial in pursuit deterrence, in that it more effectively
20 signals to a predator that it has been seen and that the individual is unprofitable prey
21 – perhaps due to hyper-aggression or ability to flee (Caro, 1995). However, this
22 hypothesis is problematic where the main predators are birds, as signalling
23 aggression or ability to flee does not seem likely to deter a bird from attacking
24 potential prey, and overall the hypothesis has been somewhat controversial (Caro,
25 1995).

26 We also found a negative relationship between chromatic contrast and habitat
27 light that is partially driven by a cluster of four taxa found in most well-lit habitats (Fig.
28 4d). Species found in open, well-lit habitats are thought to experience greater levels
29 of predation than those in closed habitats (Stuart-Fox & Ord, 2004). For three of
30 these four species, we did not have data on relative predation intensity, and the
31 fourth was found in a relatively high predation habitat. Therefore, it remains possible
32 that the low chromatic contrast for these four species in the brightest habitat reflects
33 high predation risk in these more open habitats.

1 To conclude, our study finds evidence for alternate signalling strategies of
2 increased colour contrast or increased dewlap area relative to body size, for males of
3 several *Draco* taxa, and that relative predation intensity between habitats may
4 influence the particular strategy a species employs. Furthermore, these results
5 highlight how ornaments used in communication are composed of multiple
6 components (e.g. size and colour), and that each of these components may be
7 influenced by different selection pressures. Ideally, the nature of selection acting on
8 dewlap size and coloration should be corroborated by independent measures of
9 sexual selection (e.g. mating system or testis size) and manipulative experiments
10 (e.g. male contest or mate choice experiments). Determining how selection acts on
11 different signal components will enable a fuller understanding of the evolution of
12 signal diversity, which characterises many of the world's adaptive radiations.

13

14 **Acknowledgements**

15 We are grateful to Jim McGuire for advice on the *Draco* phylogeny, Lee Grismer for
16 help in locating field sites for Malaysian *Draco* species, and Audrey Stewart and
17 Elizabeth Cassidy, and other students from Malaysia and the Philippines for
18 assistance in the field. We thank the Malaysian Economic Planning Unit, Sarawak
19 State Planning Unit, Sarawak Forestry Department, Sarawak National Parks and
20 Nature Reserves and the Philippine Department of Environment and Natural
21 Resources for facilitating research permits. This work was supported by E&ERC
22 start-up funds and a UNSW SFRGP grant to TJO, a grant from the Niche Research
23 Grant Scheme (NRGS/1087/2-13(01)) to ID and a grant from the National
24 Geographic Society (8875-11) to DSF. DAK was supported by an Australian
25 Postgraduate Award. This study was covered by the UNSW Animal Care and Ethics
26 Committee protocol #11/33b and the University of Melbourne Animal Ethics
27 Committee approval 1112003. The authors declare no conflict of interest.

28

29

30

1

2 **References**

- 3 Abramoff, M.D., Magalhaes, P.J. & Ram, S.J. 2004. Image processing with ImageJ.
4 *Biophotonics Int.* **11**: 36–42.
- 5 Akre, K.L., Farris, H.E., Lea, A.M., Page, R.A. & Ryan, M.J. 2011. Signal perception
6 in frogs and bats and the evolution of mating signals. *Science (80-.)*. **333**: 751–
7 752.
- 8 Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton.
- 9 Barbour, H.R., Archer, M.A., Hart, N.S., Thomas, N., Dunlop, S.A., Beazley, L.D., *et*
10 *al.* 2002. Retinal characteristics of the ornate dragon lizard, *Ctenophorus*
11 *ornatus*. *J. Comp. Neurol.* **450**: 334–344.
- 12 Bisazza, A. 1993. Male competition, female mate choice and sexual size dimorphism
13 in poeciliid fishes. *Mar. Behav. Physiol.* **23**: 257–286. Taylor & Francis Group.
- 14 Boughman, J.W. 2001. Divergent sexual selection enhances reproductive isolation in
15 sticklebacks. *Nature* **411**: 944–948.
- 16 Bradbury, J.W. & Vehrencamp, S.L. 1998. *Principles of Animal Communication*,
17 Second Edi. Sinauer Associates, Sunderland, Massachusetts.
- 18 Bro-Jørgensen, J. 2010. Dynamics of multiple signalling systems: animal
19 communication in a world in flux. *Trends Ecol. Evol.* **25**: 292–300.
- 20 Butler, M.A., Schoener, T.W. & Losos, J.B. 2000. The relationship between sexual
21 size dimorphism and habitat use in Greater Antillean Anolis lizards. *Evolution (N.*
22 *Y)*. **54**: 259. The Society for the Study of Evolution.
- 23 Cardoso, G.C. & Hu, Y. 2011. Birdsong Performance and the Evolution of Simple
24 (Rather than Elaborate) Sexual Signals. *Am. Nat.* **178**: 679–686.
- 25 Caro, T.M. 1995. Pursuit-deterrence revisited. *Trends Ecol. Evol.* **10**: 500–3.
- 26 Chalsurlyanun, S. 2011. Food consumed by the Great Hornbill and Rhinoceros
27 Hornbill in the tropical rainforest, Budo Su-Ngai Padi National Park, Thailand.
28 *Raffles Bull. Zool.* 123–135.
- 29 Chen, I.-P., Stuart-Fox, D., Hugall, A.F. & Symonds, M.R.E. 2012. Sexual selection

- 1 and the evolution of complex color patterns in dragon lizards. *Evolution* (N. Y.)
2 **66**: 3605–14.
- 3 Cronin, T.W., Johnsen, S., Marshall, N.J. & Warrant, E.J. 2014. *Visual Ecology*.
4 Princeton University Press, Princeton.
- 5 Dawkins, M.S. & Guilford, T. 1997. *Conspicuousness and Diversity in Animal Signals*
6 (D. H. Owings et al., eds). Springer US, Boston, MA.
- 7 Donner, K.O. 1951. The visual acuity of some passerine birds. *Acta Zool. Fenn.* **66**:
8 1–40.
- 9 Drummond, A.J., Ho, S.Y.W., Phillips, M.J. & Rambaut, A. 2006. Relaxed
10 phylogenetics and dating with confidence. *PLoS Biol.* **4**: e88.
- 11 Drummond, A.J. & Rambaut, A. 2007. BEAST: Bayesian evolutionary analysis by
12 sampling trees. *BMC Evol. Biol.* **7**: 214. BioMed Central.
- 13 Endler, J.A. 1987. Predation, light intensity and courtship behaviour in *Poecilia*
14 *reticulata* (Pisces: Poeciliidae). *Anim. Behav.* **35**: 1376–1385.
- 15 Endler, J.A. 1992. Signals, signal conditions, and the direction of evolution. *Am. Nat.*
16 **139**: S125–S153.
- 17 Endler, J.A. 1993a. Some general-comments on the evolution and design of animal
18 communication-systems. *Philos. Trans. R. Soc. London Ser. B-Biological Sci.*
19 **340**: 215–225.
- 20 Endler, J.A. 1993b. The colour of light in forests and its implications. *Ecol. Monogr.*
21 **63**: 1–27.
- 22 Endler, J.A. & Thery, M. 1996. Interacting Effects of Lek Placement, Display
23 Behavior, Ambient Light, and Color Patterns in Three Neotropical Forest-
24 Dwelling Birds on JSTOR. *Am. Nat.* **148**: 421–452.
- 25 Epsmark, Y. & Amundsen, T. 2000. Animal signals: signalling and signal design in
26 animal communication. Tapir Academy, Trondheim.
- 27 Fairbairn, D.J., Banckenhorn, W.U. & Szekely, T. (eds). 2007. *Sex, Size and Gender*
28 *Roles. Evolutionary Studies of Sexual Size Dimorphism*. Oxford University
29 Press.
- 30 Godin, J.-G.J. & Mcdonough, H.E. 2003. Predator preference for brightly colored
31 males in the guppy: a viability cost for a sexually selected trait. *Behav. Ecol.* **14**:

- 1 194–200.
- 2 Goldsmith, T.H., Collins, J.S. & Perlman, D.L. 1981. A wavelength discrimination
3 function for the hummingbird *Archilochus alexandri*. *J. Comp. Physiol. A* **143**:
4 103–110.
- 5 Hauser, M.D. 1996. *The Evolution of Communication*. MIT Press.
- 6 Hebets, E.A. & Papaj, D.R. 2005. Complex signal function: developing a framework
7 of testable hypotheses. *Behav. Ecol. Sociobiol.* **57**: 197–214.
- 8 Hebets, E.A., Vink, C.J., Sullivan-Beckers, L. & Rosenthal, M.F. 2013. The
9 dominance of seismic signaling and selection for signal complexity in
10 *Schizocosa* multimodal courtship displays. *Behav. Ecol. Sociobiol.* **67**: 1483–
11 1498.
- 12 Hill, G.E. 1999. Pairing success relative to male plumage redness and pigment
13 symmetry in the house finch: temporal and geographic constancy. *Behav. Ecol.*
14 **10**: 48–53.
- 15 Hill, G.E. & McGraw, K.J. 2006. *Bird coloration. Mechanisms and measurements*, 1st
16 ed. Cambridge: Harvard University Press, Cambridge.
- 17 Hunt, J., Breuker, C.J., Sadowski, J.A. & Moore, A.J. 2009. Male-male competition,
18 female mate choice and their interaction: determining total sexual selection. *J.*
19 *Evol. Biol.* **22**: 13–26.
- 20 Husak, J.F., Macedonia, J.M., Fox, S.F. & Saucedo, R.C. 2006. Predation cost of
21 conspicuous male coloration in collared lizards (*Crotaphytus collaris*): An
22 experimental test using clay-covered model lizards. *Ethology* **112**: 572–580.
- 23 Husak, J.F. & McGuire, J.A. 2014. Does “gliding while gravid” explain Rensch’s rule
24 in flying lizards? *Biol. J. Linn. Soc.* **113**: 270–282.
- 25 Inger, R.F. 1983. Morphological and ecological variation in the flying lizards (Genus
26 *Draco*). In: *Fieldiana*. Field Museum of Natural History.
- 27 Kelber, A., Vorobyev, M. & Osorio, D. 2003. Animal colour vision-behavioural tests
28 and physiological concepts. *Biol. Rev. Camb. Philos. Soc.* **78**: 81–118.
- 29 Kemp, D.J., Herberstein, M.F., Fleishman, L.J., Endler, J.A., Bennett, A.T.D., Dyer,
30 A.G., *et al.* 2015. An integrative framework for the appraisal of colouration in
31 nature. *Am. Nat.* **185**: 705–724.

- 1 Klomp, D.A., Stuart-Fox, D., Das, I. & Ord, T.J. 2014. Marked colour divergence in
2 the gliding membranes of a tropical lizard mirrors population differences in the
3 colour of falling leaves. *Biol. Lett.* **10**: 20140776–20140776.
- 4 Koga, T., Backwell, P.R.Y., Jennions, M.D. & Christy, J.H. 1998. Elevated predation
5 risk changes mating behaviour and courtship in a fiddler crab. *Proc. R. Soc. B*
6 *Biol. Sci.* **265**: 1385–1390.
- 7 Lea, S.E.G. & Dittrich, W.H. 2001. What do birds see in moving video images? In:
8 *Picture perception in animals* (J. Fagot, ed), pp. 143–180. Psychology Press,
9 Ltd., East Sussex, UK.
- 10 Leal, M. & Fleishman, L.J. 2004. Differences in visual signal design and detectability
11 between allopatric populations of Anolis lizards. *Am. Nat.* **163**: 26–39.
- 12 Loew, E.R., Fleishman, L.J., Foster, R.G. & Provencio, I. 2002. Visual pigments and
13 oil droplets in diurnal lizards : a comparative study of Caribbean anoles. *J. Exp.*
14 *Biol.* **205**: 927–938.
- 15 Loyau, A., Jalme, M. Saint & Sorci, G. 2005. Intra- and Intersexual Selection for
16 Multiple Traits in the Peacock (*Pavo cristatus*). *Ethology* **111**: 810–820.
- 17 Marchetti, K. 1993. Dark habitats and bright birds illustrate the role of environment in
18 species divergence. *Nature* **362**: 149–152.
- 19 Martins, E.P., Ossip-Klein, A.G., Zúñiga-Vega, J.J., Vital García, C., Campos, S.M. &
20 Hews, D.K. 2015. Evolving from static to dynamic signals: evolutionary
21 compensation between two communicative signals. *Anim. Behav.* **102**: 223–229.
- 22 Maynard Smith, J. & Harper, D. 2003. *Animal Signals* (P. H. Harvey & R. M. May,
23 eds). Oxford University Press, Oxford.
- 24 McBrayer, L.D. & Anderson, R.A. 2007. Sexual Size Dimorphisms and Bite Force in
25 the Northern Alligator Lizard, *Elgaria coerulea*. *J. Herpetol.* **41**: 554–559. Society
26 for the Study of Amphibians and Reptiles.
- 27 McElligott, A.G., Gammell, M.P., Harty, H.C., Paini, D.R., Murphy, D.T., Walsh, J.T.,
28 *et al.* 2001. Sexual size dimorphism in fallow deer (*Dama dama*): do larger,
29 heavier males gain greater mating success? *Behav. Ecol. Sociobiol.* **49**: 266–
30 272.
- 31 McGuire, J.A. & Heang, K.B. 2001. Phylogenetic systematics of Southeast Asian

- 1 flying lizards (Iguania : Agamidae : Draco) as inferred from mitochondrial DNA
2 sequence data. *Biol. J. Linn. Soc.* **72**: 203–229.
- 3 McLean, C.A., Moussalli, A. & Stuart-Fox, D. 2010. The predation cost of female
4 resistance. *Behav. Ecol.* **21**: 861–867.
- 5 Mitani, J.C., Gros-Louis, J. & Richards, A.F. 1996. Sexual dimorphism, the
6 operational sex ratio and the intensity of male competition in polygynous
7 primates. *Am. Nat.* **147**: 966–980.
- 8 Morgans, C.L. & Ord, T.J. 2013. Natural selection in novel environments: predation
9 selects for background matching in the body colour of a land fish. *Anim. Behav.*
10 **86**: 1241–1249.
- 11 Mori, A. & Hikida, T. 1994. Field observations on the social-behaviour of the Flying
12 Lizard, *Draco volans sumatranus*, in Borneo. *Copeia* 124–130.
- 13 Mori, A. & Hikida, T. 1993. Natural-history observations of the Flying Lizard, *Draco*
14 *volans sumatranus* (Agamidae, Squamata) from Sarawak, Malaysia. *Raffles*
15 *Bull. Zool.* **41**: 83–94.
- 16 Nicholson, K.E., Harmon, L.J. & Losos, J.B. 2007. Evolution of Anolis lizard dewlap
17 diversity. *PLoS One* **2**: 12.
- 18 Ord, T.J., Charles, G.K. & Hofer, R.K. 2011. The evolution of alternative adaptive
19 strategies for effective communication in noisy environments. *Am. Nat.* **177**: 54–
20 64. The University of Chicago Press.
- 21 Ord, T.J. & Martins, E.P. 2006. Tracing the origins of signal diversity in anole lizards:
22 phylogenetic approaches to inferring the evolution of complex behaviour. *Anim.*
23 *Behav.* **71**: 1411–1429.
- 24 Ord, T.J., Peters, R.A., Clucas, B. & Stamps, J.A. 2007. Lizards speed up visual
25 displays in noisy motion habitats. *Proc. R. Soc. B-Biological Sci.* **274**: 1057–
26 1062.
- 27 Osorio, D. & Vorobyev, M. 2008. A review of the evolution of animal colour vision and
28 visual communication signals. *Vision Res.* **48**: 2042–2051.
- 29 Ossip-Klein, A.G., Fuentes, J.A., Hews, D.K. & Martins, E.P. 2013. Information
30 content is more important than sensory system or physical distance in guiding
31 the long-term evolutionary relationships between signaling modalities in

- 1 Sceloporus lizards. *Behav. Ecol. Sociobiol.* **67**: 1513–1522.
- 2 Ouithavon, K. 1999. *A comparative study of the feeding ecology of two sympatric*
3 *Hornbill species (Aves: Bucerotidae) during their breeding season in Huai Kha*
4 *Khaeng Wildlife Sanctuary, Thailand.* National Parks and Wildlife Research
5 Division, Natural Research Conservation Office, Royal Forest Department,
6 Bangkok, Thailand.
- 7 Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* **401**:
8 877–84. Nature Publishing Group.
- 9 Paradis, E., Claude, J. & Strimmer, K. 2004. APE: Analyses of Phylogenetics and
10 Evolution in R language. *Bioinformatics* **20**: 289–290.
- 11 Pérez i de Lanuza, G., Font, E. & Monterde, J.L. 2013. Using visual modelling to
12 study the evolution of lizard coloration: Sexual selection drives the evolution of
13 sexual dichromatism in lacertids. *J. Evol. Biol.* **26**: 1826–1835.
- 14 Podos, J. 1997. A performance constraint on the evolution of trilled vocalizations in a
15 songbird family (Passeriformes: Emberizidae). *Evolution (N. Y.)*. **51**: 537–551.
- 16 Serrano-Meneses, M.A., Cordoba-Aguilar, A., Mendez, V., Layen, S.J. & Szekely, T.
17 2007. Sexual size dimorphism in the American rubyspot: male body size predicts
18 male competition and mating success. *Anim. Behav.* **73**: 987–997.
- 19 Shine, R. 1978. Sexual size dimorphism and male combat in snakes. *Oecologia* **33**:
20 269–277.
- 21 Shine, R., Keogh, S., Doughty, P. & Giragossyan, H. 1998. Costs of reproduction and
22 the evolution of sexual dimorphism in a “flying lizard” *Draco melanopogon*
23 (Agamidae). *J. Zool.* **246**: 203–213.
- 24 Simon, V.B. 2007. Not All Signals are Equal: Male Brown Anole Lizards (*Anolis*
25 *sagrei*) Selectively Decrease Pushup Frequency Following a Simulated
26 Predatory Attack. *Ethology* **113**: 793–801.
- 27 Slagsvold, T., Dale, S. & Kruszewicz, A. 1995. Predation favours cryptic coloration in
28 breeding male pied flycatchers. *Anim. Behav.* **50**: 1109–1121.
- 29 Smith, R.J. 1999. Statistics of sexual size dimorphism. *J. Hum. Evol.* **36**: 423–459.
- 30 Smith, R.J. 2009. Use and misuse of the reduced major axis for line-fitting. *Am. J.*
31 *Phys. Anthropol.* **140**: 476–486.

- 1 Stamps, J.A., Losos, J.B. & Andrews, R.M. 1997. A comparative study of population
2 density and sexual size dimorphism in lizards. *Am. Nat.* **149**: 64–90.
- 3 Stuart, Y.E., Dappen, N. & Losin, N. 2012. Inferring predator behavior from attack
4 rates on prey-replicas that differ in conspicuousness. *PLoS One* **7**: e48497.
5 Public Library of Science.
- 6 Stuart-Fox, D., Moussalli, A. & Whiting, M.J. 2007. Natural selection on social
7 signals: Signal efficacy and the evolution of chameleon display coloration. *Am.*
8 *Nat.* **170**: 916–930.
- 9 Stuart-Fox, D.M., Moussalli, A., Marshall, N.J. & Owens, I.P.F. 2003. Conspicuous
10 males suffer higher predation risk: visual modelling and experimental evidence
11 from lizards. *Anim. Behav.* **66**: 541–550.
- 12 Stuart-Fox, D.M. & Ord, T.J. 2004. Sexual selection, natural selection and the
13 evolution of dimorphic coloration and ornamentation in agamid lizards. *Proc. R.*
14 *Soc. London Ser. B-Biological Sci.* **271**: 2249–2255.
- 15 Taylor, A.R., Persons, M.H. & Rypstra, A.L. 2005. The effect of perceived predation
16 risk on male courtship and copulatory behaviour in the wolf spider *Pardosa*
17 *milvina* (Araneae, Lycosidae). *J. Arachnol.* **33**: 76–81. American Arachnological
18 Society.
- 19 Teasdale, L.C., Stevens, M. & Stuart-Fox, D. 2013. Discrete colour polymorphism in
20 the tawny dragon lizard (*Ctenophorus decresii*) and differences in signal
21 conspicuousness among morphs. *J. Evol. Biol.* **26**: 1035–46.
- 22 Torok, J. 2003. Depigmented wing patch size is a condition-dependent indicator of
23 viability in male collared flycatchers. *Behav. Ecol.* **14**: 382–388.
- 24 Vanhooydonck, B., Herrel, A., Meyers, J.J. & Irschick, D.J. 2009. What determines
25 dewlap diversity in Anolis lizards? An among-island comparison. *J. Evol. Biol.*
26 **22**: 293–305.
- 27 Vorobyev, M. 1997. Costs and benefits of increasing the dimensionality of colour
28 vision system. In: *Biophysics of photoreception: molecular and phototransductive*
29 *events*, pp. 280–289.
- 30 Wong, B.B.M. & Candolin, U. 2005. How is female mate choice affected by male
31 competition? *Biol. Rev. Camb. Philos. Soc.* **80**: 559–71.

- 1 Woods, W.A., Hendrickson, H., Mason, J. & Lewis, S.M. 2007. Energy and predation
2 costs of firefly courtship signals. *Am. Nat.* **170**: 702–8.
- 3 Yewers, M.S., McLean, C.A., Moussalli, A., Stuart-Fox, D., Bennett, A.T.D. & Knott,
4 B. 2015. Spectral sensitivity of cone photoreceptors and opsin expression in two
5 colour-divergent lineages of the lizard *Ctenophorus decresii*. *J. Exp. Biol.* **218**:
6 1556–63.
- 7 Zuk, M. & Kolluru, G.R. 1998. Exploitation of sexual signals by predators and
8 parasitoids. *Q. Rev. Biol.* **73**: 415–438.

11 **Supplementary material**

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

13 **Appendix S1** Visual modelling methodology.

14 **Figure S1** Photograph of plasticine lizard models used in predation experiment.

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

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

20 **Figure S4** A) Female chromatic contrast as a function of male chromatic contrast
21 (JND, log-transformed); B) female achromatic contrast as a function of male
22 achromatic contrast (JND); and C) female relative dewlap area as a function of male
23 relative dewlap area (size-free residuals, cm²).

24
25
26 Data deposited at Dryad: 10.5061/dryad.xxxx

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

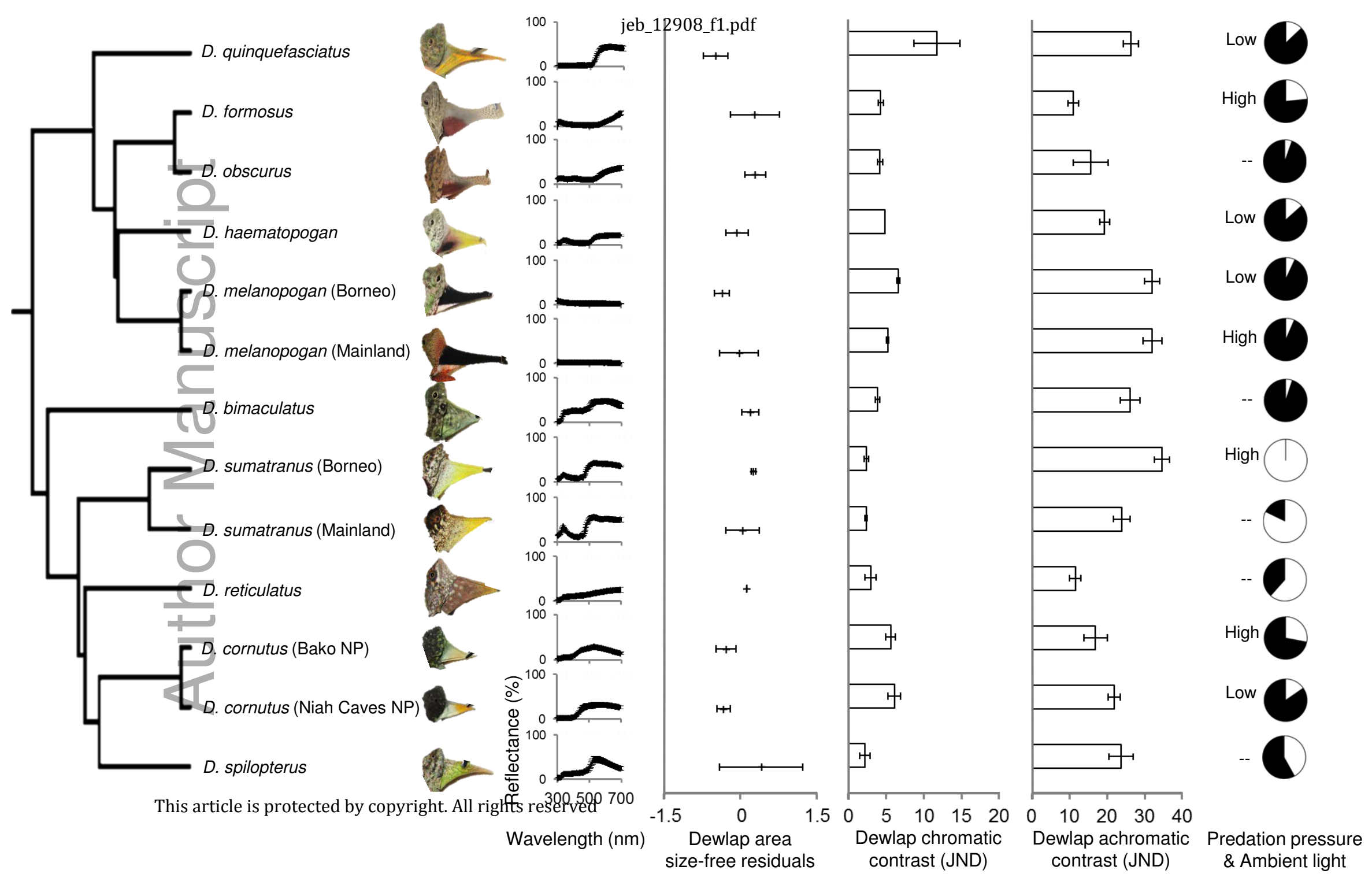
Table 2 Phylogenetic regressions of male and female dewlap traits (dewlap area size-free residuals, chromatic contrast and achromatic contrast against the background) against SSD and trait-specific sexual dimorphisms (dimorphism in dewlap area and sexual dichromatism in chromatic and achromatic contrast).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

Dewlap traits	N_{taxa}	λ	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

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	N_{taxa}	λ	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

Author Manuscript



(F1_comp.pdf)

Figure 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.

Author Manuscript

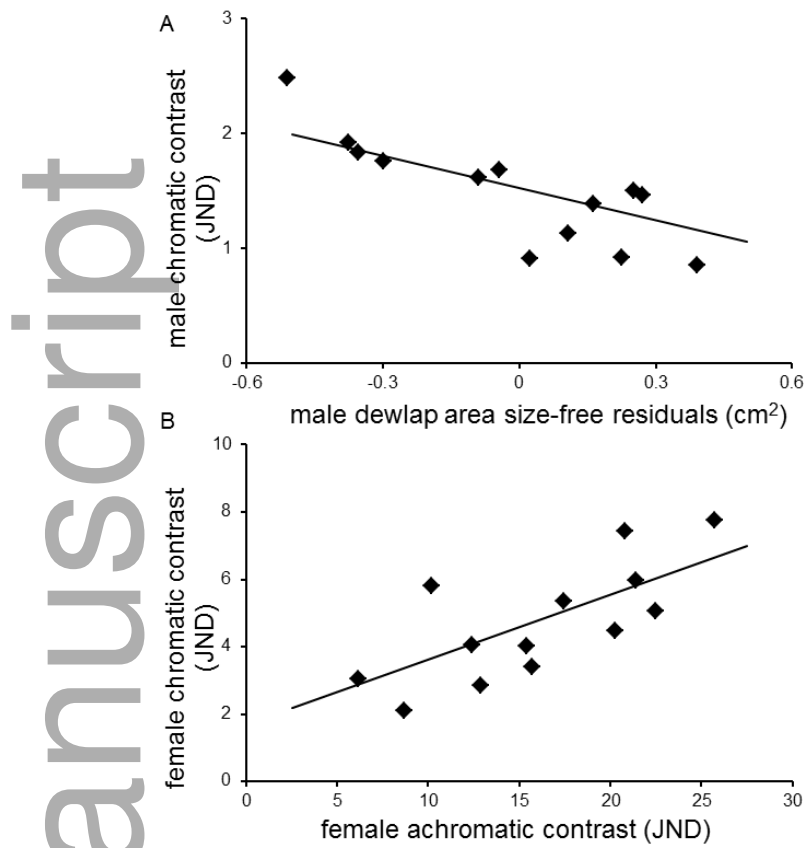


Figure 2 A) Male chromatic contrast (log-transformed) against relative dewlap area, and B) female chromatic contrast against achromatic contrast.

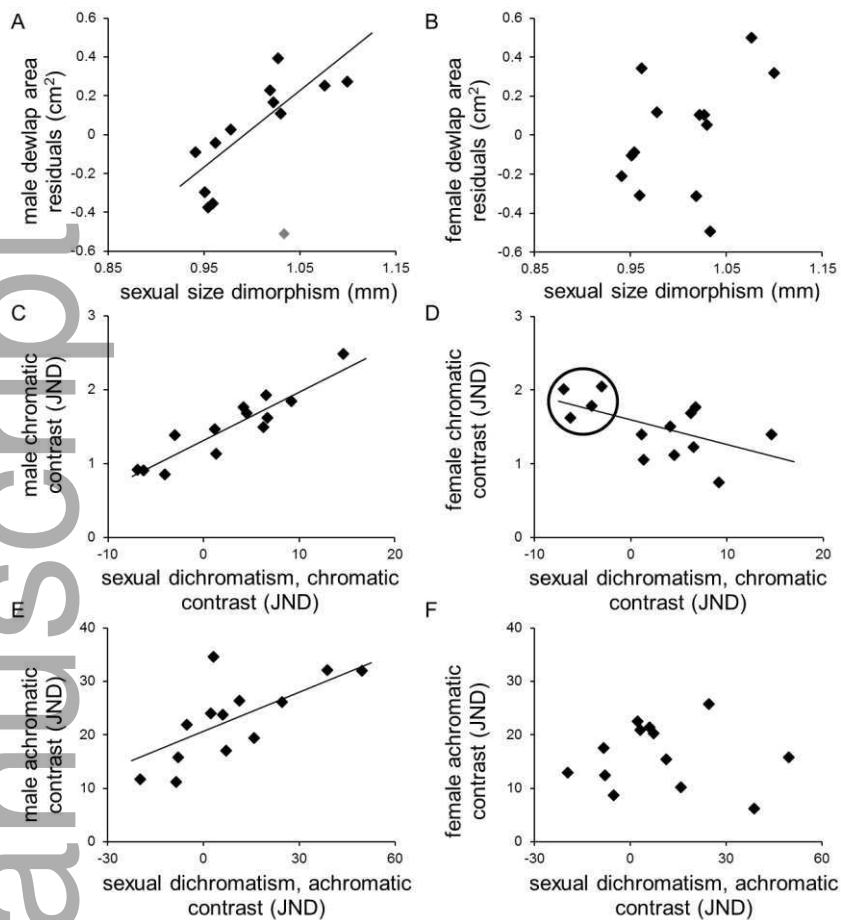


Figure 3 A) Male and B) female relative dewlap area as a function of sexual size dimorphism, C) male and D) female chromatic contrast (log-transformed) as a function of sexual dichromatism (JND, chromatic contrast between the primary dewlap colour of the sexes), and E) male and F) female achromatic contrast 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.

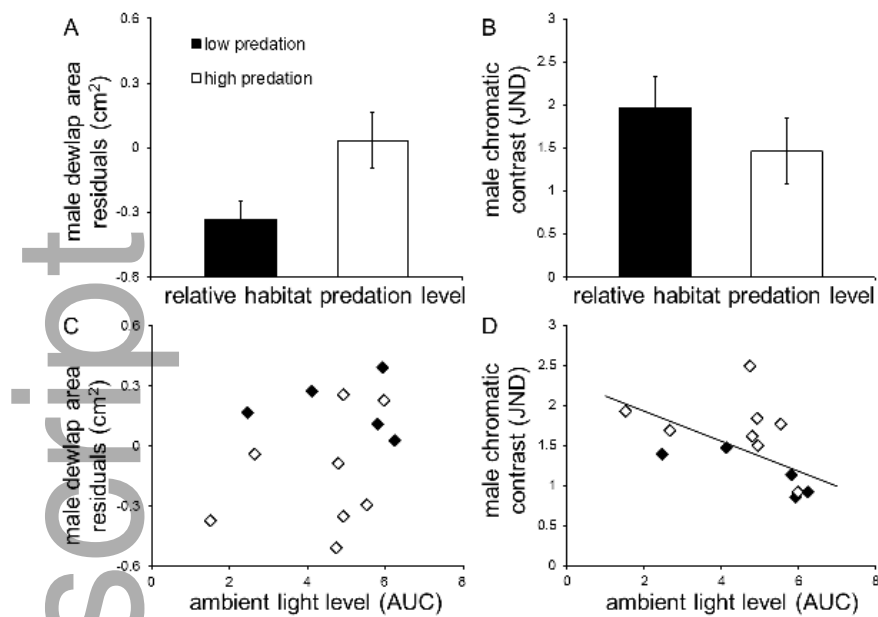


Figure 4 A) Male relative dewlap area for species sampled in high and low predation habitats ($N = 8$ taxa), B) male chromatic contrast (log-transformed) for species sampled in high and low predation habitats ($N = 8$ taxa), C) male relative dewlap area as a function of ambient light level ($N = 13$ 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).



Minerva Access is the Institutional Repository of The University of Melbourne

Author/s:

Klomp, DA; Ord, TJ; Das, I; Diesmos, A; Ahmad, N; Stuart-Fox, D

Title:

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

Date:

2016-09-01

Citation:

Klomp, D. A., Ord, T. J., Das, I., Diesmos, A., Ahmad, N. & Stuart-Fox, D. (2016). Ornament size and colour as alternative strategies for effective communication in gliding lizards. JOURNAL OF EVOLUTIONARY BIOLOGY, 29 (9), pp.1689-1700.
<https://doi.org/10.1111/jeb.12908>.

Persistent Link:

<http://hdl.handle.net/11343/291454>

File Description:

Accepted version