The Evolution of Diversity: Sexual selection and natural selection on the social signals of gliding lizards.

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THE EVOLUTION OF ORNAMENT DIVERSITY:
Sexual selection and natural selection on the social signals of gliding lizards

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Diversity in animal colour and form can often be attributed to communication signals, which play an important role in species recognition and mate choice. Divergence of signals among populations is therefore thought to be a driver of speciation. This thesis examines signalling processes in the species rich agamid genus, *Draco*, to understand their influence on signal design, signal divergence and ultimately speciation. *Draco* lizards are known as 'gliding lizards', as they have retractable gliding membranes. They communicate with extendable throat-fans, called dewlaps, which are diverse in colour, shape and size among species. Chapter two assesses the importance of dewlap signal design for detection and recognition in *Draco melanopogon*, by presenting free-living lizards with robots displaying dewlaps of different designs. Dewlap design does not affect the latency of signal detection by conspecifics, but once the robot dewlap had been detected, males responded with greater intensity to dewlaps that best resembled the species' typical design, suggesting pattern is important in species recognition. As signal components may evolve differently in populations exposed to different selection pressures, chapter three assess the relationships between the dewlap components (colour and size) and aspects of their environments. Males of different species employ colour contrast and dewlap size as alternative strategies for effective communication, and predation intensity may play a role in which strategy a species employs. Further, correlations between male dewlap components and sexual dimorphism suggest that sexual selection is also a major factor influencing dewlap design. Chapter four shows that the different gliding membrane colouration of two populations of *Draco cornutus* closely match the colours of freshly fallen leaves in their respective habitats as they appear to the visual system of predatory birds. This suggests the populations have diverged in colouration to mimic the colours of local falling leaves and thereby reduce predation by birds. Chapter five tests whether *Draco sumatranus* lizards use their position relative to the sun to enhance the transmission of light through the dewlap, and thus the apparent brightness of their dewlap during display. Lizards are significantly more likely to orientate themselves perpendicular to the sun when displaying, ensuring maximum sun exposure for the extended dewlap. This thesis confirms the centrality of sexual selection, species recognition and predation as major factors influencing signal design in *Draco*, and thereby furthers our understanding of the evolution of ornament diversity.

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For my father, who provided the inspiration,

and for Hugh, my audience of one.

<u>*Acknowledgements*</u>

Abstract

Diversity in animal colour and form can often be attributed to communication signals, which play an important role in species recognition and mate choice. Divergence of signals among populations is therefore thought to be a driver of speciation. This thesis examines signalling processes in the species rich agamid genus, *Draco*, to understand their influence on signal design, signal divergence and ultimately speciation. *Draco* lizards are known as 'gliding lizards', as they have retractable gliding membranes. They communicate with extendable throat-fans, called dewlaps, which are diverse in colour, shape and size among species.

Chapter two assesses the importance of dewlap signal design for detection and recognition in *Draco melanopogon*, by presenting free-living lizards with robots displaying dewlaps of different designs. Dewlap design does not affect the latency of signal detection by conspecifics, but once the robot dewlap had been detected, males responded with greater intensity to dewlaps that best resembled the species' typical design, suggesting pattern is important in species recognition.

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Table of Contents

Chapter One

Introduction

The incredible diversity in colour, form and behaviour of animals has both fascinated and perplexed evolutionary biologists since Charles Darwin first considered differences among species (Darwin 1859). Indeed many of the world's adaptive radiations are characterised by a great diversity of colour or ornaments among species, and explaining the evolution of this diversity is still a central focus today (Boughman 2002; Rundle and Nosil 2005; Grant and Grant 2011). Much of this diversity can be attributed to the aspects of organisms that function in communication, known as signals (Maynard Smith and Harper 2003). Signals play an important role in species recognition and mate choice, which strongly suggests that divergence of signals between populations is a principal driver in speciation (Lande 1981; Endler 1992; Leal and Losos 2010; Maan and Seehausen 2011). The use of signals may therefore contribute not just to the diversity of behaviour and form among species, but to the diversity of species themselves.

There are a few key processes that lead to signal divergence between populations of a species, including genetic drift, sexual selection for signal elaboration, and selection for effective signals in new habitats (Andersson 1994; Boughman 2002). It is suggested that the need for organisms to adapt signals to function effectively in new, heterogeneous

or fluctuating environments may be the most widely influential process for signal

divergence (Endler 1992; Marchetti 1993; Leal and Fleishman 2004; Ritchie 2007; Bro-

Jørgensen 2010). Nevertheless, all of these processes are likely to contribute in part to the

evolution of signal diversity and any subset may act in concert to shape signal phenotype

throughout the evolutionary history of an organism (Endler 1992). Once signals have

diverged, selection to minimise the risk of hybridisation reinforces reproductive isolation

between the populations (Williams and Rand, 1977). To fully understand why signals

diverge we require an in-depth knowledge of both the purpose of the signal and the

signalling process (Endler 1993). In this thesis I aim to examine the processes of

signalling in the agamid lizard genus *Draco*, to better understand the physical and social

factors that influence signal evolution.

Signals take the form of behaviours, ornaments or body colours, and allow the

transfer of information about the signaller to the receiver. This information may be the

signaller's presence, identity, or quality (in terms of body condition or resource holding

potential – Bradbury and Vehrencamp, 2011). Signals have evolved to affect the

behaviour of receivers, such that the fitness of the sender is increased (Maynard-Smith

and Harper 2003). Effective communication is crucial both in an intersexual context – to

gain matings (e.g. Seehausen and van Alphen, 1998) – and in an intrasexual context – to

avert conflict escalation and avoid injury (e.g. Hamilton *et al.*, 2013). The minimum

requirement for effective communication is a signal conspicuous enough to be easily

detected by their intended receivers (Endler 1993). Therefore, signals may be selected for

both detectability and for eliciting the desired response in the receiver (Darwin 1871;

Andersson 1982).

Conspicuousness of visual signals is determined by the properties of the signal (e.g. colour brightness or ornament size), the environmental conditions in which the signal travels to reach the receiver (e.g. ambient light or background colour), and by the perceptual ability of the receiver (e.g. visual acuity and spectral sensitivities – Endler, 2000). There are many alternative ways signals can achieve conspicuousness, such as through the amplification of display movements, ornament size, and the visibility of colours and patterns. However, in most circumstances, signals that are conspicuous to intended receivers also stand out to predators, placing the signaller at a higher risk of predation (Endler 1978; Godin and Mcdonough 2003; Stuart-Fox *et al*. 2003).

The sensory drive hypothesis posits that signals may diverge to maintain conspicuousness in new visual habitats, to the conspecific sensory system (Endler 1992; Boughman 2002). Different aspects of the environment in which signalling occurs affect signal conspicuousness, including habitat light level and spectral quality (Marchetti 1993; Leal and Fleishman 2004; Doucet *et al*. 2007) and the extent of visual noise in the background (Ord *et al*. 2007; Peters *et al*. 2007). This means that signals effective in one habitat may be ineffective in another (Fleishman 1992). Conversely, signals that are effective in one habitat may result in too great a risk of predation to be viable for communication in a new habitat with a different predation regime (Endler 1980; Zuk and Kolluru 1998). In these circumstances, organisms must adapt so that effective communication with conspecifics can be maintained. Consequently, populations that move into new habitats may also diverge in signal design.

Visual signals are complex traits comprised of many different components, for example, the colour of an ornament or its motion in display. Each component may act as a separate axis for signal divergence (Endler 2000; Grether *et al*. 2004). Components

may function in different elements of the communication process (such as detection or quality advertisement) and thus face independent selection pressures (Hebets and Papaj 2005). Alternatively, there may be redundancy in the function of components (e.g. multiple components function in signal detection), but one component is more effective in certain environmental conditions than another. As a hypothetical example, a species' ornament colour and display motion may both have the potential to function in signal detection, but in one habitat the average distances between conspecifics is too great for individuals to distinguish the ornament colour from the background. Instead, this species must rely on display motion for having their signals detected and thus selection for increased signal detectability will act more on display motion and less on ornament colour (Endler 1978; Fleishman 1992). Given the influence of the environment on signal effectiveness, signals of closely related species in different environments may diverge through the enhancement of different signal components (Endler 2000).

As most signalling environments are heterogeneous and environmental conditions may fluctuate – both rapidly (e.g. over the day) and over longer periods – having multiple signal components that are effective in different conditions can allow signals as a whole to maintain conspicuousness (Candolin 2003; Hebets and Papaj 2005). Alternatively, animals may enhance a signal by adapting display behaviour to take advantage of the most effective times and places (Endler and Thery 1996; Peters et al. 2007; Simon 2007). Individuals may only display at times when the risk of predation is low, or in the location that signal will be most reliably detected. For example, species of *Anolis* lizards on Puerto Rico enhance the conspicuousness of their motion display by avoiding visual background noise and only displaying when background vegetation is still (Ord *et al*. 2011). Although the need to signal effectively in complex and changing

environments may promote signal divergence between populations, the ability to behaviourally control signalling in response the environment could potentially reduce selection for signal divergence.

Lizards of the genus *Draco c*ommunicate with a throat-fan, called a dewlap, which is often strikingly coloured and diverse among species (fig. 1.1). There are at least 42 species of *Draco* lizards distributed across southern and eastern Asia (McGuire and Kiew, 2001). *Draco* are aboreal lizards and species are found in diverse habitats from open mangrove forests, urban environments, to primary rainforest (fig 1.2). In general *Draco* lizards show a cryptically coloured and patterned dorsum (e.g. similar patterning to tree bark), which likely functions to reduce detection by predators via surface mimicry (Stuart-Fox *et al*. 2004; Stuart-Fox and Ord 2004). *Draco* are known as the 'gliding lizards'; the only extant squamate genus with large, extendable gliding membranes, referred to as patagia (fig 1.3; McGuire and Dudley 2011). The patagia are supported by elongated ribs that extend allowing the lizards to glide between trees (Russell and Dijkstra 2001). They vary in colour among species considerably, from cryptically coloured to apparently conspicuous (fig 1.4). Both the patagia and the dewlap are only visible when extended (either during gliding or display), and when retracted they are well concealed.

The dewlap is an important component of communication in *Draco* lizards and males and females use it to communicate resource defence and mate attraction (Mori and Hikida 1993). Males, in particular, defend territories from other conspecific males in order to maintain exclusive access to females (Hairston 1957; Alcala 1967; Mori and Hikida 1993; Mori and Hikida 1994). During display the dewlap is extended and retracted at varying speeds, in varying motion patterns, and in many species the dewlap

display is accompanied by 'push ups'. Like the anoles, *Draco* lizards produce broadcast displays, to advertise continued territory ownership to conspecifics in all directions, in addition to displays for individuals in close range interactions (i.e. conflict or courtship – Mori and Hikida, 1994). In most *Draco* species, males appear to signal more frequently than females and possess larger, more conspicuously coloured dewlaps, though I have found this can vary and in some species males and females have very different but equally conspicuous dewlap colours (chapter three).
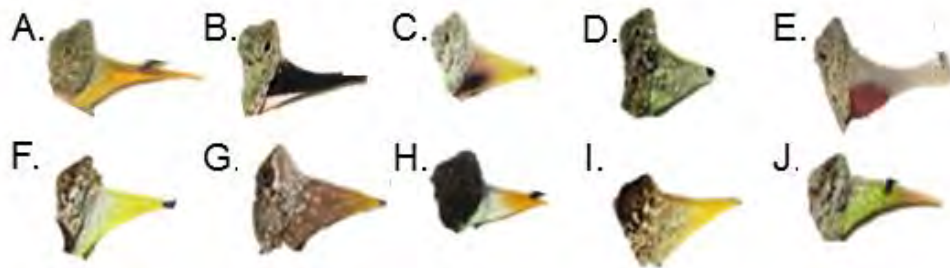
Figure 1.1   Extended dewlap of (A) *Draco quinquefasciatus* (Borneo); (B) *D. melanopogon* (Borneo); (C) *D. haematopogon* (Borneo); (D) *D. bimaculatus* (Philippines); (E) *D. formosus* (Malay Peninsula); (F) *D. sumatranus* (Borneo); (G) *D. reticulatus* (Philippines); (H) *D. cornutus* (Borneo); (I) *D. sumatranus* (Malay Peninsula); and (J) *D. spilopterus* (Philippines).

Figure 1.2   Habitat photographs of (A) *Draco melanopogon* and (B) *D. cornutus*

Figure 1.3   *Draco melanopogon* with left patagia extended.
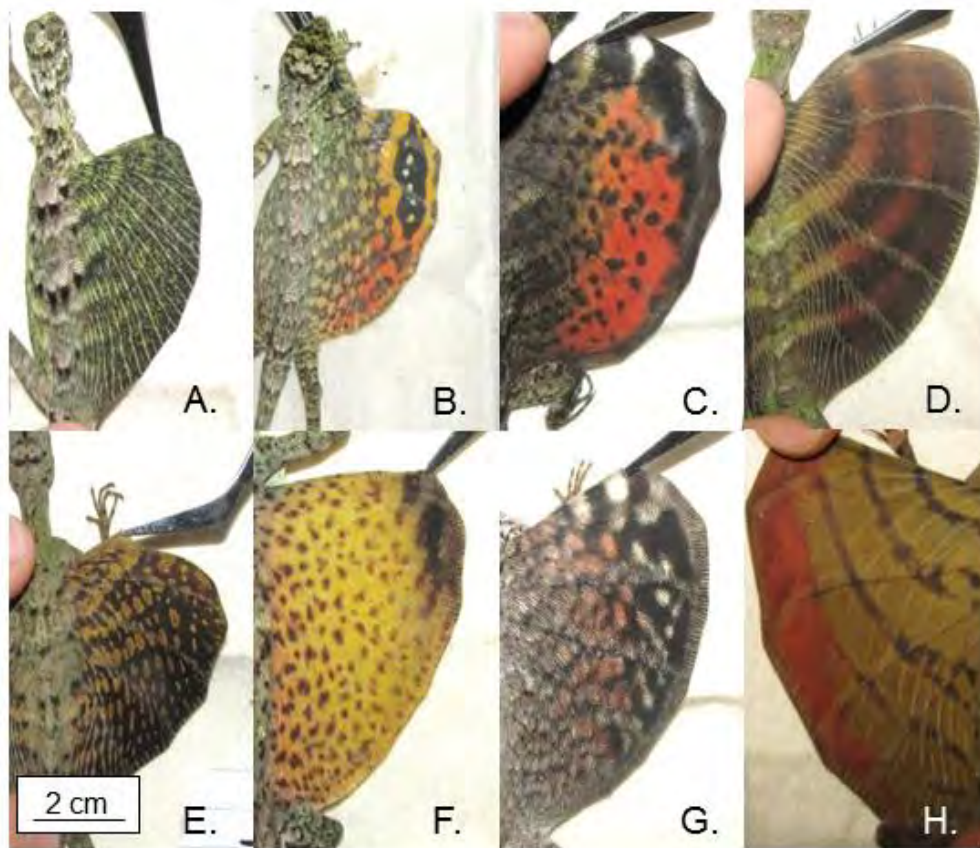
Figure 1.4   Extended patagia of (A) *Draco bimaculatus*; (B) *D. ornatus*; (C) *D. cornutus*; (D) *D. quinquefasciatus*; (E) *D. melanopogon*; (F) *D. spilopterus*; (G) *D. sumatranus*; and (H) *D. formosus*.

Given the uses of the dewlap in scenarios of mate choice and resource competition, the elaboration of the dewlap is likely to be heavily influenced by sexual selection (Andersson 1994). *Draco* species vary markedly in the colour of their dewlaps such that they are species-typical in colour and pattern. As *Draco* species frequently occur sympatrically with one or more congeners (Das, 2010; Grismer, 2011) it is likely that dewlap colour and pattern plays a large role in species recognition – a first step in identifying an appropriate mate or relevant rival (Ryan and Rand 1993) – and thus an essential component of the communication process. For these reasons *Draco* is an ideal genus for studying selection on visual signalling under different regimes. Despite this, the

only studies examining *Draco* signalling behaviour to date have been descriptive. For example, papers by Mori and Hikida (1993; 1994) describe the diurnal activity of one population of *Draco sumatranus*, including signalling and territorial behaviour. But this thesis therefore exhibits the first studies on the evolution of the *Draco* dewlap display.

In chapter two I use robotic playback of realistic *D. melanopogon* display, with different dewlap pattern treatments, to investigate the function of dewlap colouration. I test two non-mutually exclusive hypotheses: (1) that colour and pattern contrast enhances signal detection; and (2) that the specific colour pattern of the *D. melanopogon* dewlap facilitates species recognition. I also assess sex differences in responses to the dewlap treatments as males and females may respond to different components in multicomponent signals (Hebets and Papaj 2005; Searcy and Nowicki 2005).

Employing phylogenetic comparative methods in chapter three, I test whether multiple dewlap traits of different *Draco* species are enhanced together in response to selection for signal conspicuousness, or whether they function as alternative strategies, by examining the relationship between colour and brightness contrast of the dewlap against the background and its area relative to body size. As these traits are likely to be under sexual selection for elaboration, I also test whether they were associated with potential indicators of sexual selection. Finally, to understand how the relationships between dewlap traits may be influenced by environmental factors, I test whether dewlap conspicuousness is predicted by habitat light or potential predation intensity.

In a further investigation of *Draco* colouration, in chapter four I study two populations of *D. cornutus* which differ markedly in the colour of their patagia. They also differ in local vegetation type (mangrove forest versus lowland rainforest) and

consequently, the colour of falling leaves. Though the bright coloured of the patagia are often thought to be selected for conspicuous signalling, I test the idea that instead the colouration is selected for crypsis, by determining whether the colours of falling leaves in each habitat are distinguishable from the colours of the patagia to the spectral sensitivities of a predatory bird.

As some environmental conditions, such as light intensity, may enhance the visibility of colour signals, in chapter five I test the idea that *Draco sumatranus* lizards use their position relative to the sun to enhance the apparent brightness of their dewlap during broadcast display to conspecifics. Finally, in chapter six I synthesize my findings and present the broader relevance of my work to our general understanding of the evolution of signal diversity.

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Chapter Two

Colour pattern facilitates species recognition but not signal detection: a field test using robots

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Behavioral Ecology (In Review)

Abstract

There are many factors that affect signal design, including the need for rapid signal detection and the ability to identify the signal as conspecific. Understanding these different sources of selection on signal design is essential to explain the evolution of both signal complexity and signal diversity. We assessed the relative importance of detection and recognition for signal design in the black-bearded gliding lizard, *Draco*

melanopogon, which uses the extension and retraction of a large, black and white dewlap (or throat fan) in territorial communication. We presented free-living lizards with robots displaying dewlaps of different designs that varied in the proportion of the black and white components. We found no effect of dewlap colour or design on the time it took for a lizard to detect the robot, consistent with the view that initial detection is likely to be primarily elicited by movement rather than specific colour pattern. However, males (but not females) responded with a greater intensity to the dewlap treatment that most resembled the natural dewlap colour and design of the species. Furthermore, males were more likely to display to any dewlap colour in the presence of a neighbour. These results suggest that colour pattern may play an important role in species recognition, but does not influence the initial detection of the signal. Importantly, our results also highlight that factors unrelated to discrimination, such as social cues and individual motivational state, may affect responses to species identity cues.

Introduction

Visual signals used in intraspecific social displays are often complex, comprising multiple components, such as the size of a morphological structure, its colour and pattern, and accompanying behavioural displays (Hebets and Papaj 2005). Each component may be under selection for both the efficacy with which it is detected by the intended receiver and the information it conveys (Endler 1992; Andersson 2000; Maynard Smith and Harper 2003; Searcy and Nowicki 2005). An effective visual signal must first be easily detected by the receiver's visual system in the environment in which the display is typically given. Once the signal is detected, the receiver must recognise the signal as

conspecific (Cronin 1993; Andersson 1994) and may assess additional information encoded in the signal such as signaller quality (Ryan and Rand 1993a; Hebets and Papaj 2005). Understanding the relative contribution of selection for efficient detection and selection for information content on various signal components is critical to explain the evolution of both signal complexity and signal diversity (Espmark et al. 2000; Fleishman 2000; Fleishman et al. 2015).

Detectable visual signals are those with colours, patterns or movements that stand out to receivers in the habitat in which the signal is typically given (Dawkins and Guilford 1997). In the specific case of colour, the conspicuousness of a visual signal can be dependent on its contrast against the environmental background, where greater colour contrast results in greater conspicuousness (Fleishman, 1992; Fleishman & Persons, 2001; Stuart-Fox *et al.*, 2003; Hebets & Papaj, 2005). Colour contrast can be further enhanced in multicomponent colour signals through increased internal contrast between colour patches within the signal (Marshall 2000; Bohlin et al. 2008). This additionally ensures that the signal is conspicuous against variable backgrounds (Renoult et al. 2015). However, the appearance of the signal will depend on the size and configuration of individual colour patches, in relation to the distance of the receiver, as the receiver's visual acuity determines whether adjacent colour patches can be distinguished (Endler 1987; Cronin et al. 2014). Many species also combine conspicuously coloured ornaments with display motion, which helps capture the attention of conspecifics in complex visual environments by triggering the 'visual grasp reflex' – an automatic response to orientate towards movement in the periphery of the visual field (Fleishman 1992; Peters and Evans 2003a; Steinberg and Leal 2013). However, the extent to which conspicuous colouration

enhances signal detection (i.e. probability of triggering the 'visual grasp reflex') is unclear (Persons et al. 1999; Fleishman and Persons 2001).

Once the receiver detects and orients towards a signaller, the signal must be recognised as 'conspecific'. For example, females will assess a signal for conspecific cues in order to avoid wasteful heterospecific matings (Servedio and Noor 2003). Territorial males may also evaluate these cues to avoid aggressive interaction and minimise energy expended on defending a territory or other resource against heterospecific males with which they are not in direct competition for reproduction (Servedio & Noor, 2003; Gröning & Hochkirch, 2008; but see Ord King, L. & Young, A. R., 2011, Drury *et al.*, 2015). Signals important for species recognition are expected to be under stabilising selection, whereby signals that deviate from the species typical signal are selected against (Pryke and Andersson 2008).

Taken together, both detection and species recognition are important aspects of the signalling process (in addition to subsequent mate or rival assessment) and different components of multicomponent signals may function to enhance detection, species recognition or both. In this study, we tested how the design of a multicomponent ornament functions in signal detection and recognition in a lizard. The black-bearded gliding lizard, *Draco melanopogon,* from Southeast Asia is a good model for addressing questions on signal detectability and species recognition because they possess a large extendable throat fan or dewlap that is species-typical in colour and pattern. The species also occurs syntopically with as many as four other congeners at many locations (*D. formosus*, *D. quinquefasciatus, D. sumatranus* and *D. maximus*; Das, 2010; Grismer, 2011). Male *Draco* lizards defend territories from other conspecific males to maintain exclusive access to females (Hairston 1957; Alcala 1967; Mori and Hikida 1993; Mori

and Hikida 1994), and the extension of the dewlap is central to communicating

aggression in territory defence (indeed, it appears to be the only social signal used in

Draco melanopogon, whereas in other species a push-up or head-bob display is also

performed; D. A. Klomp & T. J. Ord, personal observation). *Draco melanopogon* males

have long black dewlaps with a bright white base, which provides a strong achromatic

contrast both internally and against the background (fig. 2.1). The high achromatic

contrast of the dewlap may be important in initial signal detection (initiation of the visual

grasp reflex) because the achromatic visual channel is associated with the perception of

movement (Kelber et al. 2003; Osorio and Vorobyev 2005). Furthermore, the dewlap of

D. melanopogon differs by a lesser or greater degree from those of the four sympatric

species at our field site—*D. formosus*: off-white and red dewlap; *D. quinqufasciatus*: a

pale yellow dewlap; *D. sumatranus*: a bright yellow and white dewlap; *D. maximus*: a

black dewlap with white rim—which implies dewlap colour pattern could also be

influential in species recognition and that deviating away from the population average

design could begin to overlap with one or more congeners.

We used robotic playback of realistic *D. melanopogon* displays, with different

dewlap pattern treatments, to investigate the function of dewlap colouration and infer its

potential adaptive significance. For this purpose our robots included only the moving

dewlap to circumvent any species identity cues that might be associated with morphology

(e.g. body size or shape; Hankison & Morris, 2003; Ord & Stamps, 2009). We tested two

non-mutually exclusive hypotheses: (1) that achromatic contrast (both internal

achromatic contrast and contrast with the background) enhances signal detection;
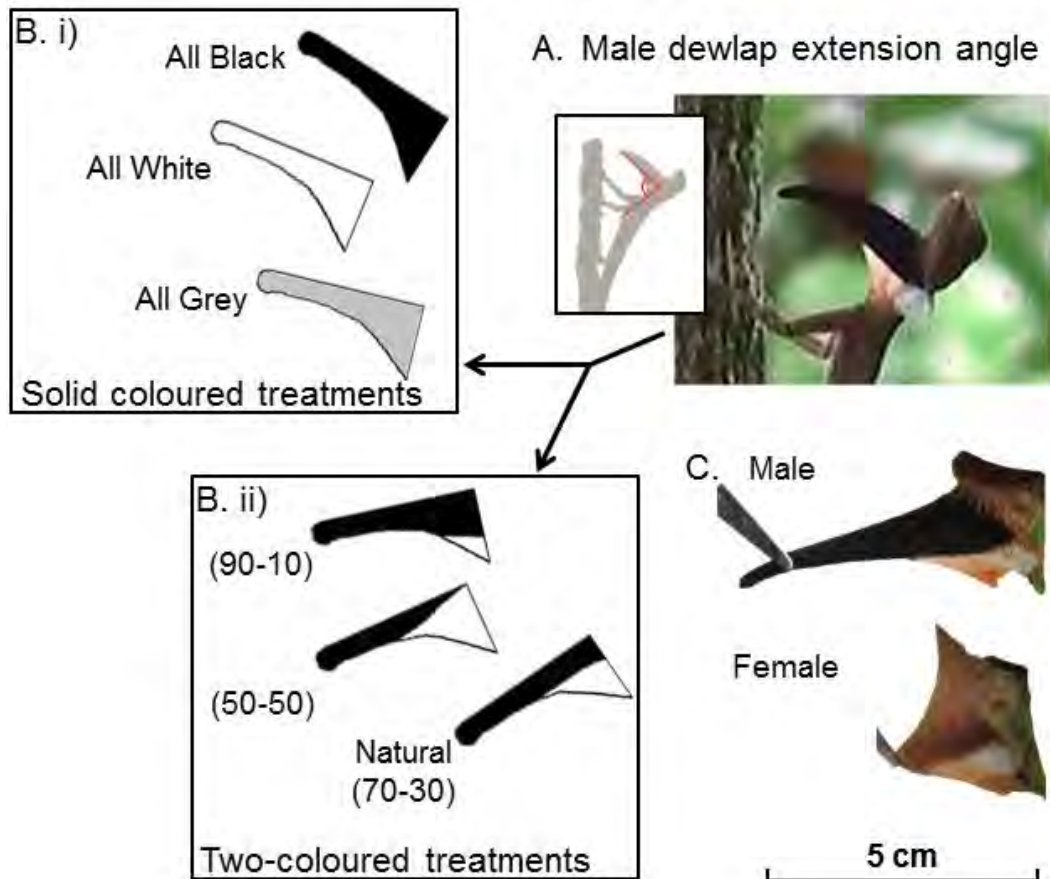
Figure 2.1 (A) Male *D. melanopogon*, dewlap naturally extended (image a still from behavioural trials) and the angle of dewlap extension as measured from still; (B) robot, dewlap treatments (B)i. solid colour and (B)ii. two-coloured); and (C) artificially extended dewlaps of a male and female *D. melanopogon*.

and (2) that the specific colour pattern of the *D. melanopogon* dewlap facilitates species recognition. We presented territorial males in the wild with six different treatments in which we varied the proportion of black and white on the dewlap (including a solid grey treatment) and estimated achromatic contrast using models of *Draco* vision, taking into account the distance of the receiver. The first hypothesis predicts that treatments with higher achromatic contrast should be detected sooner by conspecific male and female lizards (i.e. receivers orient toward the robot more quickly). If colour pattern is unimportant for detection, then we expect no difference in detection time between treatments. The second hypothesis predicts that lizards will be more likely to respond (i.e. display to the robot), to respond sooner or with greater intensity to the most population-typical (or 'natural') dewlap colour pattern, while responding least to the treatments that deviate away from the population-typical dewlap colour pattern. Additionally, presenting dewlaps that varied along a gradient from more to less similar to the population-typical design allowed us to assess possible stabilising selection on dewlap pattern. We also assessed sex differences in responses to the dewlap treatments as different receivers may exert variable selection on multicomponent signals (e.g., males and females may attend to different cues within multicomponent signals; Hebets & Papaj, 2005; Searcy & Nowicki, 2005).

Methods

Quantifying the colour and behaviour of free-ranging lizards

We studied a wild population of *D. melanopogon* at Ulu Gombak forest reserve, north of Kuala Lumpur (Peninsula Malaysia) between May 14 and May 22, 2011, to collect baseline habitat colour, and behaviour data for visual modelling of dewlap

conspicuousness, programming of the robot and creating its dewlap treatments. The dewlap colours of five free-living adult male lizards 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). The spectrometer's probe holder limited the measurements taken to a standard distance of 1 cm from the surface, and the angle of surface illumination and reflectance measurement to a 45° angle, relative to the surface, following (Endler 1990; Stuart-Fox et al. 2003). Background colour can be classified into four groups (green, brown, dark brown/black and white/ pale green), covering the predominant background colours of leaves, bark and lichen. A minimum of 10 measurements for each colour group were also taken with the spectrometer, and averaged for use in visual modelling (see appendix to this chapter). 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 framing the lizard's perch to the side as conspecifics are likely to view the signal perpendicular to the lizard (see Chapter 4). These photographs captured representative background vegetation colour and density (fig 2.2), and were used to calculate the proportions of each colour in the background (e.g. bark, lichen, ground, fallen leaves, standing foliage and other vegetation), using a 1 cm^2 grid overlaid on the photographs (see Klomp *et al.*, 2014).

Side welling absolute irradiance (90° from the ground) was measured with a JAZ–ULM–200 spectrometer and cosine corrected irradiance probe (Ocean Optics) from the position of capture facing away from the sun to not saturate the sensor, as described in Klomp *et al.* (2014). We used side-welling irradiance rather than downwelling irradiance as this better represents illumination of the dewlap.

Figure 2.2 Photographs framing the lizard's perch to the side (indicated by the yellow flag), capturing representative background vegetation colour and density.

Details of visual modelling to estimate the achromatic contrast of natural dewlaps and dewlap treatments are given in the appendix to this chapter.

In order to mimic the movement of the dewlap during its display sequence, we collected data on display bout duration, interval length and dewlap extension frequency, angle and speed. These data were collected from videos of 18 free-living lizards displaying recorded using a Sony Handycam HDR-XR550VE digital camcorder mounted on a tripod. Following video recording we calibrated the image by placing a ping-pong

ball of known size attached to an extendable pole at the same perch site from which the lizard was recorded to have displayed (see Ord *et al.* 2007). We were then able to use stills from the size-calibrated footage to measure dewlap length, area, natural extension angle and the proportions of each colour in the dewlap, using ImageJ (Abramoff et al. 2004). We obtained information on the speed and temporal pattern of the dewlap extension using the MATLAB based program 'Analysis of Image Motion' v 1.2 (Peters *et al.*, 2002) and frame-by-frame analysis using video time codes from QuickTime clips of video recordings (see Ord *et al*. 2010). Only stills where lizards and extended dewlaps are orthogonal to the camera were used in size measurements.

Robot construction

We constructed three programmable robots, each consisting of a plain plywood box from which a dewlap extended and retracted on a simple wire mechanism controlled by a stepper-motor powered by several batteries (fig. S2.1). The robots had Arduino Pro Mini microcontrollers that we programmed with the population typical speed, dewlap extension angle and temporal movement patterns of *D. melanopogon* (fig. S2.2), such that only the colour and pattern of the dewlap varied among our treatments (table S2.1, S2.2). The robot boxes were mounted on poles with quick-release pads that connected to a tripod below to enable the robot to be presented at a height (3.2 m) comparable to the natural perch height of the lizards. The colour of the plywood box was designed to blend in with the background, by closely matching the average spectra of the habitat (fig. S2.3).

Experimental dewlap treatments

We varied the achromatic component of the signal by altering the proportion of black and white across five dewlap types, with a sixth treatment included of solid grey. Specifically, three treatments were solid colours—black, white and grey (20% reflectance)—and therefore lacked internal contrast, while the remaining three were two-coloured treatments—70% black and 30% white (the population-typical), 50% black and 50% white, and 90% black and 10% white (fig. 2.1)—that varied in internal contrast. The black and white colours for all treatments matched the natural black and white colours of the *D. melanopogon* dewlap (fig. S2.3). These six treatments were chosen to provide variation in achromatic contrast (internal contrast and contrast with the background) and gradual variations along a scale from population-typical, or 'natural', to unnatural.

Appearance of dewlap treatments to receivers

Of the solid coloured dewlap treatments, both white and black produce high achromatic contrast against the background while the grey achromatically matches the background very closely (table 2.1). For the two-coloured treatments, black and white together in the dewlap produces a high achromatic internal contrast (table 2.1), which increases the conspicuousness of the signal, so long as the receiver is close enough to distinguish the two colours (Marshall, 2000; Bohlin *et al.*, 2008; McLean *et al.*, 2014). Whether the black and white components can be distinguished depends on the size of the colour patches and the distance and visual acuity of the receiver (Endler 1987; Fleishman 1992).

Table 2.1 Achromatic contrast against the background and internal contrast of the black

and white colour patches, in Just Noticeable Differences (JND), for natural dewlaps and

dewlap treatments.

	mean JND (range)*
Viewed close enough for colour patches to be resolved:	
i. Natural dewlap, contrast against the background	
black	33.25 (25.36 - 42.67)
white	24.28 (21.84 - 27.51)
overall, weighted	30.56 (24.30 - 37.60)
ii. Dewlap treatments, weighted contrast against the background	
solid black	39.02
solid white	36.00
solid grey	3.21
70% black 30% white (natural)	38.11
50% black 50% white	38.65
90% black 10% white	38.72
iii. Achromatic contrast between internal colour patches (black and white)	
natural dewlap	60.76
two-coloured dewlap treatments	75.02
Viewed from a distance, colour patches blend together:	
iv. Natural dewlap, contrast against the background	5.16 (2.98 - 7.33)
v. Dewlap treatments, contrast against the background	
70% black 30% white (natural)	13.40
50% black 50% white	22.61
90% black 10% white	7.05

* JND values are only indicative of relative differences in achromatic contrast - see appendix for
extended discussion.
** Weighted contrasts against the background for dewlap treatments are all approximately the same
except for solid grey because the contrast of the solid white and solid black components are very similar.
However, contrasts of two-coloured treatments are expected to be higher than solid colours when the
two colour patches can be resolved because of high internal contrast.

When colour patches are indistinguishable from one another, either because the receiver's visual acuity is too low to resolve small colour patches or the receiver is at too great a distance from the signaller, colour patches appear as a 'blended' average weighted by the relative proportions of the constituent colours. This is important because where the colour patches are distinguishable the treatment is more conspicuous than when are not distinguishable– both because of the internal contrast and because both black and white are individually more conspicuous than an average grey (see *'Dewlap treatments, weighted contrast against the background'* table 2.1).

Dewlap treatments – predictions

Assuming that the black and white components of the signal can be resolved, in terms of signal detectability, we would predict that the 50% black 50% white treatment should be detected most readily, followed by the natural and the 90% black 10% white treatments, followed by the solid black and solid white treatments, and that the solid grey treatment would be the least readily detected.

In terms of species recognition, we predict that the natural and the 50% black 50% white treatments will appear most similar to a *D. melanopogon* dewlap and thus will illicit the greatest response from conspecifics. The solid black and the 90% black 10% white treatment resemble the primary black component of the *D. melanopogon* dewlap, but with no or minimal white, and thus we predict that they will elicit the next greatest response. Finally, we predict the least response to the solid white and grey dewlap treatments, which least resemble the natural dewlap. If there is strong stabilising selection to only respond to conspecifics (i.e. heterospecific interaction is particularly costly) then we expect little to no response to the treatments which deviate from the population

typical dewlap (i.e. natural treatment). In our experiments, robots were presented at a range of distances (1.9 - 9.5 m, table S2.1) and under some circumstances (e.g. at relatively great receiver distances), the constituent colour patches may appear as a 'blended' average. In this case, the natural treatment would appear similar to the solid grey treatment (see fig. S2.3). Therefore, the natural dewlap treatment, together with the solid grey, would be least detectable (see table 2.1) but should elicit a similarly strong response once detected.

Field robot playback experiments

We returned to the same field site at Ulu Gombak between June 17 and July 31, 2013 and presented the robots with different dewlap treatments to free living *D. melanopogon*. Robots were positioned at approximately 5 metres from the focal lizard (fig. S2.4) and away from nearby trees. This was done because previous studies have suggested that lizards may respond to any stimulus, irrespective of its conspecific or heterospecific cues, simply because it is positioned in an area of the environment that is typical for a conspecific male rival or mate (Ord & Stamps 2009).

The robots were programmed with an initial 7-minute no-display period to allow the lizard to recover from any disturbance experienced during the set-up of the robot in its immediate environment. Focal lizards were video recorded at a distance of at least 6 metres (and at least 5 metres away from the robot). To prevent further disruption of the lizard, the observer remained entirely still and quiet for the duration of the trial. Setting up in the same way for each trail meant that the initial disruption to the lizard was consistent across all trails and treatments. The position of the robot relative to the focal lizard was recorded and this allowed us to be confident about the direction in which the

focal lizard would need to look in order to be orientating toward the robot. Video recording continued once the robot began to display for 5 minutes, after which the presentation was terminated. Playbacks were made to 218 lizards. The trees on which focal lizards were found were flagged to ensure that each new trial was out of visual range of all previous trials.

During filming we noted the presence and location of any neighbours as well as species and sex, in a 10 metre radius from the focal lizard. As ambient light level can influence detectability of visual signals (Mottram 1916; Endler 2000), immediately following each playback trial we measured light level at the site of first display using a LI-250A light meter fitted with a LI-190SA Quantum Sensor (LI-COR, Inc.). The average of two light readings taken over a 15-second period with the sensor positioned perpendicular to the ground was used to approximate the amount of light that would enter a lizard's left and right eye. At the end of the trial, we then measured the distance between the robot and the lizard and the distance between the lizard and any neighbours that were seen, using a measuring tape.

Analysis and statistical methods

All footage was reviewed in real-time using the event recorder 'Jwatcher' (version 0.9 – Blumstein & Daniel, 2007). We recorded the time it took for the lizard to move its eye towards the robot ('latency to orientate'), as per Fleishman (1992). We then recorded whether or not the lizard displayed once detection was assumed to have occurred ('display post orientation') and, for those that did display, the time it took for the lizard to start to display ('latency to display'). Finally, we recorded the overall display level as the number of dewlap extensions in a 2.5 minute period from the first display ('number of

displays'), which represents the intensity of the response of individuals to the robot stimulus. Two lizards that took over 5 minutes to orientate to the robot were excluded from the analysis.

We tested the effect of dewlap treatment on each variable using generalized linear models in R version 3.0.3 (2014-03-06). The variables 'latency to orientate' and 'latency to display' were modelled with a Gamma error distribution and log link function because they are strictly positive and continuous, but left-skewed. The variable 'display post orientation' was either 'yes' or 'no', and thus modelled with a binomial distribution, and 'number of displays' was modeled using a negative binomial distribution (as count data that was over-dispersed), following Zuur *et al.* (2013).

We then compared the computed values of AICc (Akaike's Information Criterion, corrected for small sample size; Akaike (1974), Burnham & Anderson (2002)) and their relative weights for a set of models in which predictor variables differed. To determine the best model to explain a lizard's detection time (latency to orientate) we assessed the relative support of models including dewlap treatment, robot distance from the focal lizard and light level as well as null model (intercept only). As we expect that the detection of different colours and patterns to be worse at greater distances and with lower light levels, we also included models with the interaction of dewlap treatment with robot distance and dewlap treatment with light level in the candidate set. Additionally, recent work by Nava *et al.*, (2009) found sex differences in the likelihood of response to motion signals in the Sagebrush lizard (*Sceloporus graciosus*), so for this set of models we also included 'sex' as a factor on its own, as well as with the interactions between sex and treatment, robot distance and light.

To determine the best-supported model for the effect of dewlap treatment on each of the lizard 'response' variables (i.e. 'display post orientation', 'latency to display', and 'number of displays') we compared AICc model values, weights and effect sizes between a set of candidate models which included robot distance from the focal lizard, the presence (or absence) of neighbours, and a null model. Again, as responses to a stimulus can be affected by social factors such as the sex of the receiver, the distance to the stimulus and the presence of other observers, we also included the interaction of dewlap treatment with sex, robot distance and the presence of a neighbour in this candidate set.

Results

Latency to orientate

Male and female *D. melanopogon* lizards detected the robot stimulus with similar latency, with none of the models that included 'sex' as a factor ranking highly (table 2.2). The best supported models were those that included an interaction of dewlap treatment with robot distance and the dewlap treatment considered alone. However, both models had low effect sizes and there were no obvious patterns for treatment across different distances in plots of the data (fig. 2.3). The 'all white' treatment seemed to have been detected with slightly longer latencies at a distance, which might account for the treatment by robot distance model ranking highly. Regardless, overall detection times were generally comparable across all treatments suggesting that all dewlap patterns were similarly detectable.

Display response following detection

In assessing the salience of the different dewlap treatments to *D. melanopogon* males and females, we first looked at the factors affecting whether or not an individual displayed to robot stimuli. Dewlap treatment had little effect and instead males were more likely to display to any treatment in the presence of a neighbour (table 2.3i, fig. S2.5). Second, latency to display was not well predicted by any of the candidate models and the intercept-only model ranked the highest for both males and females (table 2.3ii). Finally, there was a strong effect on the overall intensity of response (number of dewlap extensions performed by focal lizards). The model that included an interaction term between dewlap treatment and sex ranked the highest of all models considered and was supported by a large effect size (table 2.3iii). More specifically, males displayed the most to the population-typical dewlap pattern (fig. 2.4A), whereas the intensity of response in females was generally low and unrelated to dewlap pattern (fig. 2.4B).

Table 2.2 Candidate model set for detection of the robot ('latency to orientate'; N = 218).

Compelling models with ΔAICc ≤ 2.0 are highlighted in bold.

Model	AIC_c	ΔAIC_c	AIC_W	F (effect size)
intercept only	1830.27	2.94	0.08	
sex	1830.40	3.06	0.08	1.23
treatment	**1827.74**	**0.40**	**0.30**	**1.84**
treatment * sex	1833.41	6.08	0.02	0.77
robot distance	1832.21	4.87	0.03	0.07
robot distance * sex	1831.02	3.69	0.06	1.99
light	1832.28	4.94	0.03	0.02
light * sex	1833.44	6.11	0.02	0.63
treatment * robot distance	**1827.33**	**0.00**	**0.36**	**1.76**
treatment * robot distance * sex	1834.15	6.82	0.01	0.86
treatment * light	1834.83	7.50	0.009	0.69
treatment * light * sex	1849.40	22.07	0.000006	0.34
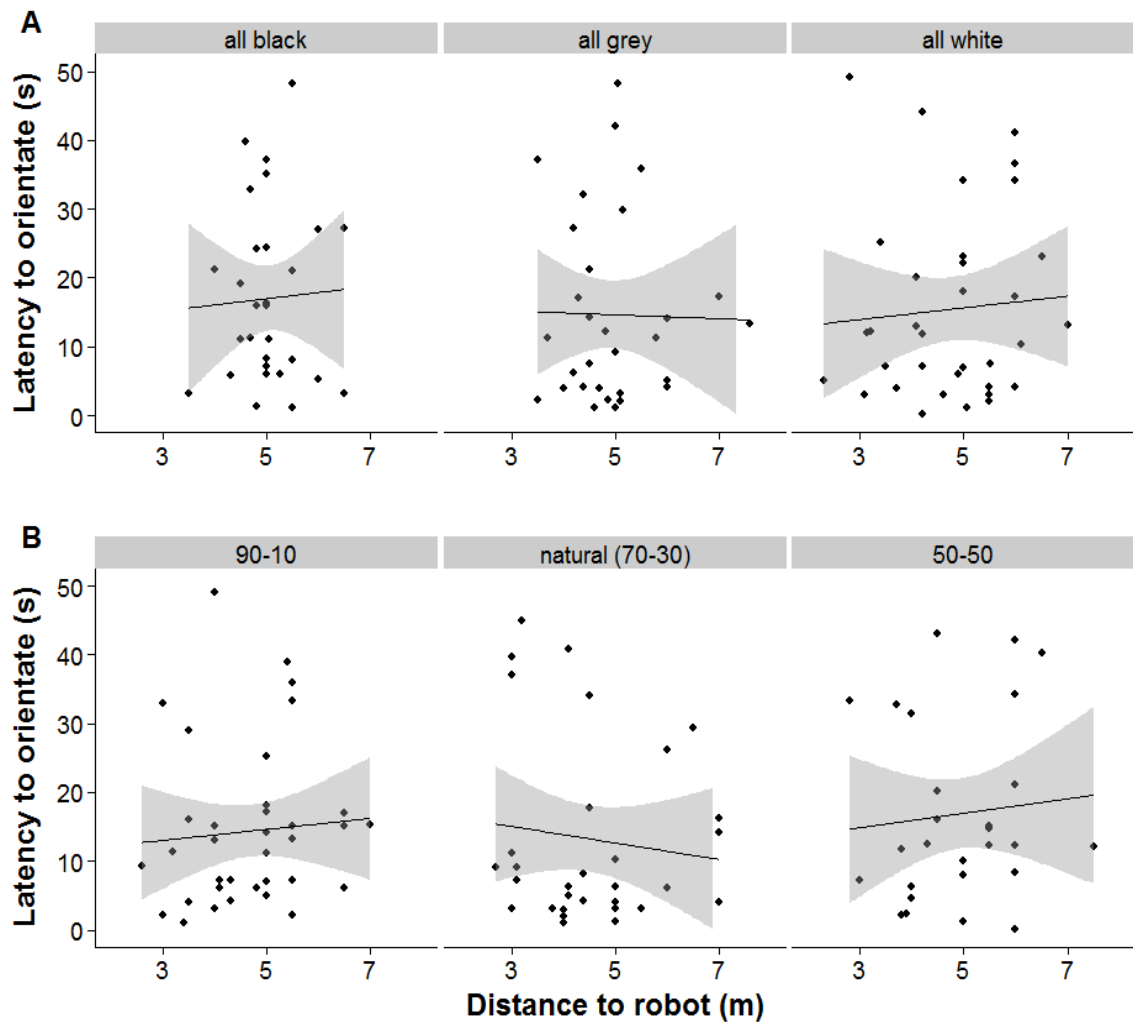
Figure 2.3 Latency to orientate to each treatment as a function of robot distance from the focal lizard (males and females combined), (A) solid coloured treatments and (B) two-coloured treatments. Each dot represents the response of an individual lizard to the robot. Trend lines represent the mean orientation time as a function of robot distance, with grey bands representing 95 % confidence intervals.

Table 2.3 Candidate model sets for response to the robot. Compelling models with

ΔAICc $\leq$ 2.0 are highlighted in bold.

Model	AICc	ΔAIC	AIC_W	F (effect size)
i. Display post orientation (yes/no, $N = 218$)				
intercept only	298.44	6.96	0.02	
sex	**292.39**	**0.91**	**0.34**	**8.16**
treatment	302.86	11.38	0.002	1.14
treatment * sex	305.46	13.98	0.0005	0.40
robot distance	300.55	9.07	0.006	0.00
robot distance * sex	295.72	4.24	0.06	0.86
neighbour present	297.50	6.02	0.03	3.06
neighbour present * sex	**291.48**	**0.00**	**0.54**	**0.15**
treatment * robot distance	309.30	17.82	0.00007	1.13
treatment * robot distance * sex	312.49	21.01	0.00001	2.16
treatment * neighbour present	309.37	17.89	0.0007	0.59
treatment * neighbour present * sex	320.90	29.42	0.0000002	0.20
ii. Latency to display ($N = 93$)				
intercept only	**964.12**	**0.00**	**0.46**	
sex	966.23	2.12	0.02	0.004
treatment	970.77	6.66	0.02	0.82
treatment * sex	979.95	15.83	0.0002	0.63
robot distance	966.12	2.01	0.17	0.14
robot distance * sex	970.02	5.90	0.02	0.35
neighbour present	966.22	2.11	0.16	0.01
neighbour present * sex	970.29	6.17	0.02	0.13
treatment * robot distance	981.34	17.22	0.00008	0.35
treatment * robot distance * sex	989.65	25.53	0.000001	1.37
treatment * neighbour present	978.08	13.96	0.0004	1.07
treatment * neighbour present * sex	985.58	21.46	0.00001	2.56

iii. Number of displays in 2.5 min post initial display (*N* = 64)

intercept only	414.31	15.53	0.0004	
sex	406.15	7.37	0.02	11.10
treatment	410.80	12.02	0.002	3.05
treatment * sex	**398.78**	**0.00**	**0.86**	**2.77**
robot distance	414.96	16.18	0.0003	1.48
robot distance * sex	403.81	5.03	0.07	3.30
neighbour present	416.35	17.57	0.0001	0.07
neighbour present * sex	409.81	11.03	0.003	0.34
treatment * robot distance	417.86	19.08	0.00006	1.07
treatment * robot distance * sex	405.15	6.37	0.04	2.27
treatment * neighbour present	419.16	20.38	0.00003	0.68
treatment * neighbour present * sex	410.61	11.83	0.002	1.54
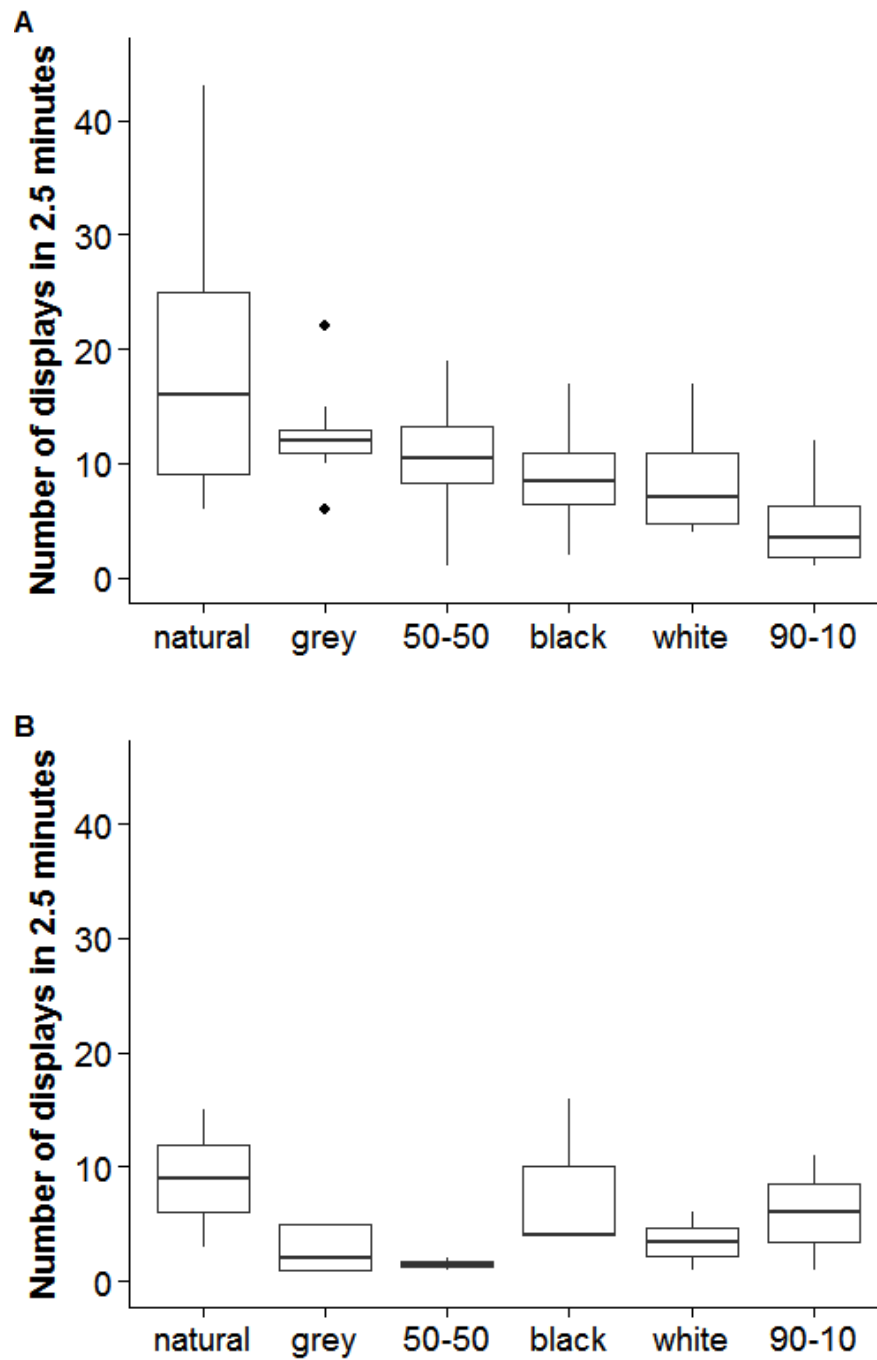
Figure 2.4   Boxplot showing the number of dewlap displays performed by lizards in 2.5 minutes following detection for (A) males and (B) females.

Discussion

We examined the possible functions of the black and white components of a visual ornament, the dewlap, in *Draco melanopogon* to shed light on the evolution of signal complexity and signal diversity in gliding lizards more broadly. There has been an extensive radiation of this single genus throughout Southeast Asia, resulting in over 40 recognised species (McGuire and Heang 2001), all of which differ in some aspect of the colour and pattern of the dewlap. Given the range of habitats occupied by different species and the frequency of sympatric occurrence, differences in dewlap design could reflect differences in signal detection requirements or the need for improved species recognition.

Despite large differences in the computed conspicuousness of the achromatic contrast of our dewlap treatments, our experiment revealed that dewlap pattern had little impact on detection under the same environmental conditions that *D. melanopogon* communicate with one another. The achromatic visual channel is known to be associated with the perception of movement (Fleishman 2000; Kelber et al. 2003; Osorio and Vorobyev 2005), but the *D. melanpogon* visual grasp response appears to be activated by the motion of the dewlap and not enhanced by dewlap colour. This is consistent with the argument that signal detection in visually communicating species relies more on conspicuous movement—the way in which the visual signal is presented to social partners—rather than colouration per se (Fleishman 1992). In our system of lizards, the dewlap is rapidly extended and retracted in repeated bouts of display. This dynamic aspect of the dewlap display was consistent across all of our treatments. Our results therefore suggest that selection for efficient detection has not played a large role in the

evolution of colour signals, and signal detection is probably dependent on the speed and repetition of movement associated with the dewlap display. Similar findings have been found for other lizards that use large conspicuously coloured dewlaps for territorial communication (Caribbean *Anolis* lizards; Ord & Stamps 2008). Though the movement patterns of dewlap display are mostly species typical, some variation between individuals exists (Ord, Klomp & Summers, unpublished data) and this could potentially be an important axis for sexual selection.

Species recognition, however, does appear to play a role in colour signal evolution in *Draco*. Species recognition is important for reducing costly heterospecific aggression in many animals (Lorenz 1962; Losos 1985; Alatalo et al. 1994). We found that males responded with the greatest intensity to the population-typical dewlap design, suggesting that male lizards identified the stimulus as a dewlap belonging to an individual with whom they are in competition for resources (i.e. most likely a conspecific male). Additionally, focal lizards responded to the grey dewlap treatment with a similar intensity to the natural dewlap treatment, which appear similar when the two colours cannot be resolved and instead appear as a 'blended average'. This suggests that lizards may not be able to resolve the two colours of the *D. melanopogon* dewlap in natural conditions for distances at which broadcast displays are typically given. Instead, the two colours may be more important in close-range interactions (during which the black and white components may be resolved), such as aggressive competition and courtship. Given that dewlap stimuli deviating away from the species norm (apart from grey) were clearly less evocative to males and would presumably be signals less effective at maintaining territory boundaries, our data also suggest that dewlap design is probably subject to stabilising selection. Nevertheless, males did respond to non-species typical

dewlap designs, albeit at lower response intensities. Whether or not this reflects some level of selection resulting from interspecific territoriality among sympatric congeners that overlap in resource use (e.g., Orians & Willson, 1964; Cody, 1969; Grether *et al.*, 2009; Peiman & Robinson, 2010) is unclear and requires further investigation.

We also found no effect of treatment on whether or not focal lizards responded to the robot stimulus in the first place, nor on the time it took for lizards to respond. That is, colour pattern only seems to affect the level of response once a male has decided to respond. Whether or not animals ultimately decide to respond to conspecific and non-conspecific signals can be affected by many factors and is a separate question to whether those animals discriminate differences in the signals presented (e.g., see Ord & Stamps (2009), Ord *et al.* (2011) and Drury *et al.*, (2015b) for discussion). For example, our experiment revealed that the presence of a neighbour during robot presentations increased the likelihood of the focal lizard responding to the robot. This is consistent with many other taxa, in which the presence and sex of a neighbour has been shown to influence mating and territorial behaviour (Matos and McGregor 2002; Striedter et al. 2003; Wich and Sterck 2003; Matos and Schlupp 2005). It suggests that recent or ongoing activity in the surrounding social environment can have an important motivating influence on an individual's decision to respond to any form of social stimulus.

Though species recognition is important in preventing costly heterospecific mating (Servedio and Noor 2003; Gröning and Hochkirch 2008) we did not find the same strong effect for females. Female reproductive status and motivation may strongly influence female response to a conspecific male signal (Shine 1980), so a lack of response does not imply that females are not using the dewlap signal in species recognition. Female receptivity to males is also likely to be influenced by many

42

additional cues (body size, territory quality; Candolin, 2003) that were absent in our stimuli. How females discriminate among conspecific males or choose areas to establish home ranges will require further study, but our results suggest that reproduction in these lizards is likely centered on male-male competition for the monopolization of access to females, rather than female mate choice per se.

Research on the mechanisms leading to diversity in colour signals in groups of closely related species has often focussed on (among other things) selection for detectable signals in diverse visual habitats (i.e. Sensory Drive hypothesis: Endler, 1992, 1993). Comparative studies on terrestrial species have shown some support for this hypothesis (Gomez et al. 2004; Leal and Fleishman 2004; Stuart-Fox et al. 2007; Fleishman et al. 2009; Macedonia et al. 2014). Furthermore, in a laboratory study on *Anolis cristatellus*, Fleishman & Persons (2001) found that visual flags (resembling dewlaps) with greater chromatic contrast or achromatic contrast were detected sooner than those with lower contrast; yet our field experiment showed that even large differences in achromatic contrast had no influence on detection. This suggests that in real-world conditions, the evolution of conspicuous signals is unlikely to be driven by selection for signal detectability alone. Instead, conspicuous signals may increase the reliability of information transfer during display (i.e., post detection; Endler, 1993). That information may include cues on species or sex identity, individual condition or quality, motivational state, or any combination of these factors (Maynard Smith and Harper 2003).

The evolution of colour signal diversity is therefore likely to be driven by multiple forms of selection, and their interaction, and particularly the interaction between sexual and natural selection (Endler 1984; Stuart-Fox and Moussalli 2008; Chen et al.

43

2012; Heinen-Kay et al. 2014; Marshall and Stevens 2014) and sexual selection and species recognition (Ryan and Rand 1993b; Ellers and Boggs 2003; Nicholson et al. 2007; Pryke and Andersson 2008; Rosenthal and Ryan 2011; Pike et al. 2014). Although signal detection is critical for effective communication (Fleishman et al. 2009), in *D. melanopogon* achromatic contrast does not appear to be used in conjunction with motion based display to increase signal detectability. Instead, the initial grasp reflex is likely to be primarily elicited by movement. Overall, therefore, our study provides no support for the hypothesis that diversity in colour patterns between groups of closely related species is due to selection for detectability in different visual habitats. Signal colour pattern likely plays an important role in advertising species identity in *Draco*, and the need for improved species recognition is believed to have contributed to the evolution of signal complexity and diversity in communities with several sympatric congeners (Stegmann 2013). However, our results also highlight that a receiver's decision to respond to a signal depends on other factors as well, such as the presence of a neighbour or motivational state. This presents a challenge for playback experiments and the study of species recognition more generally, because consistent responses to both conspecific and non-conspecific signals could reflect lack of discrimination of species identity cues or a host of other factors that are unrelated specifically to discrimination (Ord & Stamps 2009).

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Chapter Two Appendix

Visual Modelling

To measure dewlap conspicuousness, we calculated achromatic contrast values of the dewlap against the background, from the perspective of *Draco* conspecifics. We calculated these values for the natural dewlap as well as dewlap treatments (solid black, white and grey, and the three black and white treatments).

To calculate conspicuousness for the natural dewlap, and the two-coloured (black and white) dewlap treatments as seen in close range were the colour patches can be individually resolved, we calculated contrast values against the background for each colour individually and then weighted those values by the relative area each colour occupied. We also calculated the internal contrast between the black and white components for the natural dewlap and two-coloured dewlap treatments. To calculate the conspicuousness of the natural and two-coloured dewlap treatments as viewed from a distance (i.e. where the colours patches are indistinguishable), we took a weighted proportion of the spectra of each of the two colours and calculated the contrast values for the resultant spectra against the background.

To model how *Draco* are likely to perceive achromatic contrast we used data on an agamid lizard, *Ctenophorus ornatus*. Barbour et al. (2002) found that *C. ornatus* has a pure cone retina containing both single and double cones – and the double cone is thought to be responsible for luminance perception in birds, and probably lizards (Osorio and Vorobyev 2005). The double cone contains a long-wavelength sensitive (LWS) visual pigment with $\lambda_{max} = 571$ nm. Yewers et al (2015) similarly identified double cones

with LWS λ_{max} = 569 nm in the closely related agamid *C. decresii*. Double cones have no associated coloured oil droplet (Barbour et al 2002).

Spectra of the dewlap colours and representative background vegetation colours (green, brown, dark brown/black and white/ pale green) were smoothed over 5 nm intervals between the range 300 and 700 nm. A representative irradiance spectra was taken in at the site of capture for one *D. melanopogon* lizard, between 0830 and 1030 (which is a period of heightened activity for diurnal dragons). This spectra was similarly smoothed over 5 nm intervals and normalised to a maximum of one.

First, we calculated photoreceptor quantum catches (Q_D) for the double cone (D) for dewlap and background colour with the equation:

$$Q_D = \int R_D(\lambda)S(\lambda)I(\lambda)\mathrm{d}\lambda$$

where $R_D(\lambda)$ is the spectral sensitivity of the double cone D, $S(\lambda)$ is the spectral reflectance of the colour patch and $I(\lambda)$ is irradiance.

Achromatic contrast for each dewlap reflectance spectrum against the mean reflectance of each of the four principal types of background colour (green, brown, dark brown/black and white/pale green) was calculated as:

$$f_D = (\Delta f_D)/\omega_D$$

where the receptor signal (f_D) is proportional to the natural logarithm of the quantum catch: $f_D = \log(Q_D)$), and ω_D is the Weber fraction – a measure of photoreceptor noise within the receptor field. We assumed that the double cone has a $\omega_D = 0.05$ (Siddiqi et al. 2004). Although the Vorobyev and Osorio model was not formulated for comparisons of

luminance, and absolute values should be interpreted with caution, results of the model should still be indicative of perceived achromatic differences.

In order to quantify the proportions in which each colour (green, brown, dark brown/black and white/ pale green) was present in the background to the lizard's dewlap display, we took digital photographs 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 cm^2 grid overlaid on the background photographs (as per Klomp *et al.*, 2014).

This estimate of achromatic contrast assumes that, on average, the contrast is a weighted average of the contrast of the dewlap against the immediate vegetation background comprising leaves and tree trunks. In reality, however, the background is likely to consist of a highly heterogeneous mosaic of radiance patches including light passing through the vegetation or reflecting specularly off of leaves. Background radiance and contrast will also depend greatly on the direction of illumination relative to the dewlap (Fleishman et al. 2006). Despite the complexities of estimating realistic contrasts in natural environments, black and white should, on average, produce the highest achromatic contrast against any collection of background luminance patches and produce the highest internal achromatic contrast. The overall contrasts will also vary in relation to the relative size of the black and white dewlap components. Therefore relative differences in achromatic JNDs should provide a reasonable indication of relative differences in achromatic contrast of the natural dewlaps and dewlap treatments against the environmental background.

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Supplementary tables and figures

Table S2.1 Dewlap extension angles, perch heights and neighbour distances for free-living *D. melanopogon* lizards and robot presentations

Comparisons	
i. Perch height	
natural mean (*N = 220*)	4.0 m
95% CI	2.1 m
minimum	0.6 m
maximum	9.0 m
robot	3.2 m
ii. Neighbour distance	
natural mean (*N = 121*)	3.8 m
95% CI	0.7 m
minimum	0.2 m
maximum	15.0 m
iii. Robot presentation distance	
mean (*N = 223*)	4.9 m
95% CI	0.2 m
minimum	1.9 m
maximum	9.5 m
iv. Dewlap extension angle	
natural mean (*N = 21*)	88.76°
95% CI	3.70°
minimum	77.82°
maximum	107.84°
robot	90.00°

Measurements were taken from the lizards during the robot presentation field trip.

Table S2.2 Length, area, white colour patch area and proportion of the dewlap area coloured black, for natural dewlaps and dewlap treatments.

	dewlap length (mm)	total area (mm²)	'white colour patch' area (mm²)	% 'black'
i. Natural male dewlap ($N = 21$)				
average	22.81	95.69	39.26	71.18
95% CI, upper limit	23.69	104.95	44.37	73.71
95% CI, lower limit	21.94	86.44	34.15	68.66
maximum	27.38	140.39	60.71	84.91
minimum	19.12	62.09	15.64	56.98
ii. Dewlap treatments				
solid black	23	99.96	00.00	100.00
solid white	23	99.96	99.96	00.00
solid grey	23	99.96	00.00	00.00
70% black 30% white (natural)	23	99.96	29.99	70.00
50% black 50% white	23	99.96	49.98	50.00
90% black 90% white	23	99.96	10.00	90.00
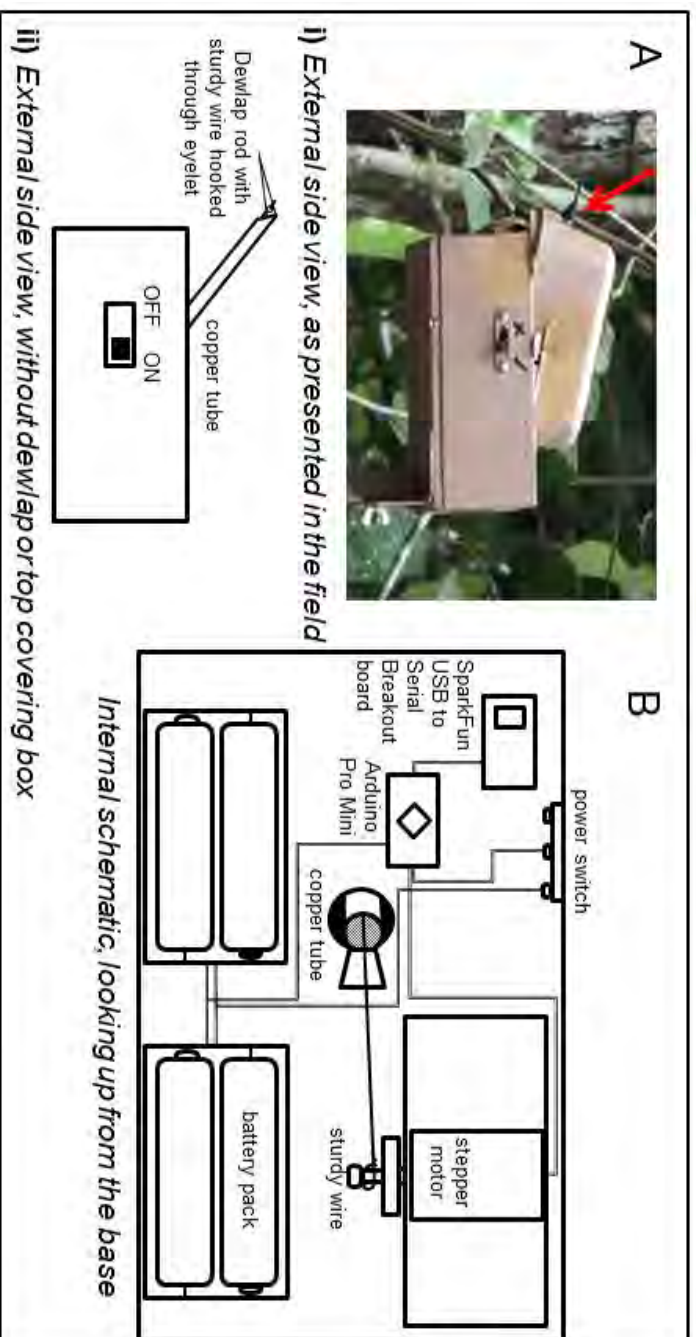
Figure S2.1 (A) i. Photograph of the robot with dewlap extended and ii. the external side view without the dewlap or covering box. The sturdy length of wire protrudes from the end of the copper tube and hooks through the eyelet of the dewlap rod. (B) the internal set-up viewed from the base looking upwards, showing the stepper motor connected to a length of sturdy wire that passes through a copper tube and drives the dewlap.
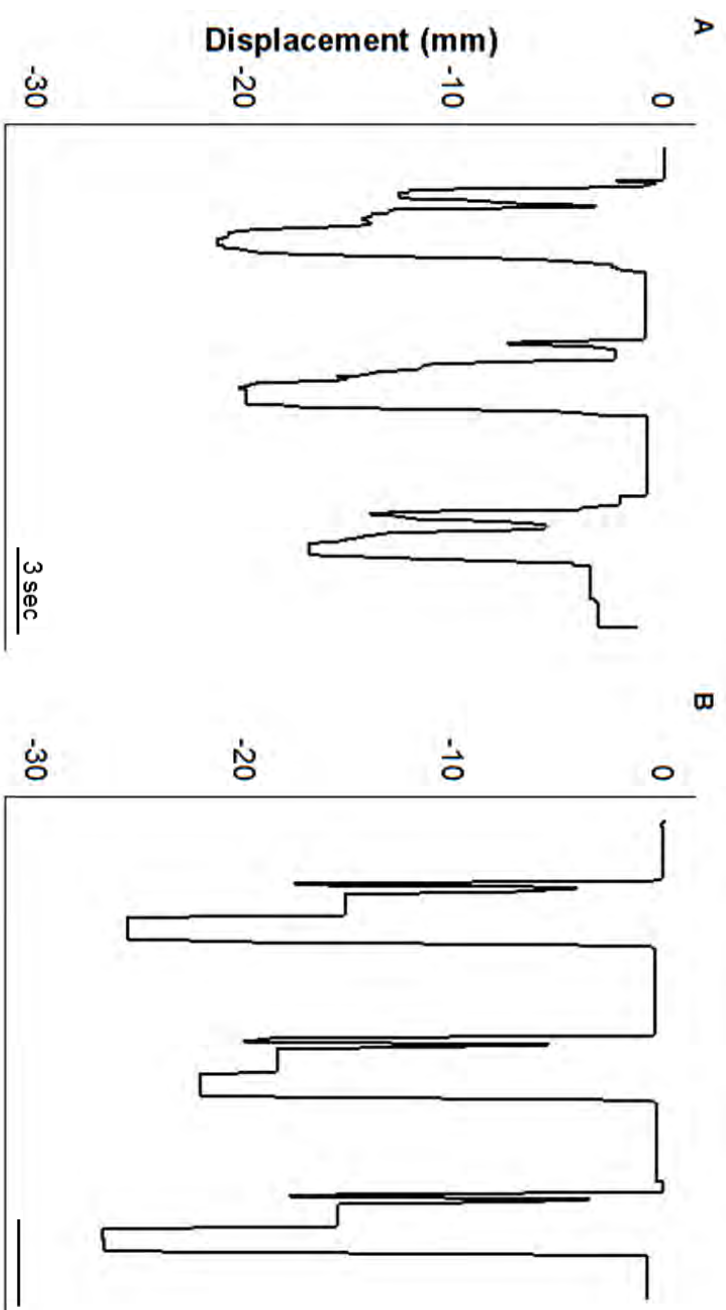
Figure S2.2   Display-Action-Pattern graphs, for (A) a representative example of the natural *D. melanopogon* display and (B) the programmed robot display Displacement (y-axis) refers to the distance the tip of the dewlap travels during display, in relation to its point of origin, over time (x-axis).
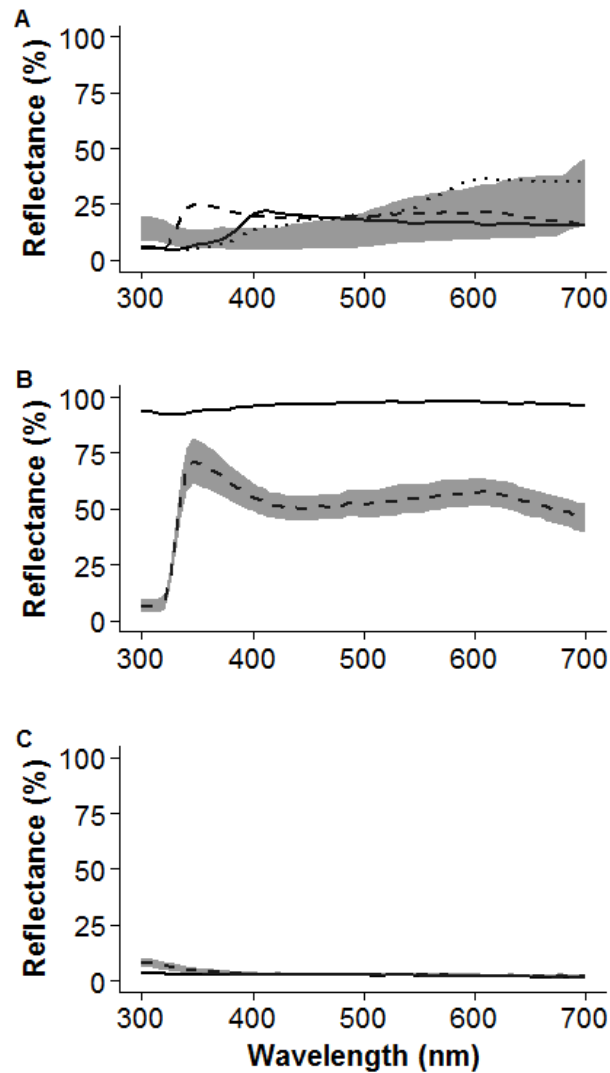
Figure S2.3   Reflectance spectra of the habitat background and dewlap. (A) The grey ribbon represents limits of average habitat spectra (dark brown, brown and green) and dotted line indicates robot box and pole colour (khaki). The solid line indicates grey dewlap treatment and dashed line indicates the appearance of the natural dewlap with the colours blended together (i.e. viewed from a distance); (B) dashed line and grey ribbon represents natural white dewlap spectra and its 95% CI, while the solid line indicates the white dewlap treatment; (C) dashed line and grey ribbon represent natural black dewlap spectra and its 95% CI, while the solid line indicates black dewlap treatment.

Figure S2.4   Robot and video recording set-up. The robot is indicated by the red arrow while the direction of the camcorder shows the general position of the focal lizard on the adjacent tree.
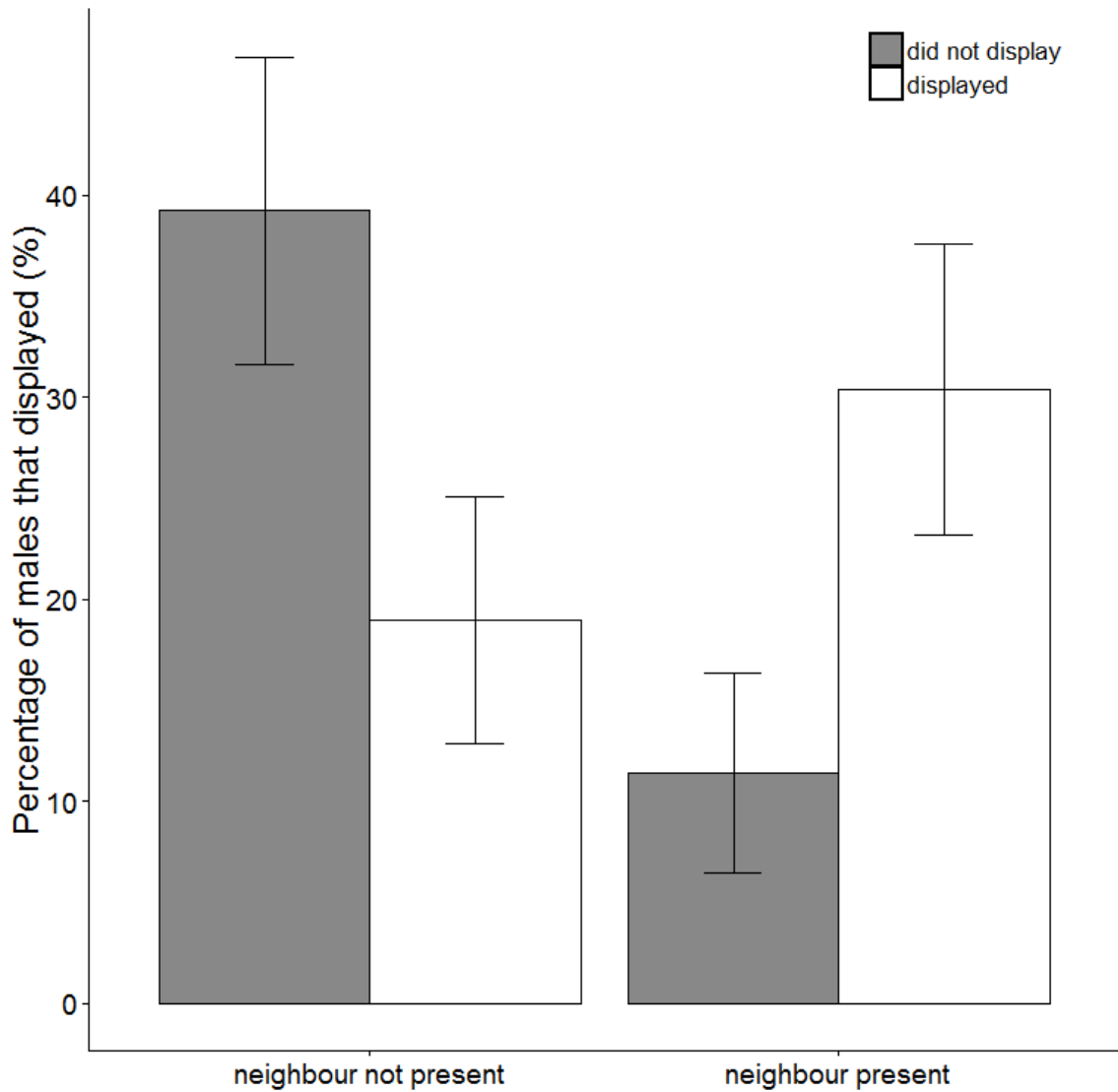
Figure S2.5   The percentage of male lizards that displayed (grey bars) and did not

display (white bars) in the presence and absence of neighbours in a 10 metre radius of the

focal lizard. Error bars represent 95% confidence intervals.

Chapter Three

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

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This study was conceived and designed by DAK, TJO and DS-F. DAK, TJO and DS-F collected the data, with assistance from ID, AD and NA. DAK analysed the data and wrote the manuscript with supervision and guidance from DS-F and TJO.

Abstract

Sexual ornamentation needs to be conspicuous to be effective in attracting potential mates and defending territories and indeed, a multitude of ways exist 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; Espmark et al. 2000; Maynard Smith and Harper 2003; Bradbury and Vehrencamp 2011); 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 (Maynard Smith and Harper 2003; Bradbury and Vehrencamp 2011). 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

characterises some groups of closely related species (Endler 1992; Leal and Fleishman 2004;

Nicholson et al. 2007).

Even phylogenetically closely related species may optimise signal conspicuousness

through alternative means. For instance, species that use a similar ornament in display may

evolve different but equally 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 and

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 and Mcdonough 2003; Hill and

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 and 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 and 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 and 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 signal aspects that can be behaviourally controlled (Zuk and 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 and 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 and Kiew,

2001), and whilst 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 and 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 and 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. 3.1) which are mostly conspicuous in males (though only visible during

display). In most *Draco* species, males appear to signal more frequently than females and

possess larger, more conspicuously coloured dewlaps, though this does vary and in some

species males and females have very different but equally conspicuous dewlap colours (Mori

and 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

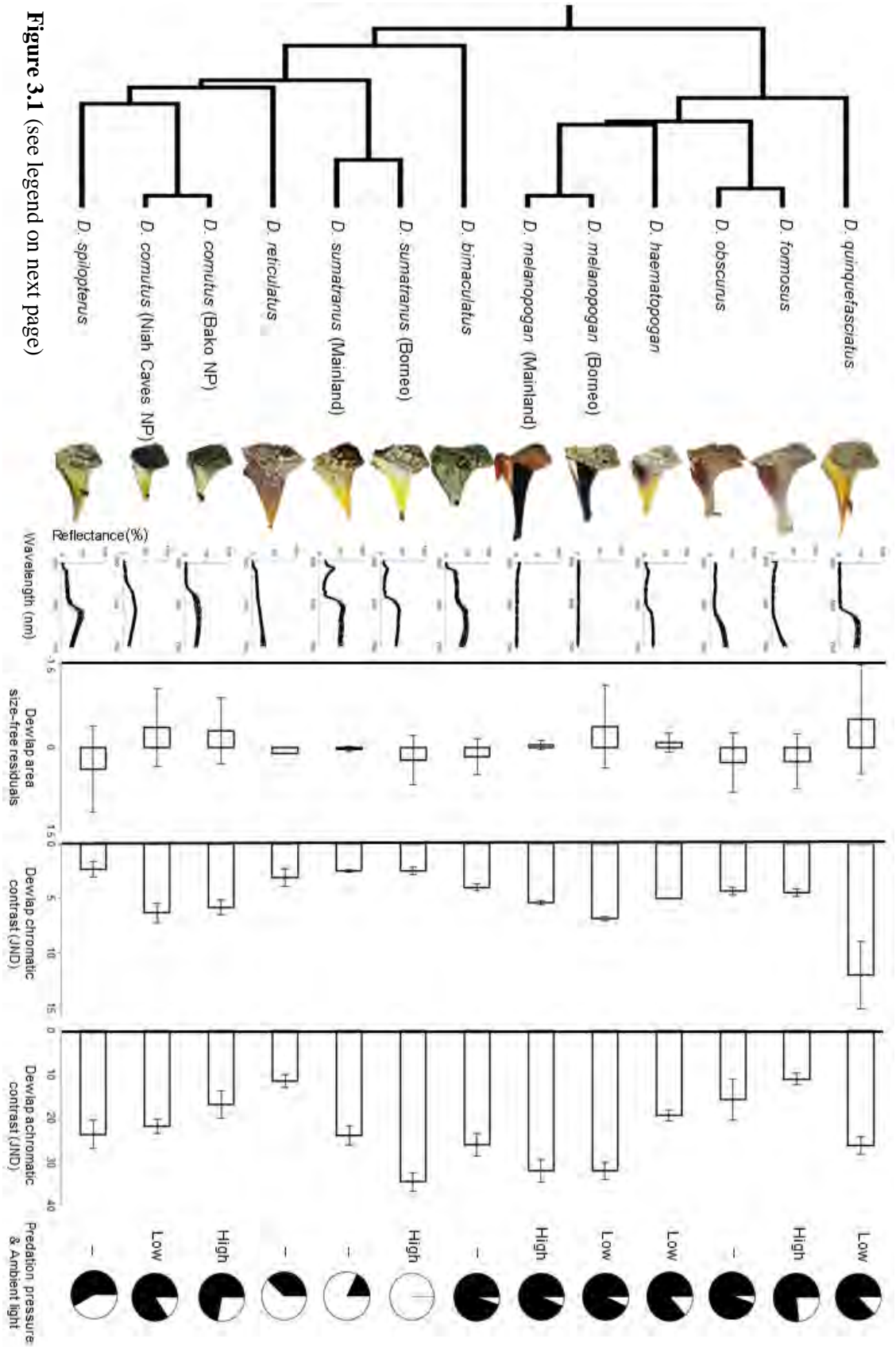dimorphism, sexual dichromatism in dewlap colour and brightness and dimorphism in relative

Figure 3.1 (see legend on next page)

Figure 3.1   Phylogeny of *Draco* species sampled (far left, then proceeding in order from left to right); images of the male dewlaps; spectral reflectance of the primary dewlap colour (with standard errors); male dewlap area size-free residuals (with 95% confidence intervals); male dewlap chromatic contrast (species means and 95% confidence intervals); male dewlap achromatic contrast (species means and 95% confidence intervals); relative predation pressure (high or low, where sampled); and ambient light level (as a proportion of 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.

Methods

Data collection

Between April 2011 and June 2012, we captured 122 individuals of 13 *Draco* taxa (fig. 3.1), from locations on Borneo, Peninsula Malaysia, and the islands of Luzon and Bohol in the Philippines. Though 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

300–700 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 $1cm^2$ grid. The photos included a

scale and were also used to measure the area of individual dewlaps using the 'freehand

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 $1 cm^2$ 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 in order to standardise 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 300–700 nm, denoted by 'AUC') as well as being normalised 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' (JND). 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 and 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 the appendix to this chapter.

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 intra-sexual 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 and 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 greater than one (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 hours 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 and 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. S3.1).

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. S3.2 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 hours and took detailed notes of all markings present.

Upon collection, the state of each model was characterised as: (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. S3.3) 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 and 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. In order 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 and 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. 3.1) 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 and Kiew, 2001), following Ord and 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 3.1; fig. 3.2A), 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 3.1; fig. 3.2B), indicating that females of some species have dewlaps that are conspicuous in terms of both chromatic and achromatic contrast against the background. Female chromatic and achromatic contrast was uncorrelated with that of males (fig. S3.4A, B), but female relative dewlap area increased with male relative dewlap area ($t_{13} = 2.89$, $p = 0.01$; fig. S3.4C), raising the possibility that dewlap size is evolutionarily coupled between the sexes.

Table 3.1 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.

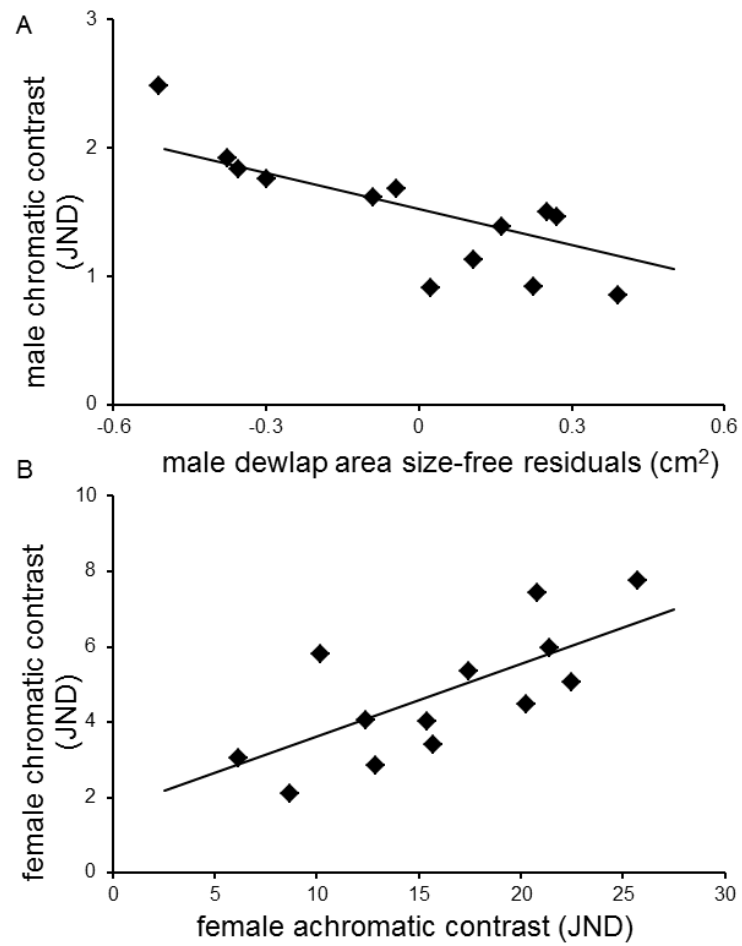| Dewlap traits	N_{taxa}	λ	r	p
i. Male dewlaps				
area vs. chromatic contrast	13	0.93	0.87	< 0.0001
area vs. achromatic contrast	13	1.10	0.14	0.62
chromatic vs. achromatic contrast	13	0.97	0.13	0.63
ii. Female dewlaps				
area vs. chromatic contrast	13	0.33	0.02	0.94
area vs. achromatic contrast	13	0.23	0.06	0.85
chromatic vs. achromatic contrast	13	0.06	0.70	0.005

Figure 3.2   (A) Male chromatic contrast (log-transformed) against relative dewlap

area, and (B) female chromatic contrast against achromatic contrast.

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 3.2). 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. 3.3A). *Draco quinquefasciatus* was excluded from this regression as an obvious model outlier, though 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), while female chromatic contrast decreased with increasing sexual dichromatism (males: fig. 3.3C; females: fig. 3.3D). 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, while 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. 3.3E; females: fig. 3.3F).

Table 3.2 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. 3.3A).

Dewlap traits	N_{taxa}	λ	t	p
i. 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)
ii. 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
iii. 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
iv. 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
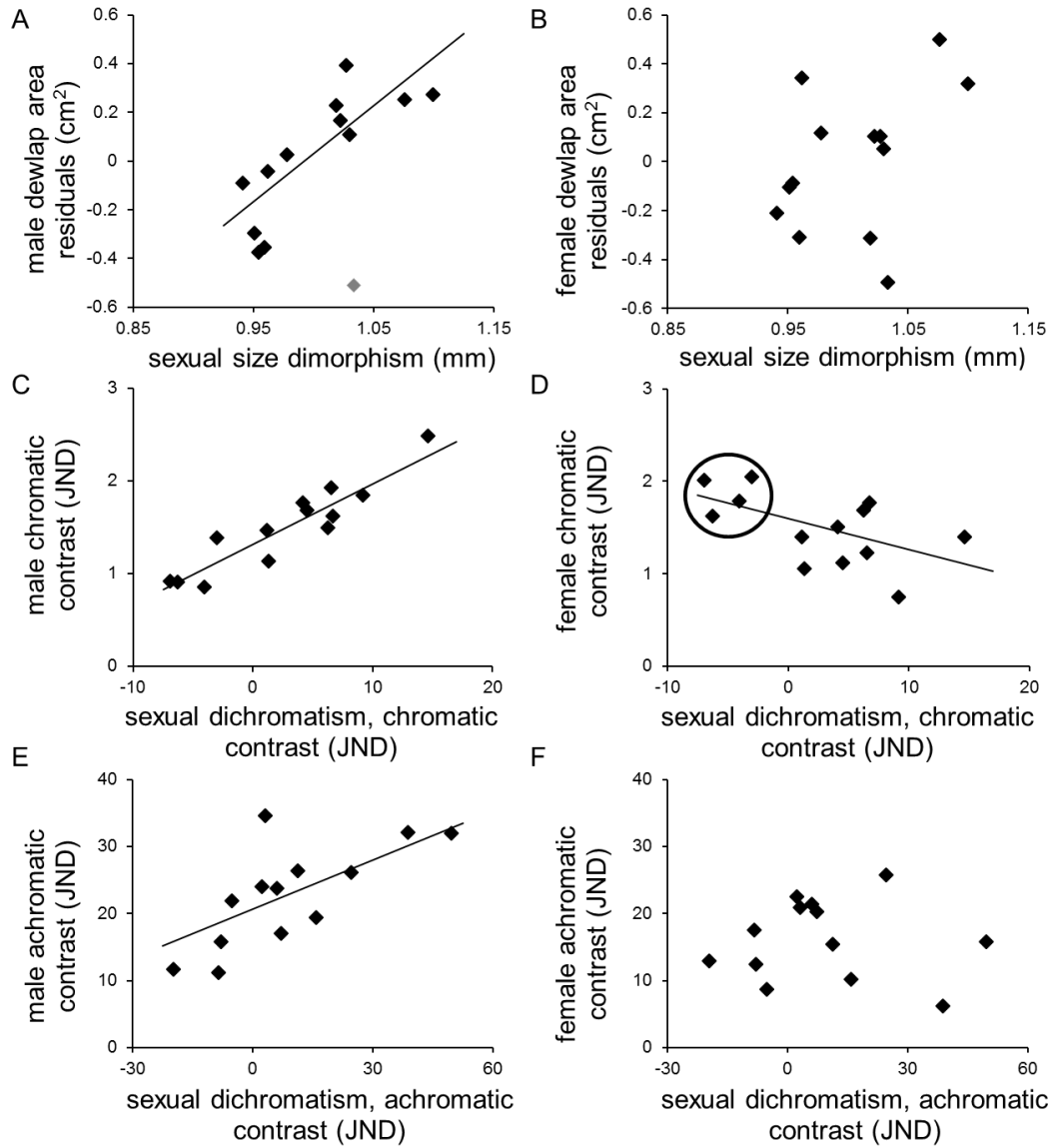
Figure 3.3 (A) Male and (B) female relative dewlap area as a function of sexual size dimorphism, (C) male and (D) female chromatic contrast (log-transformed) as a function of sexual dichromatism (JND, chromatic contrast between the primary dewlap colour of the sexes), and (E) male and (F) female achromatic contrast as a function of sexual dichromatism (JND, achromatic contrast between the primary dewlap colour of the sexes. An outlier species (*D. quinquefasciatus*) is in grey, panel A.

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. 3.4A, table 3.3ii). Male chromatic contrast was negatively correlated with habitat light (fig. 3.4D, table 3.3i), and whilst the relationship between chromatic contrast and predation pressure was not statistically significant (table 3.3ii), there was a trend for chromatic contrast to decrease with predation (fig. 3.4B).

Table 3.3 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.

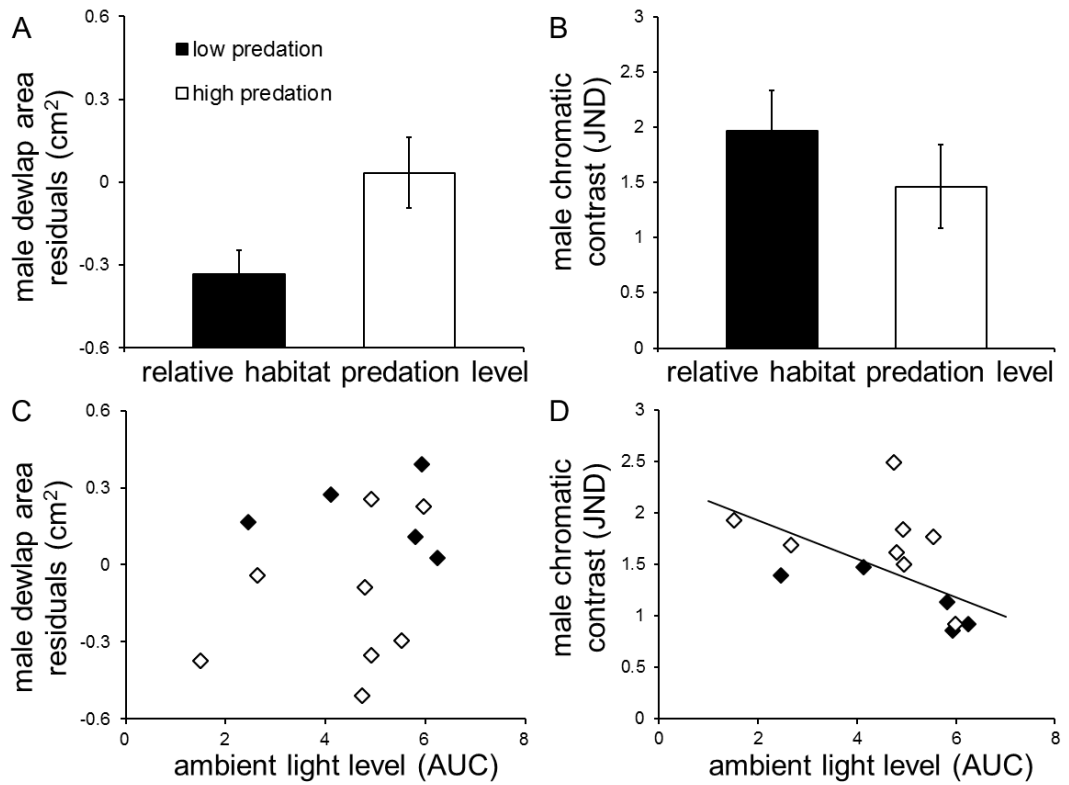| Dewlap traits	N_{taxa}	λ	t	p
i. Habitat light				
area	13	1.24	0.25	0.81
chromatic contrast	13	1.02	-5.98	0.0001
ii. Relative predation pressure				
area	8	-0.19	2.27	0.06
chromatic contrast	8	-2.42	-2.12	0.08

Figure 3.4 (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).

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 environmental selective pressures, both at the individual and population level (Hill 1999; Torok 2003; Loyau et al. 2005; Hebets et al. 2013), though 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 and Vehrencamp 2011).

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. Though 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 and 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 hypothesised 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 and McGuire 2014).

96

Husak and 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 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.

Though 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. spilopterus* 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

97

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 (though the relationship was certainly in the right direction, figure 3.4b). 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 and Ord, 2013). Diurnal birds are perhaps the most common 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 and Dittrich 2001; Osorio and 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 anti-predator 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 hyper-aggression 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. 2.7D). Species found in open, well-lit habitats are thought to experience greater levels of predation than those in closed habitats (Stuart-Fox and 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; see Prum *et al* 2010) 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 characterises many of the world's adaptive radiations.

Acknowledgements

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Chapter Three Appendix

Visual Modelling

The Vorobyev and Osorio model (1998) calculates a receiver's ability to discriminate between two colours in units of just noticeable differences. The model requires the spectral sensitivities of the receiver – in this case, conspecific *Draco* lizards. As photoreceptor spectral sensitivities of *Draco* species have not been determined, we used data on an agamid lizard, *Ctenophorus ornatus*. Barbour et al. (2002) found that *C. ornatus* has a pure cone retina containing both single and double cones, and identified three single cones with visual pigments sensitive to long-wavelengths (LWS: $\lambda_{max} = 571$ nm), medium wavelengths (MWS: $\lambda_{max} = 493$ nm) and short wavelengths (SWS: $\lambda_{max} = 440$ nm), but did not find a fourth ultra-violet sensitive photoreceptor (UVS). UVS photoreceptors are generally the rarest within the retina and it is likely that these were not detected due to small sample sizes (Barbour *et al.*, 2002). Yewers *et al.* (2015) similarly identified three visual pigments with very similar spectral sensitivities as C. ornatus in the closely related agamid *C. decresii* using microspectrophotometry. However, Yewers *et al*. also clearly identified a UVS photoreceptor (SWS1) from opsin gene expression data. Given that UVS photoreceptors have been identified in all other related diurnal lizards (Loew et al. 2002; Bowmaker et al. 2005; Fleishman et al. 2011), including the agamid lizard *Ctenophorus decresii* (Yewers et al. 2015), it is likely that other agamid lizards, including *Draco* species, do perceive UV wavelengths (Barbour et al. 2002).

The sensitivity of the UVS cone is the mean of published UVS cone sensitivities for diurnal lizards of the infraorder Iguania (Loew et al. 2002). Visual pigment absorbance curves were also corrected for the ocular media (lens and cornea; $\lambda_{cutoff} = 350$ nm), multiplied by the transmission of oil droplets associated with each of the single cones (Barbour *et al*. 2002; see also Chan *et al.*, 2009) and normalised to equal area under the curve (Endler and Mielke, 2005). Double cones have no associated coloured oil droplet (Barbour *et al*. 2002).

Spectra of the dewlap colours and representative background vegetation colours (green, brown, dark brown/black and white/ pale green) were smoothed over 5 nm intervals between the range 300 and 700 nm. Irradiance spectra were similarly smoothed over 5 nm intervals and normalized to a maximum of one. The irradiance used was always that of the local habitat (see Klomp *et al.*, 2014).

First, we calculated photoreceptor quantum catches (Q_i) for each cone type (i) for dewlap and background colour with the equation:

$$Q_i = \int R_i(\lambda)S(\lambda)I(\lambda)\mathrm{d}\,\lambda$$

where $R_i(\lambda)$ is the spectral sensitivity of cone i, $S(\lambda)$ is the spectral reflectance of the colour patch and $I(\lambda)$ is irradiance. We then applied the von Kries transformation which accounts for the receptors' adaption to the light environment and contributes to colour constancy (Vorobyev and Osorio, 1998; Siddiqi *et al.*, 2004). This entailed normalizing quantum catches (Q_i) to the background:

$$q_i = k_i Q_i$$

where

$$k_i = 1/\int R_i(\lambda)S^b(\lambda)I(\lambda)\mathrm{d}\,\lambda$$

and $S^b(\lambda)$ is the reflectance of the background.

The receptor signal (f_i) is proportional to the natural logarithm of the quantum catch: $f_i = \log(q_i)$). The contrast for a tetrachromatic visual system can then be calculated using the following equation:

$$(\Delta S)^2 = (\omega_1\omega_2)^2\,(\Delta f_4 \Delta f_3)^2 + (\omega_1\omega_3)^2\,(\Delta f_4 \Delta f_2)^2 +$$

$$(\omega_1\omega_4)^2\,(\Delta f_3 \Delta f_2)^2 + (\omega_2\omega_3)^2\,(\Delta f_4 \Delta f_1)^2 +$$

$$(\omega_2\omega_4)^2\,(\Delta f_3 \Delta f_1)^2 + (\omega_3\omega_4)^2\,(\Delta f_2 \Delta f_1)^2 \,/$$

$$((\omega_1\omega_2\omega_3)^2 + (\omega_1\omega_2\omega_4)^2 + (\omega_1\omega_3\omega_4)^2 + (\omega_2\omega_3\omega_4)^2)$$

where ΔS is the contrast between any two colours in units of JNDs and ω_i is the noise-to-signal ratio (Weber fraction). The higher the value of ΔS, the more distinguishable the two spectra, at least for values close to the discrimination threshold (Kemp et al. 2015). The Weber fraction is a measure of photoreceptor noise within the receptor field, and can be calculated by:

$$\omega_i = v_i/\sqrt{\eta_i}$$

under bright illumination, where v_i is the noise-to-signal ratio of a single cone and η_i is the number of photoreceptors of type i. It was assumed that photoreceptor noise for the LWS photoreceptors $\omega_L = 0.1$ and ω_i for the remaining photoreceptor types was calculated assuming a photoreceptor ratio of 1: 1: 3.5: 6, based on *Ctenophorus ornatus*

(Barbour *et al.*, 2002; see also Chan *et al.*, 2009; Teasdale *et al.*, 2013; Stuart-Fox and Goode, 2014), giving values for remaining photoreceptor classes or $w_U = 0.245$, $w_S = 0.245$, and $w_M = 0.131$.

Achromatic contrast was calculated as:

$$f_D = (\Delta f_D)/\omega_D$$

where we assumed that the double cone has a $\omega_D = 0.05$ (Siddiqi et al. 2004). Although the Vorobyev and Osorio model was not formulated for comparisons of luminance, and absolute values should be interpreted with caution, results of the model should still be indicative of perceived relative differences between colours.

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Supplementary figures

Figure S3.1   Photographs of predation models (dark grey and light grey).
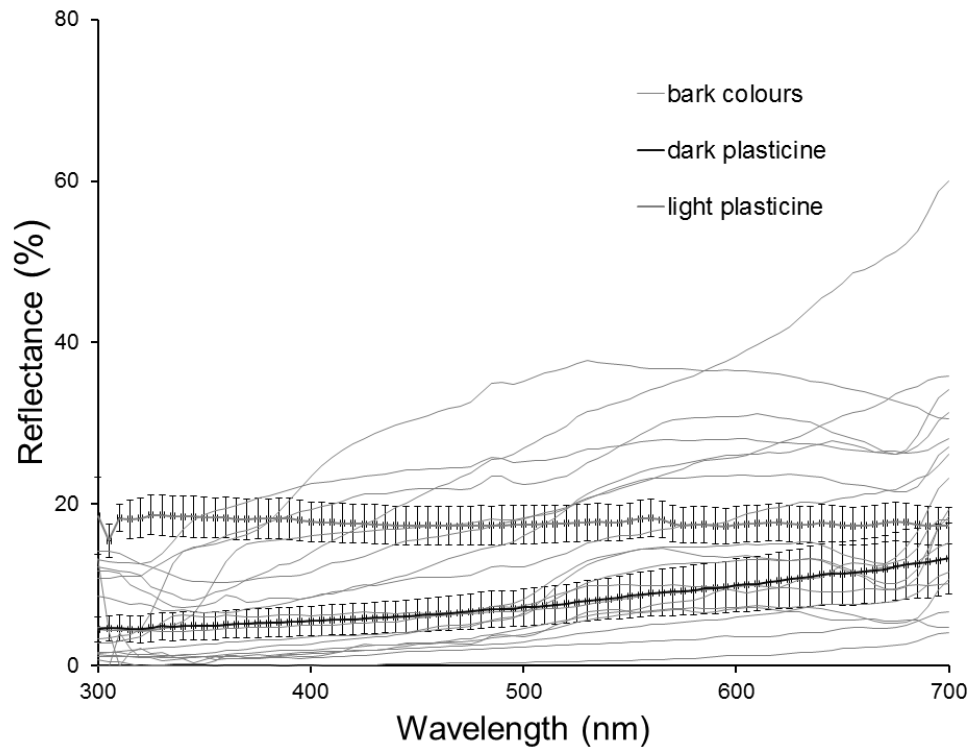
Figure S3.2 Mean spectra of predation models (dark grey and light grey plasticine) with 95% confidence intervals, and example bark spectra from all six habitats where relative predation was measured.

Figure S3.3   Frequency histogram of relative predation levels of all habitats studied, showing bimodal distribution.

Figure S3.4 (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, cm^2).

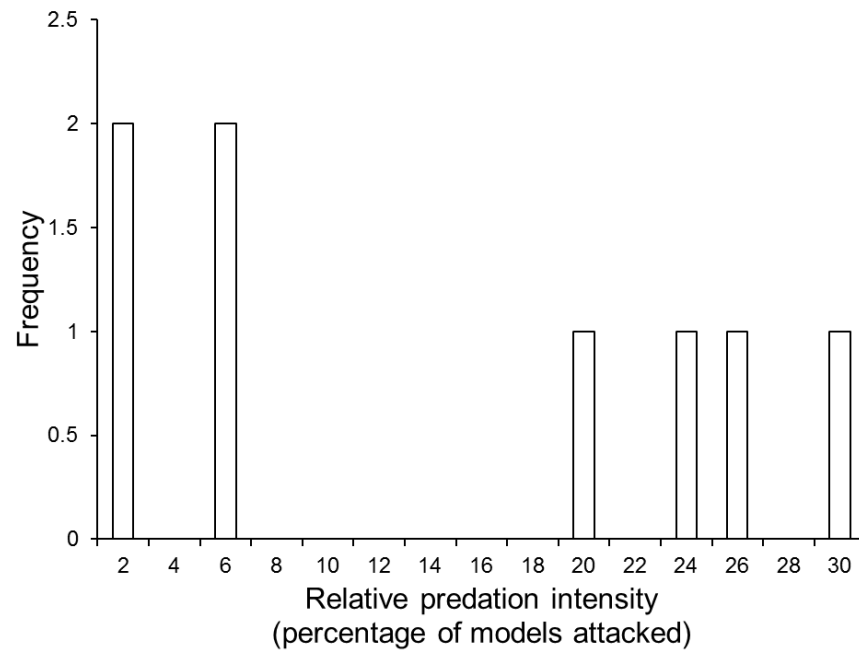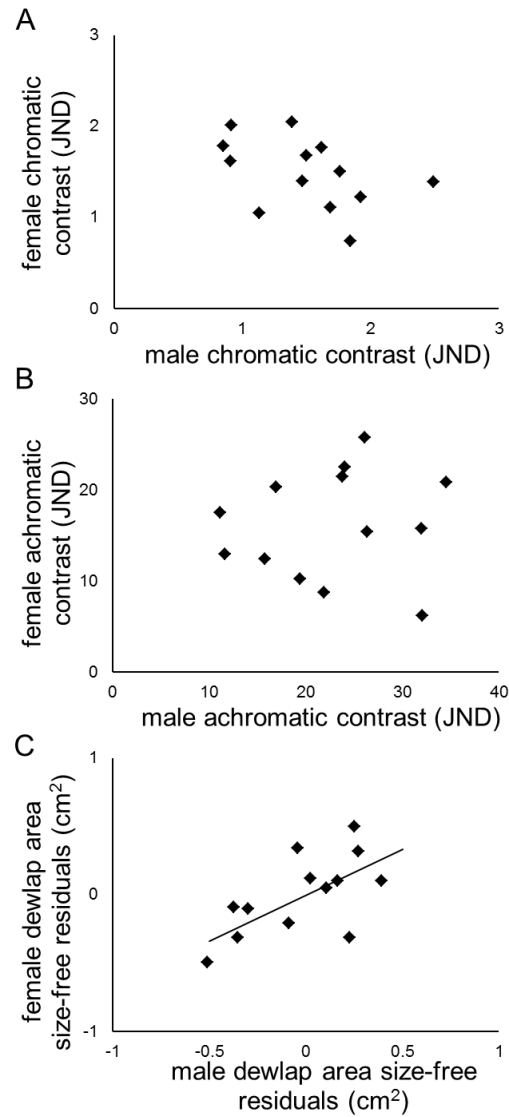## *Chapter Four*

Marked colour divergence in the gliding membranes of a lizard mirrors population differences in the colour of falling leaves

Danielle Klomp, Devi Stuart-Fox, Indraneil Das and Terry J. Ord

This study was conceived and designed by DAK, TJO and DS-F. DAK and TJO collected the data, with assistance from ID. DAK analysed the data and wrote the manuscript with supervision and guidance from DS-F and TJO.

Abstract

Populations of the Bornean gliding lizard, *Draco cornutus*, differ markedly in the colour of their gliding membranes. They also differ in local vegetation type (mangrove forest versus lowland rainforest) and consequently, the colour of falling leaves (red and brown/black in mangrove versus green, brown and black in rainforest). We show that the gliding membranes of these lizards closely match the colours of freshly fallen leaves in the local habitat as they appear to the visual system of birds (their probable predators).

Furthermore, gliding membranes more closely resembled colours of local fallen leaves than standing foliage or fallen leaves in the other population's habitat. This suggests the two populations have diverged in gliding membrane colouration in order to match the colours of their local falling leaves, and that mimicking falling leaves is an adaptation that functions to reduce predation by birds.

Introduction

Draco is the only extant genus of lizards with extensible gliding membranes (patagia), supported by elongated ribs. Patagia extend to permit glides between trees but are otherwise kept retracted at the lizard's flank (Shine *et al*. 1998; McGuire and Dudley 2011). Patagia are often strikingly coloured when extended, and vary markedly among the 40 described species. Given the apparently conspicuous and diverse colouration of patagia, an obvious hypothesis is that patagial function is associated with social communication (McGuire and Dudley 2011). An alternative hypothesis for the colouration of patagia in *Draco* is that it provides camouflage during gliding by resembling falling leaves (fig. S4.1) to reduce the probability of detection by predators. The size of *Draco* lizards, and their shape when gliding with outstretched patagia, is comparable to that of falling leaves. Birds probably constitute the greatest risk for *Draco* whilst gliding due to their likely vantage points and mobility (Chalsurlyanun 2011).

To test the hypothesis that *Draco* patagia show local adaptation to the colour of falling leaves, we compared two populations of the Bornean endemic *Draco cornutus*, which have diverged markedly in patagia colouration and occupy two different habitats. *Draco cornutus* occurs in coastal mangrove forest dominated by *Rhizophora apiculata*,

which have bright red falling leaves (in contrast to the green standing foliage), similar to the red patagia of resident *D. cornutus* (fig. S4.2). The species also occurs in lowland forest, in which falling leaves range from black to yellowish-green, especially *Calophyllum inophyllum* and *D. cornutus* has dark brown patagia with extended green body colouration in males. By assessing behavioural footage for several species of *Draco*, we first verified that patagia are rarely extended during display and therefore do not feature prominently in social communication. We then quantified the spectral properties and proportions of falling leaves and patagia colours from coastal mangrove (Bako National Park) and lowland forest (Niah Caves National Park) populations in Borneo and used models of animal colour vision to assess how distinguishable the colour of the patagia were from the colour of falling leaves and standing foliage from the point of view of a predatory bird. If selection for resemblance to local falling leaf colouration has driven divergence in patagial colouration in *D. cornutus*, we predicted the colours of the patagia should be indistinguishable from the colours of the local falling leaves specifically, and not the standing foliage of their native habitats nor falling leaves in a non-native habitat.

Methods

Over 32 hours of footage was compiled for males of six *Draco* species (table 4.1) by opportunistically recording lizards in their natural habitats. Upon sighting, a video camera was set-up on a tripod at a distance of 5-6 meters from the focal lizard and recording continued for 30 minutes or as long as the lizard remained in view. Footage was analysed for the frequency of patagia extensions. We captured six male and ten

female *Draco cornutus* from Bako National Park, and six males and five females from Niah Caves National Park. Patagia reflectance (300 – 700 nm) and sidewelling irradiance were measured as described in Stuart-Fox *et al.* (2007), and detailed in the appendix to this chapter.

Table 4.1 Frequency of patagia extension (excluding those involved in gliding) from over 32 hours of behavioural footage of *Draco* species.

Population	Number of patagia extensions min^{-1} (median [range])	Number of individuals surveyed
D. cornutus (Niah)	0 (0)	17
D. cornutus (Bako)	0 (0 – 0.15)	14
D. haematopogon	0	1
D. melanopogon (Gombak)	0 (0 – 0.31)	21
D. melanopogon (Niah)	0 (0)	4
D. obscurus	0 (0)	3
D. quinquefasciatus (Gombak)	0 (0)	3
D. quinquefasciatus (Niah)	0 (0 – 0.033)	4
D. sumatranus	0 (0)	16

A refuse bag (1.02 x 1.22 m quadrat) was laid flat at the foot of the trees in which lizards were caught, to collect freshly fallen leaves over 48 hours. Reflectance was measured for all leaf colour patches immediately after collection, as well as for the standing foliage on the same trees. The nine quadrats (three at Niah, six at Bako) had an average of six leaves (range: 1 – 14, total: 55). The proportions of each colour (red, green or dark) present in the leaves, patagia and standing foliage were calculated using a 1 cm^2 grid overlaid on

photographs. We focused on the colour of the central component of the patagia, which differs most prominently between the sexes and populations (fig. 4.1).

To determine how patagia colours would be perceived by predatory birds 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' (JND). One JND is the threshold of discrimination for a visual system to distinguish two colours. Model calculations followed those in Siddiqi *et al.* (2004) and McLean *et al.* (2010) and are detailed in the appendix to this chapter.

We calculated chromatic (colour) and achromatic (luminance) contrasts of the predominant patagia colours viewed against three backgrounds: the predominant colours of the fallen leaves of the local habitat, the predominant colours of the standing foliage of the local habitat, and the predominant colours of the fallen leaves in the habitat of the other population. While both sexes at Bako had a single predominant patagia colour (fig. 4.1A), at Niah, there were two main colours in male patagia and two main fallen leaf colours: dark grey-brown and green (fig. 4.1B). We therefore contrasted the dark and green male patagia colours against the dark and green parts of local fallen leaves respectively. As Niah females have only dark grey-brown, that was contrasted against the dark of fallen leaves. We used general linear mixed models (SAS 9.3 [SAS Institute, Cary, NC]; PROC MIXED) to test for effects of sex and background (local falling leaf, standing foliage and non-native falling leaf) on contrasts of patagia (JNDs). Individual identity was included as a random factor, and significant effects were assessed using Tukey's post-hoc tests. We ran a separate model for chromatic and achromatic contrast for each population. Niah achromatic JND values were log-transformed to meet model assumptions.

126
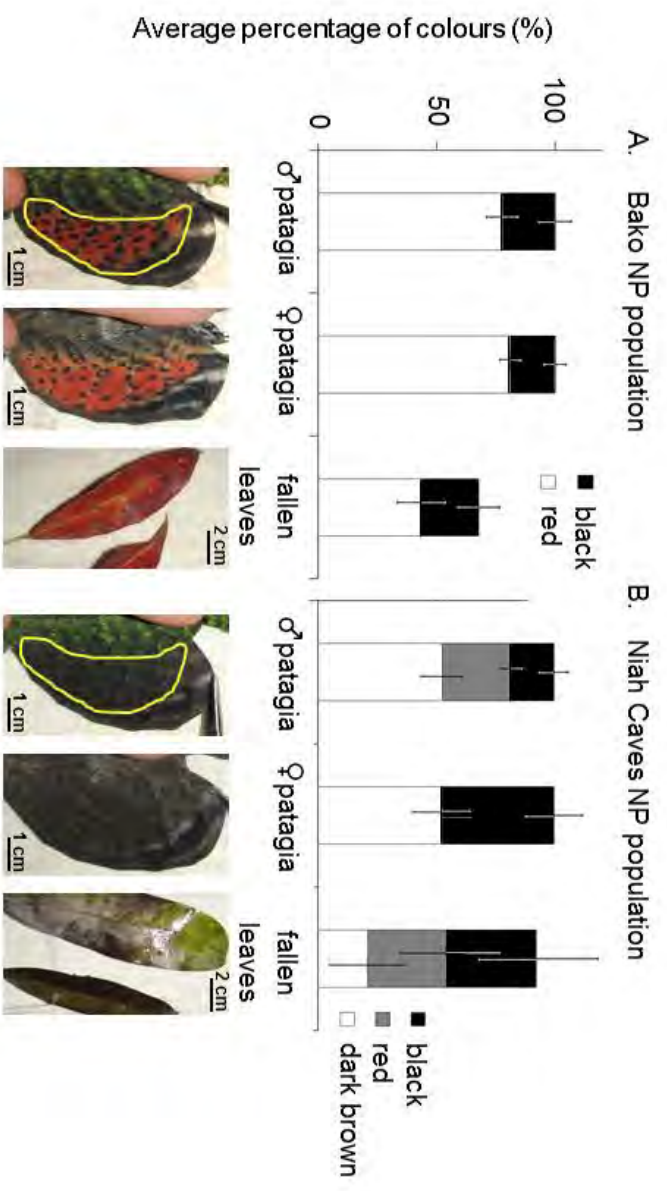
Figure 4.1 The proportions (and 95% confidence intervals) of colours in the central patagia section for *Draco cornutus* males and females, and the proportions of predominant colours of fallen leaves at (A) Bako National Park and (B) Niah Caves National Park. The falling leaf colours with the smallest proportions are not shown (yellow and brown for Bako, and yellow for Niah). The yellow outline in the patagia photographs indicates the central component, used to calculate colour proportions for both males and females.

Results

The behavioural observations of six Malaysian *Draco* species indicate the patagia are very rarely extended during social displays (table 4.1). We found that the proportions of the colours in the patagia were similar to the proportions of those in the local fallen leaves (fig. 4.1) and the colour with the greatest proportion in the patagia was also the colour with the greatest proportion in the local falling leaves. The contrast values for the patagia and the local falling leaves were low (approximately 4 JND; fig. 4.2A, B). There was no significant difference between the sexes at Bako in the conspicuousness of patagia, but there were significant differences in chromatic contrast against different backgrounds (table 4.2).

Predominant patagia colours matched those of local falling leaves significantly better than local standing foliage (Tukey posthoc test: $p < 0.0001$) or either falling leaf colour from the other (Niah) population (dark brown: $p = 0.023$; green: $p < 0.0001$; fig. 4.2A). The patagia of both Bako males and females had significantly lower achromatic contrast against local falling leaves than the green falling leaves from Niah ($p = 0.0093$), but not the dark falling leaves from Niah nor the local standing foliage (Niah, dark brown: $p = 0.47$; Bako, local standing foliage: $p = 0.75$; fig. 4.2C).

At Niah, there was a significant interaction between sex and background for both chromatic and achromatic contrasts (table 4.2). The dark brown component of male and female patagia chromatically matched the dark component of local falling leaves better than the falling leaves at the other population (both sexes: $p < 0.0001$), or the green local standing foliage (both sexes: $p < 0.0001$). The green component in the male patagia matched the local green falling leaves significantly better than the falling leaves at Bako

($p = 0.0005$), but matched the green of local falling leaves similarly to the green standing foliage ($p = 0.54$; fig 4.2B). In terms of achromatic contrast, neither the dark brown patagia colour of males or females better matched the dark local falling leaves than the falling leaves from the other population (males: $p = 0.053$; females: $p = 0.88$), and there was no difference in the contrasts of the male green patches against either background (Males, green: $p = 0.47$). The dark brown patches of the patagia of Niah males matched the local falling leaves better than the local standing foliage ($p = 0.0004$), but not for that of females ($p = 0.99$) nor for the green patches of the male patagia against the green local falling leaves ($p = 1.00$; fig. 4.2C), as the greens of falling leaves and standing foliage are similar.
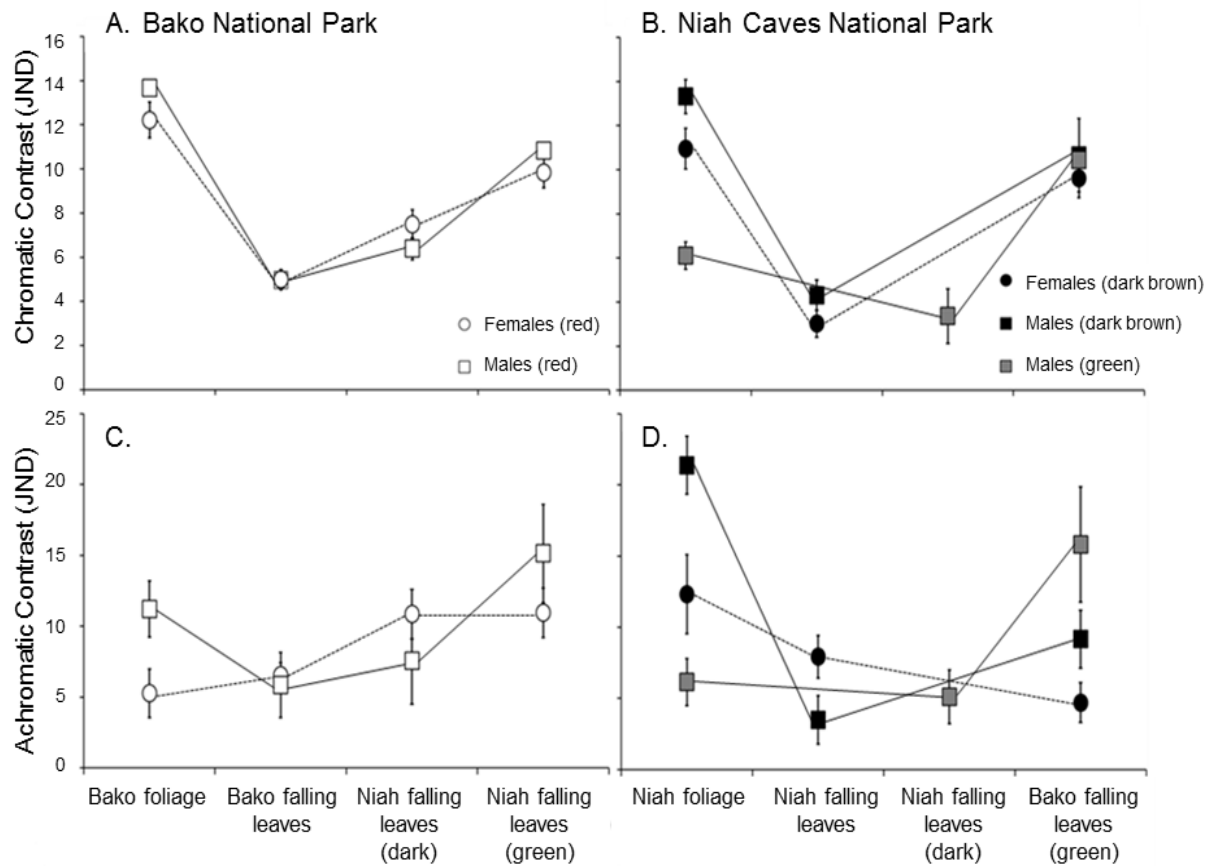
Figure 4.2 Chromatic contrast for the population at (A) Bako National Park and

(B) Niah Caves National Park and achromatic contrast for (C) Bako and (D) Niah populations

(means, 95% confidence intervals) in Just Noticeable Differences (JND). Values represent

contrasts between colours of the patagia of *Draco cornutus* at Bako and Niah, colours of the

local falling leaves (Bako fallen leaves / Niah fallen leaves (dark) / Niah fallen leaves (green))

and colours of standing foliage (Bako foliage / Niah foliage).

Table 4.2 The effects of sex and background on patagia conspicuousness (chromatic and achromatic contrast). The backgrounds were: local falling leaves, local standing foliage and falling leaves from the other population

	Chromatic Contrast		Achromatic Contrast	
	F_{df}	p	F_{df}	p
Bako National Park:				
sex	$.62_{(1,47)}$	.43	$1.10_{(1,47)}$	.30
background	$57.85_{(3,47)}$	$< .0001$	$3.86_{(3,47)}$	.015
sex*background	$1.49_{(3,47)}$	.23	$2.14_{(3,47)}$	.11
Niah Caves National Park:				
sex	$5.39_{(2,26)}$	.011	$.01_{(2,26)}$	.99
background	$65.12_{(2,26)}$	$< .0001$	$6.98_{(2,26)}$	.0038
sex*background	$5.34_{(4,26)}$	.0028	$5.54_{(4,26)}$	.0023

For the Niah population, 'sex' refers to three categories: female (dark brown), male (dark brown), and male (green). For the Bako population 'sex' refers to two categories: female (red) and male (red).

Discussion

The colours of the patagia of *D. cornutus* have diverged markedly between the two different populations and correspond closely to the differences in the falling leaf colours and proportions of those colours in their local habitats. Patagia colours of each population also matched local falling leaves more closely than falling leaves in the other population or local standing foliage, particularly in terms of chromatic contrast. Behavioural observations indicate that gliding membranes of *D. cornutus* are rarely used for communication, reinforcing the view that patagia colouration has instead been selected to specifically resemble the colours of falling leaves.

This study recorded an average of six leaves falling onto a 1.24m^2 quadrat over 48 hours – equivalent to 1,008 leaves falling in any given hectare every hour – and leaves fall continuously across the year from mostly non-deciduous trees at Niah and Bako. The pattern of movement of falling leaves is extremely variable, but commonly includes a gliding motion akin to the directed gliding in *Draco*. Indeed other falling leaf mimicry, functioning to reduce predation, has been recorded in other tropical rainforest settings (Cintra 1990; Greeney *et al*. 2006), suggesting that falling leaves are sufficiently common for mimicry to confer a survival benefit. Additionally, gliding is an integral part of *Draco* ecology (Mori and Hikida 1993; McGuire and Dudley 2011). Our behavioural observations of these populations recorded a combined average of 3.8 glides per hour indicating that vulnerability to predation whilst gliding would constitute a considerable selection pressure. Although motion plays an important role in prey detection by birds (Lea and Dittrich 2001), colour matching is likely to enhance mimicry of falling leaves, thereby providing an advantage in reducing detection by aerial predators.

Draco have prominent, sexually dichromatic dewlaps used solely for social communication (Mori and Hikida 1994). In contrast, the limited or absent sexual dichromatism in the patagia provides further, indirect support for the hypothesis that patagia colouration functions in camouflage rather than social communication. However, these hypotheses are not mutually exclusive and McGuire and Dudley (2011), who have worked extensively on *Draco*, have observed the patagia used in display. We found limited evidence of this in the Malaysian *Draco* species we have studied (table 4.1), but it may be that other *Draco* species extend patagia during social displays. For example, extending patagia in close range display could increase the apparent size of the lizard, and this could be beneficial during aggressive encounters. Patagia colouration may therefore have multiple functions, and our study suggests that one of these functions is probably camouflage.

Results of this study clearly show that the marked divergence in patagial colouration of two *D. cornutus* populations corresponds with differences in the colours of leaves that fall in each population's habitat. Our observations suggest that this is not an isolated example. Our opportunistic examination of patagia and falling leaf coloration for four other species (*D. melanopogon* at Niah, *D. spilopterus* in the Philippines, *D. quinquefasciatus* at Niah and *D. formosus* on the Malay Peninsula*;* fig. S4.1) shows a similarly remarkable match between the coloration of patagia and local falling leaves. We predict that falling leaf colour matching would be important for species where the spacing among trees results in longer glides and greater visibility to overhead predators. Similarly, habitats that are dominated by a single tree species (and thus falling leaf colour) should also promote falling leaf colour matching in the patagia of *Draco* lizards.

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Chapter Four Appendix

Visual Modelling

Patagial reflectance (300 – 700 nm) was 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. Sidewelling irradiance (90° from the ground) was measured with a JAZ–ULM–200 spectrometer and cosine corrected irradiance probe (Ocean Optics), and were normalised to a maximum of one for use in visual modelling. Irradiance measurements were taken at capture, between 0830 and 1030h (a period of heightened activity for the diurnal lizards).

A predatory bird's eye view

The Vorobyev and Osorio (1998) model calculates a receiver's ability to discriminate between two colours in units of just noticeable differences (JND). The model requires the spectral sensitivities of the receiver – in this case birds, which have a tetrachromatic visual system with four single cones (UVS/VS, SWS, MWS, and LWS) and a double cone, used to detect luminance variation (v. Campenhausen and Kirschfeld 1998; Hart 2001; Osorio and Vorobyev 2005; Hart and Hunt 2007). The spectral sensitivities were corrected for transmission of associated oil droplets (data from Endler and Mielke 2005). Although the spectral sensitivities of birds are either ultraviolet sensitive (UVS) with a UVS cone that peaks in sensitivity at 360 nm, or violet sensitive (VS) with a VS cone that peaks in sensitivity at 410 nm (Hart 2001), we present results for the UVS system only. This is because all relevant spectra have low reflectance in the UV and violet

wavelengths (thus there was no qualitative difference between results for the two visual systems) and the UVS system provides a more conservative estimate of colour differences across the full spectrum potentially visible to birds.

Spectra of the patagia colour and background colour (fallen leaves or foliage) were smoothed over 5 nm intervals between the range 300 and 700 nm, which corresponds to the visual system of birds. Irradiance spectra were similarly smoothed over 5 nm intervals and normalized to a maximum of 1. The irradiance used was always that of the local habitat.

First, we calculated photoreceptor quantum catches (Q_i) for each cone type (i) for patagia, fallen leaf and foliage colour with the equation:

$$Q_i = \int R_i(\lambda)S(\lambda)I(\lambda)\mathrm{d}\lambda$$

where $R_i(\lambda)$ is the spectral sensitivity of cone i, $S(\lambda)$ is the spectral reflectance of the colour patch and $I(\lambda)$ is irradiance. We then applied the von Kries transformation which accounts for the receptors' adaption to the light environment and contributes to colour constancy (Vorobyev *et al*. 1998; Siddiqi *et al*. 2004). This entailed normalizing quantum catches (Q_i) to the background:

$$q_i = k_i Q_i$$

where

$$k_i = 1/\int R_i(\lambda)S^b(\lambda)I(\lambda)\mathrm{d}\lambda$$

and $S^b(\lambda)$ is the reflectance of the background.

The receptor signal (f_i) is proportional to the natural logarithm of the quantum catch: $f_i = \log(q_i)$). The contrast for a tetrachromatic visual system can then be calculated using the following equation:

$$(\Delta S)^2 = (\omega_1\omega_2)^2 \, (\Delta f_4 \Delta f_3)^2 + (\omega_1\omega_3)^2 \, (\Delta f_4 \Delta f_2)^2 +$$

$$(\omega_1\omega_4)^2 \, (\Delta f_3 \Delta f_2)^2 + (\omega_2\omega_3)^2 \, (\Delta f_4 \Delta f_1)^2 +$$

$$(\omega_2\omega_4)^2 \, (\Delta f_3 \Delta f_1)^2 + (\omega_3\omega_4)^2 \, (\Delta f_2 \Delta f_1)^2 \, /$$

$$((\omega_1\omega_2\omega_3)^2 + (\omega_1\omega_2\omega_4)^2 + (\omega_1\omega_3\omega_4)^2 + (\omega_2\omega_3\omega_4)^2)$$

where ΔS is the contrast between any two colours in units of JNDs and ω_i is the noise-to-signal ratio (Weber fraction). The higher the value of ΔS, the more distinguishable the two spectra. The Weber fraction is a measure of photoreceptor noise, which determines the discriminability of two colours. The Weber fraction can be calculated by:

$$\omega_i = v_i / \sqrt{\eta_i}$$

under bright illumination, where v_i is the noise-to-signal ratio of a single cone and η_i is the number of photoreceptors of type i. To calculate chromatic contrast (ΔS) we assumed that $\omega_i = 0.1$ for the long-wavelength sensitive (LWS) cone (Vorobyev and Osorio 1998; Siddiqi *et al*. 2004) and derived ω_i values for the each other photoreceptor types using the equation above and a ratio of 1 ultraviolet sensitive (UVS) cone: 2 short-wavelength sensitive (SWS): 3.4 medium-wavelength sensitive (MWS): 3 LWS (for the UVS visual system) as outlined in Hart and Hunt (2007). Achromatic contrast was calculated as:

$$f_D = (\Delta f_D)/\omega_D$$

where we assumed that the double cone has a $\omega_i = 0.05$ (McLean *et al.* 2010). Although the Vorobyev and Osorio model may not have been designed for comparisons of luminance, and absolute values should be interpreted with caution, results of the model are still indicative of real differences between colours.

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Supplementary figures

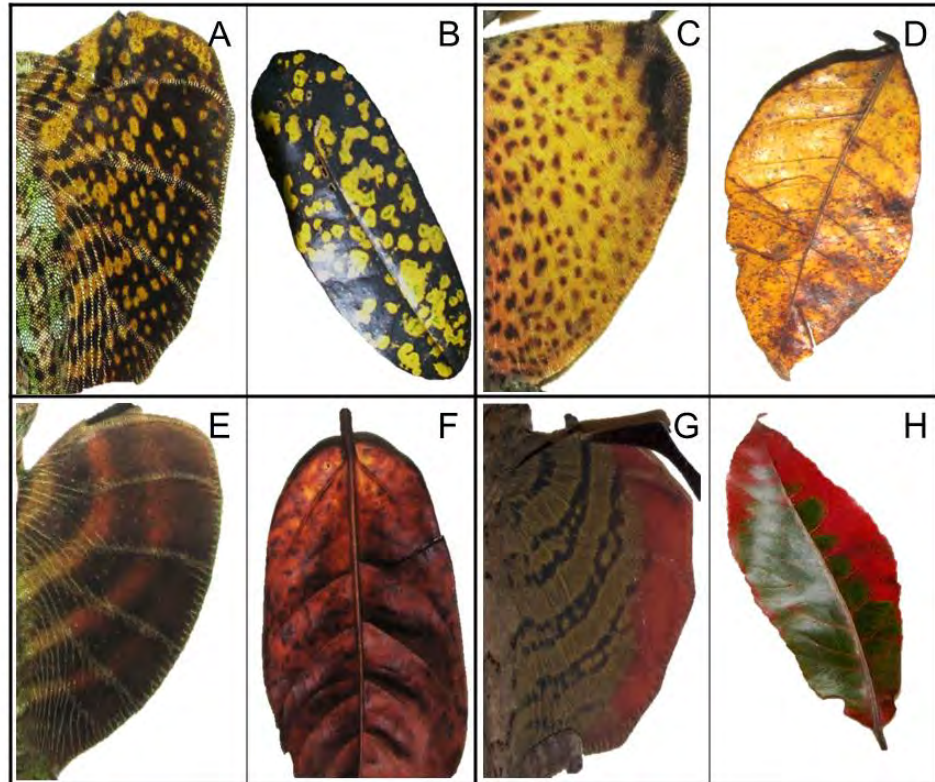**Figure S4.1** The patagia (A) of *Draco melanopogan*, the falling leaves in the immediate habitat of *Draco melanopogan* (B); the patagia of *Draco spilopterus* (C) and the falling leaves in its immediate habitat (D); the patagia of *Draco quinquefasciatus* (E) and the falling leaves in its immediate habitat (F); the patagia of *Draco formosus* (G) and the falling leaves in its immediate habitat (H).
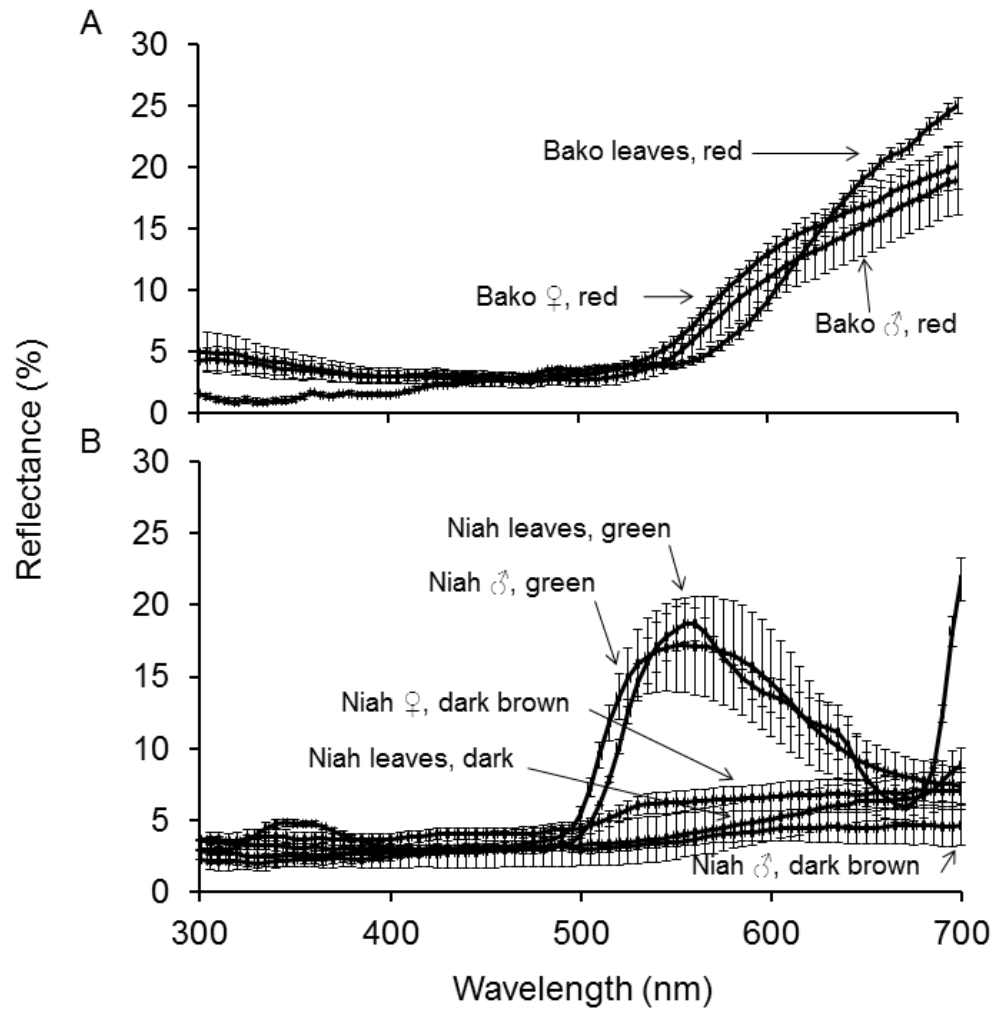
Figure S4.2 Spectra of predominant patagia colours of *Draco cornutus* and predominant falling leaf colours of (A) the Bako population and (B) the Niah population (means and standard error confidence intervals).

Chapter Five

Gliding lizards use the position of the sun to enhance a social display

Danielle Klomp, Devi Stuart-Fox, Indraneil Das and Terry J. Ord

Abstract

Effective communication with conspecifics is critical to individual fitness, and to achieve this, animals must produce signals that are readily detected in the environments in which they are given. Certain environmental conditions, such as light intensity, may enhance the visibility of colour signals and animals may therefore choose to present the signal at a time or place in which it will be most effective. Here we test the idea that *Draco sumatranus* lizards use their position relative to the sun to enhance the apparent brightness of their throat-fan (or dewlap), used in display to conspecifics. The dewlap is translucent and increased exposure to the sun increases its apparent brightness due to the light transmitted through the dewlap. We find that both males and females are

significantly more likely to orientate themselves perpendicular to the sun when

displaying, thereby ensuring maximum sun exposure for the extended dewlap. This is one

of the rare studies to describe behavioural adaptation for enhancing signalling, outside of

birds.

Introduction

Ornaments and body colours used in visual signalling are selected for detectability and

the capacity to reliably convey information (Epsmark et al. 2000). To be effective, a

signal needs to be obvious in the environment in which it is typically given (Endler 1992;

Endler 2000). The ease with which a signal may be detected can be reduced or enhanced

by different environmental conditions, such as light intensity, habitat complexity (causing

visual obstructions), and the proximity of the receiver to the signaller (Vorobyev and

Osorio 1998; Aspbury and Gibson 2004; How et al. 2008). Extensive research on species

that communicate acoustically has shown that individuals are able to adapt signalling

behaviour to mitigate effects of environmental conditions that reduce signal efficacy

(Brumm and Slabbekoorn 2005). For example, silvereyes are able to adjust their call

frequency, amplitude and duration to compensate for increases in background noise to

improve the effectiveness of their calls (Potvin and Mulder 2013). However, analogous

changes to the structure of signals have also been documented in animals that use visual

displays to communicate in visually noisy environments of windblown vegetation (e.g.,

increasing the speed/duration of display movements; Ord *et al.*, 2007; Peters *et al.*, 2007).

In addition to changes in the structure of signals, animals can increase the

conspicuousness of their signals by choosing certain places and times to signal (Endler

and Thery 1996; Doucet and Montgomerie 2003; Penteriani and Delgado 2009). In the case of colour signals, communication is more effective if colours stand out against those appearing in the background, and this can be enhanced if the signaller positions itself in front of a high contrast background (Uy and Endler 2004). Similarly, to avoid distracting motion from wind-blown vegetation (see above), animals can wait for periods when vegetation is still before displaying (Ord et al. 2011). The purpose of these behavioural strategies is to increase the visibility of signals to conspecifics (thus the likelihood of successful communication) and reduce energy wasted on signalling ineffectively.

An important factor influencing the effectiveness of visual signals is ambient light (both intensity and spectral composition – Endler, 1993; Marchetti, 1993). Iridescent or other specularly reflective colours and ornaments may increase in conspicuousness with direct sun exposure (Osorio and Ham 2002), and animals communicating with these types of ornaments may take advantage of this effect by orientating them relative to the position of the sun (Dakin and Montgomerie 2009; Sicsú et al. 2013). For example, Sicsú *et al.*, 2013 found that male blue-black grassquits perform displays more frequently when bathed in sunlight (which increases the conspicuousness of their iridescent plumage). Additionally, ornaments that reflect in shorter wavelengths may also appear more conspicuous in direct sunlight, as direct sunlight is richer in shorter wavelengths than the light beneath a forest canopy. This may create a greater contrast between the ornament and its typical background, such as bark and vegetation which generally have minimal short wavelength reflectance (Endler 1993). Most studies that have previously identified animals exploiting the position of the sun for increasing the conspicuousness of ornaments have focused on birds, however, in

principle any animal occupying an open environment might also orient their ornaments strategically towards the sun to enhance signal effectiveness.

The conspicuousness of translucent ornaments, such as the *Anolis* or *Draco* dewlap, can be particularly enhanced by orientation relative to the sun because the radiance of translucent objects (light reaching the receiver's eye) is the sum of light transmitted and reflected from the object (Fleishman et al. 2006; Fleishman et al. 2015). However, this effect is directional and relies on the position of the sun because the receiver must be on the opposite side of the signal than the source of illumination (Fleishman et al. 2006). This implies that animals with translucent visual signals may enhance signal conspicuousness by strategically orienting themselves perpendicular to the sun when displaying.

The arboreal gliding lizard, *Draco sumatranus*, which is common throughout Malaysia, lives in open areas with intermediate to full sun exposure (Das 2010; Grismer 2011). Both males and females possess throat-fans, or dewlaps, that are extended and retracted as part of a territorial or courtship broadcast display (Mori and Hikida 1993; Mori and Hikida 1994). The male dewlap is yellow and significantly larger in size than the female dewlap, which is grey/blue (Grismer, 2011 – fig. S5.1). Our extensive observation of these lizards also indicates that the male dewlap is translucent and light is transmitted through the skin (DAK personal observation; see also fig. 5.1A), whilst it is unclear if the female dewlap does as well. The male dewlap is also larger, appears to be stretched thinner than the female dewlap, which appears to be opaque (though this has not been directly measured).
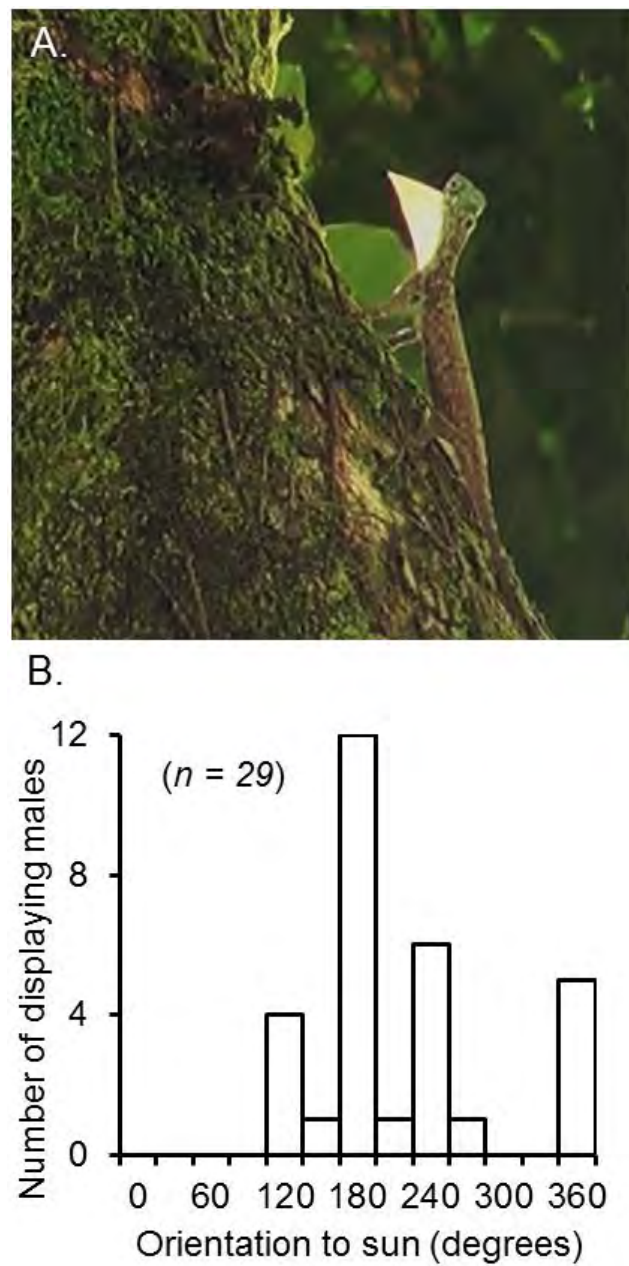
Figure 5.1   (A) *Draco sumatranus* male displaying, showing the transmission of sunlight through the dewlap; (B) Perch angle for displaying males, measured in relation to the sun (photo: T. J. Ord).

When the lizard is positioned on the trunk perpendicular to the sun, the surface of the extended dewlap is exposed to the maximum amount of light. In this case, *D. sumatranus* males that orient perpendicular to the sun would increase the amount of light transmitted through the dewlap to receivers on the opposite side and this in turn should increase the radiance of the dewlap to those receivers. Given the potential improvements to signal conspicuousness from the transmission of sunlight off or through the dewlap, we predict that males should orientate perpendicular to the sun when displaying. As transmission of light through the female dewlap appears to be minimal and notably less than that of the male dewlap, whether or not they should orientate perpendicular to the sun when displaying depends on how reflection of direct sunlight affects signal conspicuousness.

Methods

We observed free-living *D. sumatranus* lizards on the University of Malaysia Sarawak, Kota Samarahan campus in Kuching, Borneo between June and July, 2015. The lizards live on rows of trees lining both sides of roads throughout the campus, and were sighted by walking up and down the roads between 07.30 and 13.30 every day (when broadcast signals are most often produced – Mori and Hikida, 1994). It is unlikely that orientation to the sun was a secondary consequence of the spatial arrangement of the habitat. Though lizards live on trees arranged in linear rows, the habitat is still three-dimensional, with lizards interacting with each other over roads and in some instances with lizards in the forest or on other landscaped trees further back from the roads. Additionally, we sampled

several roads with different linear directions (two running north-south, one east-west and one undulating northwest-southeast, covering approximately 6 km in total).

When a lizard was spotted we recorded the sex, whether or not it was displaying (i.e. extending and retracting its dewlap), and its position on the tree trunk relative to the sun. Sex was determined by body morphology which differs between the sexes (Das 2010) and by dewlap colour and size, when lizards were displaying. In recording the position of the lizard we took the center of the trunk surface directly facing the sun to be the 0° point, and we estimated the angle between that point and the position of the lizard on the trunk (around the circumference of the tree: see fig. 5.2). This meant that a lizard positioned at 0° has their back to the sun and at 180° on the trunk the lizard is entirely shaded from the sun. At 90° the sun shines directly on the flank of the lizard and a single side of the extended dewlap. Angles around the trunk were estimated in 15° bins, by eye. *Draco* lizards are predominantly positioned vertically on the tree trunk, and broadcast displays are performed with their heads in line with the body. As sunlight is diffusely transmitted through the dewlap, the dewlap therefore transmits light in all directions regardless of the angle at which the sunlight first enters the dewlap (Fleishman 2006). As *Draco* lizards are territorial and can be observed in the same two to three tree radius on consecutive days (Mori and Hikida 1993), in order to reduce the likelihood of inadvertently re-sampling a lizard, we systematically surveyed lizards such that we did not return to the same group of trees twice.
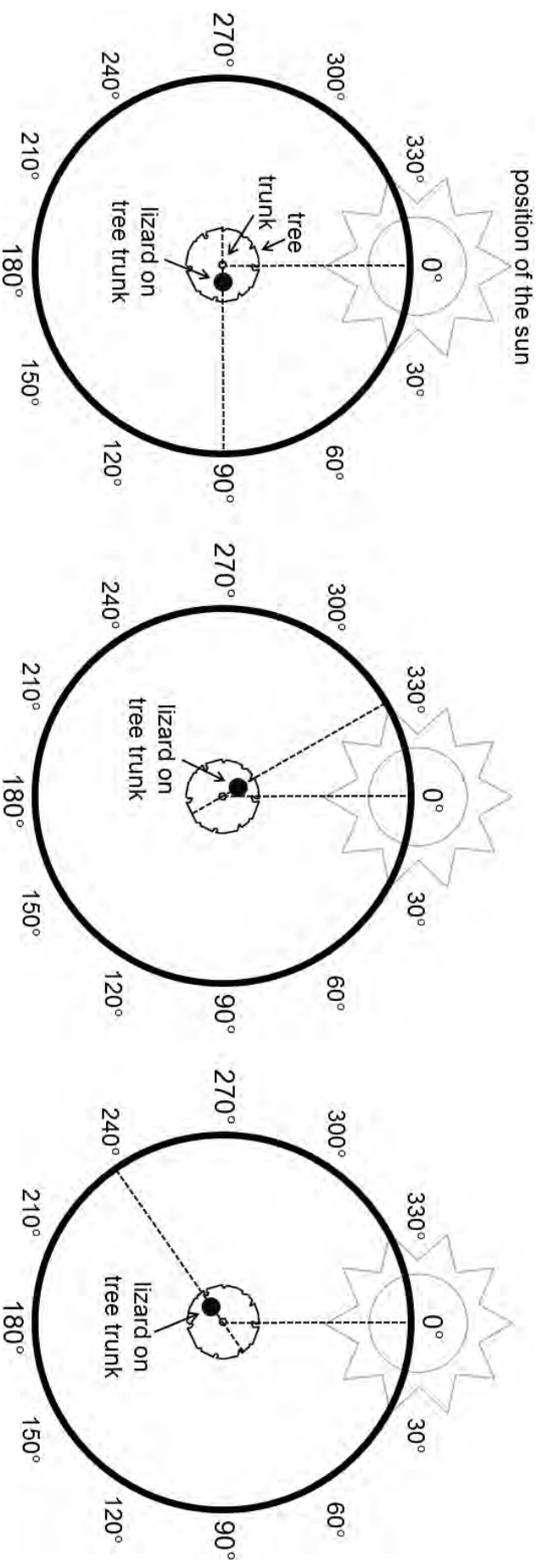
Figure 5.2 Top down view of lizard perch angles in relation to the position of the sun

We predicted lizards should orient perpendicular to the sun during displays that included the extension of the dewlap, which could either be 90° or 270° relative to the sun, making the data axially bimodal. For statistical analysis, therefore, we multiplied our data by two and subtracted 360° from all resulting angles greater than 360°, as outlined by Batschelet (1981). To test whether orientations clustered on a common mean (specifically, we predicted values corresponding to perpendicular to the sun), we used the *V* test (a modified Rayleigh test) which tests circular uniformity against non-uniformity with a specified mean angle (Durand and Greenwood 1958; Zar 2010). Analysis was performed in the program ORIANA 4.0 (Kovach Computing Services, Wales, UK).

Results

The *V* test showed males were significantly more likely to orientate themselves perpendicular to the sun when extending the dewlap in display (fig. 5.1B), but did not orientate perpendicular to the sun when not displaying (table 5.1i). The proportion of males seen displaying was higher for males than for females (males: 0.71; females: 0.28). Despite the small number of females displaying, those that did still orientated perpendicular to the sun more often than expected by chance (table 5.1ii). Again, when not displaying, females did not orientate perpendicular to the sun.

Table 5.1   *V* tests (*V*), effect size (*u*) and *p* values for displaying and non-displaying males and females. Values of *V* converging on 1 indicate orientations cluster around the expected angle of 90°, while values converging on -1 indicate orientations do not cluster at the expected angle.

	V	*u*	*p*
i. Males			
displaying (*n = 29*)	0.46	3.55	0.0001*
not displaying (*n = 12*)	-0.22	-1.075	0.86
ii. Females			
displaying (*n = 7*)	0.70	2.60	0.003*
not displaying (*n = 18*)	-0.74	-4.46	1

False discovery rate (FDR) threshold was calculated for four tests.
* *P* values that remain significant controlling for FDR, following Benjamini and Hochberg (1995).

Discussion

The clear orientation of displaying *D. sumatranus* perpendicular to the sun seems to represent a deliberate behavioural strategy for increasing the amount of light transmitted through the dewlap (at least for males) to maximize the effectiveness of the display. These types of visual broadcast displays in lizards are predominantly used by males to advertise continued territory ownership to surrounding male neighbours and potential female mates in a variety of directions and at a range of distances (Jenssen et al. 1995; Ord et al. 2007). As recent studies in birds have indicated (Olea et al. 2010; Bortolotti et al. 2011), orientating a signal to exploit direct sunlight may function to increase the effectiveness of the signal. Here we show that a similar strategy occurs in lizards – specifically that *D. sumatranus* males behaviourally enhance the conspicuousness of their ornament (the dewlap) by orienting themselves perpendicular to the sun.

Behavioral thermoregulation is an important behaviour in lizards that can influence how lizards position themselves in the environment relative to the sun (Huey et al. 2003); however it is unlikely to account for the orientation behavior we describe here for two reasons. First, lizards only orientated perpendicular to the sun when displaying, suggesting the strategy is specific to communication and not thermoregulation. Second, thermoregulation would generally be more effective for lizards orientated with the larger surface area of their backs facing the sun (if warming; Norris and Kunz, 2012) or on the opposite, shaded side of the tree (if cooling Huey and Montgomery, 1976). The more plausible explanation for this behaviour, then, is for improving the effectiveness of the broadcast displays to conspecifics in the surrounding environment.

While it is intuitive that transmission should increase the apparent brightness of the dewlap, it remains to be tested in this system. We are aware of only one study that has explicitly tested the possible signal function of light transmission through a transparent ornament. Fleishman *et al.* (2015) examined the translucent dewlap of *Anolis lineatopus*, a genus ecologically similar to *Draco* that also uses the dewlap for broadcast communication. Dewlap transmission in *Anolis* was not found to increase conspicuousness through luminance contrast of the dewlap against the background, as the broad signal background often consists of many small patches of radiance (such as the light shining through small gaps between leaves). However dewlap transmission does facilitate a receiver's ability to discriminate the dewlap colour from background colours, which could aid in the signal being detected and identified as conspecific, especially in low light habitats (Fleishman et al. 2015). It is not clear how transmission may affect the conspicuousness of signals in different habitats and light environments, and thus more work is required to understand how the transmission of light through translucent ornaments functions in communication.

Light transmission only increases conspicuousness for receivers viewing the dewlap from one side. Also, female dewlaps appear to have minimal transmission compared to males, yet both sexes orient the dewlap perpendicular to the sun. This may be because direct sunlight increases dewlap conspicuousness even when only reflected light, rather than both transmitted and reflected light, reaches the receiver's eye. Specifically direct sunlight may increase the apparent brightness of an ornament if the surface of the ornament is specularly reflective; that is, when light is reflected by a surface at a specific angle (Osorio and Ham 2002); or if the sunlight illuminates the ornament differently to the ornament's background, resulting in a greater brightness

contrast. Additionally, as the spectrum of direct sunlight is richer in shorter wavelengths than the light in canopy shade, ultraviolet and blue peaks may appear brighter in direct sunlight than in the shade (Endler 1993). Both the female and male dewlaps reflect UV light (fig. S5.1), but the female dewlap more so. Specifically, the male dewlap is yellow with a secondary UV peak, while the female dewlap is UV-blue. Therefore, orientating to maximize direct sun exposure of the dewlap likely increases the visibility of these wavelengths to receivers, particularly in the case of the female dewlap.

If transmission does enhance signal effectiveness, why don't females have more translucent dewlaps similar to those of males? Males have larger dewlaps, increasing the potential for signal transmission to enhance conspicuousness and increasing the distance at which it can be seen (Endler 1978). Females may be under weaker selection for conspicuous broadcast signals than males and our results show that females display less frequently. Though female-female conflict is occasionally observed, female *D. sumatranus* lizards are often seen in closer proximity to other females than males would tolerate from other males (personal observation), suggesting that females potentially have less impetus to defend territories. Broadcast signals are thought to be specifically associated with advertising continued territory ownership, so females may instead be reserving displays for more restricted circumstances or for communicating with specific receivers, and therefore don't require translucent dewlaps which potentially function to enhance wide-ranging broadcast signals.

Flexible behavioural strategies to increase the effectiveness of colour patterns are commonly reported in contexts other than signalling. Many recent studies have shown that in response to predation, animals are able to ingrate information both about their own appearance and their surroundings to modulate behaviour and reduce risk of detection by

predators (Briffa and Twyman 2011; Kang et al. 2014; Nafus et al. 2015; Marshall et al. 2016). However, studies addressing the interaction between colour and behavior in signalling are comparatively rare, even though modelling the appearance of the signal in the eyes of a receiver is often an objective (Bortolotti et al. 2011). The few studies addressing behavioural plasticity in communicative display confirm that some animals have the capacity to select display locations and orientations that improve signal effectiveness (Endler and Thery 1996; Endler and Basolo 1998; Campioni et al. 2010; Bortolotti et al. 2011; Sicsú et al. 2013). This study presents one of few examples outside of birds. By explicitly considering the strategies signallers might use to enhance conspicuousness, we can obtain a clearer understanding of the selection pressures that can produce novel signalling behaviours, as well as those that act on the design or structure of the signal itself.

Acknowledgments

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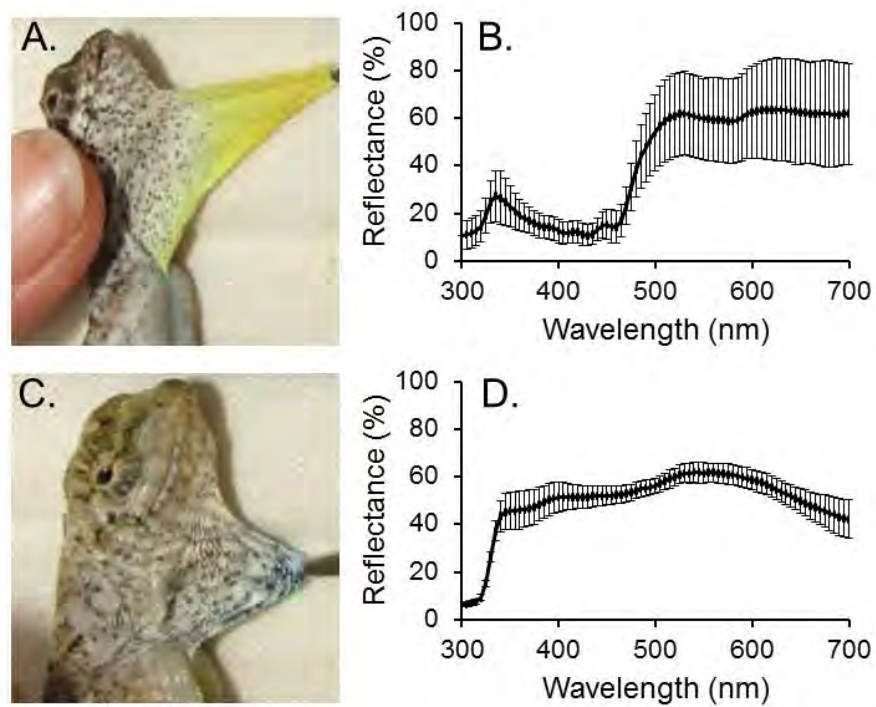
Supplementary figures

Figure S5.1   (A) *Draco sumatranus* male with dewlap out stretched; (B) male yellow dewlap colour reflectance spectrum; (C) female *Draco sumatranus* with dewlap out stretched; and (D) female blue dewlap colour reflectance spectrum.

Chapter Six

Conclusion

On understanding the role of signal design in the genus *Draco*

My thesis explored multiple factors influencing visual signalling in *Draco* to provide a greater understanding of the physical and behavioural factors that influence the evolution of visual signals. Signal components have evolved to function in various aspects of the communication process and are shaped by environmental constraints, such that when populations diverge in the type of habitat occupied, they may also diverge in signal design. By examining how different signal components function in different habitats, we stand to gain a better understanding of the specific selection pressures that influence signal evolution.

Contrary to expectation, the field-based playback experiments of chapter two found that achromatic contrast within the dewlap and of the dewlap against the background in *Draco melanopogon* does not appear to play a significant role in signal detection. Instead, I suggest that the movement of the dewlap during display is of primary importance in eliciting conspecific attention. Many vertebrates rely on the automatic 'visual grasp reflex' to bring moving stimuli detected in the periphery of their field of vision to the centre of their retina – the central fovea – with which they have a much better ability to resolve image details (Fleishman 1992; Peters and Evans 2003a; Steinberg and Leal 2013). In dynamic signals, movement is likely to play a significant role in initial detection, and studies have identified aspects such as speed, amplitude and duration as important factors in the detectability of movement (Peters and Evans 2003b; Ord and Stamps 2008; Fleishman and Pallus 2010).

Whether conspicuous colours work in conjunction with display movements to increase signal detectability has long been a topic of interest. A previous study in anoles showed an increase in both chromatic or achromatic contrast of the signal against the background improves the probability of signal detection in laboratory conditions (Persons et al. 1999). But in the field, the experiment described in chapter two found that even treatments of extreme differences in contrast are detected equally well. This may be because at ecologically relevant display distances, *Draco* lizards are not able to easily distinguish colours from their backgrounds at least when positioned in the periphery of their field of view. Once the dewlap had been detected, males responded with the greatest intensity to the conspecific dewlap treatment (70% black and 30% white) and next most to a grey dewlap treatment that was similar in appearance to the conspecific dewlap if the black and white patches cannot be distinguished from one another. This may suggest that

both treatments are interpreted as conspecific, because at farther more commonly encountered receiver distances, *D. melanopogon* lizards don't have sufficient visual acuity to resolve the individual colour components of the dewlap pattern. Therefore understanding the limits of receiver visual perception and receiver visual ecology more generally is essential for understanding the function and evolution of visual signals, as described in more detail later.

Even if dewlap movement is the primary factor eliciting the initial detection of the signal, other aspects of the dewlap signal, such as colour pattern and size are still likely to carry information and be important in communication. The alternative strategies for male conspicuousness (size vs colour contrast) between species reported in chapter three suggest that both of these aspects are important in dewlap design. That is, males of some species rely on dewlap size for conspicuousness whilst males of other species rely on dewlap colour contrast against the background. This may be because these components carry information (e.g. on individual identity or quality) and/or increase the efficacy with which the signal is transmitted (Endler 2000). Dewlap size could potentially indicate individual quality and function to determine the outcome of competitive interactions with conspecific males. Anole dewlap size has been proposed to reliably indicate bite force (Vanhooydonck et al. 2005), and thus be an honest signal of resource holding potential (Maynard-Smith and Harper 2003). The specific information content of *Draco* dewlap components has not been investigated in detail, nor was it the focus of this thesis; however it's clear from the results of chapter two that the dewlap colour pattern does function in species recognition for *D. melanopogon*, which plays an important role in intra- and inter-sexual interactions and may reinforce reproductive isolation between species.

The results from chapter three suggest that increases in either the size or colour contrast of the *Draco* dewlap are selected for in habitats with different predation intensities, but across species (regardless of habitat) dewlap size and colour contrast increase in response to the increasing strength of sexual selection. This is the case for visual ornaments in many taxa (Andersson 1994), and it suggests that in *Draco*, sexual selection may be the most consistent single pressure in the evolution of the male dewlap across the genus. Unlike that of males, female dewlaps show no relationship to the potential indicators of sexual selection, perhaps because the impetus to defend territories is not as great for females as it is for males, and/or males show minimal mate choice. Males that successfully defend territories gain exclusive matings with the females that reside within those territories. In many vertebrate systems larger or conspicuous male signals are the result of female mate choice, but this has not been shown to play a role in many reptile species (Tokarz 1995).

However, sexual selection is unlikely to be the sole driver of the repeated signal divergence that has occurred in *Draco*. Divergence in signals is more often due to the interaction between environmental factors and sexual selection (Ritchie 2007). The sensory drive hypothesis – suggesting that the environment plays an important role in the divergence of sexual signals – has garnered considerable support since it was first proposed nearly twenty-five years ago (Marchetti 1993; Leal and Fleishman 2004; Maan et al. 2006; Rosenblum 2006; Uy and Stein 2007; Seehausen et al. 2008; Harrison and Poe 2012). However, evidence of the effect of visual environments on signal efficacy is much clearer in studies of aquatic systems than those of terrestrial systems (Fleishman et al. 2009; Ng et al. 2013). This may be because ambient light is considerably more variable between aquatic habitats than terrestrial habitats. Signals in clear water are often

viewed against a blue or green-shifted background, due to the attenuation of longer

wavelengths over distance, and this effect increases as the water depth or receiver

distance increases. In turbid water this effect is reversed, as suspended particles attenuate

the shorter wavelengths of light (Boughman 2001). Light in terrestrial systems varies less

significantly in spectral shape and given that photoreceptors adapt to the ambient level of

illumination (Endler 1993a; Vorobyev and Osorio 1998), differences in ambient light is

less likely to be the sole or most important cause of signal divergence between

populations occupying different habitats.

In terrestrial systems, the more relevant selection pressure on signal design seems

to be the intensity of predation. Different predator communities in different habitats have

a major impact on which signals are viable for communication (Endler 1978; Endler

1993b; Godin and Mcdonough 2003; Stuart-Fox et al. 2003; Stobbe and Schaefer 2008).

Populations in habitats with different predation intensities, or differences in predator

communities (and therefore the ways predators locate and identify prey), would

experience very different constraints on signal design which may lead to signal

divergence. Of the two alternative strategies that *Draco* species use for dewlap

conspicuousness revealed in chapter three (increased size or increased chromatic contrast

against the background), species that relied on dewlap size (and not colour contrast) were

those found in habitats with the highest predation intensities. This suggests that

chromatic contrast may increase predation risk more than relative dewlap size. Many

predatory birds have good colour vision (Osorio and Vorobyev 2005), which may explain

this result, but the visual ecology and behaviour of the specific predators of *Draco* (and

many other taxa) is not well known, making detailed assessments of the impact of

predation on signal design difficult. The idea that chromatic contrast may increase

predation risk more than dewlap size has not been formally tested, and would require experimental tests of predation risk in response to independent manipulations of dewlap colour contrast and size.

It is apparent that predation is a significant selection pressure in *Draco* species. Despite the gliding membranes of some *Draco* species potentially being used in signalling, the results of chapter four strongly suggest that patagia colouration in two populations of *D. cornutus* has instead been selected to camouflage lizards gliding between trees. The habitats of the two populations differ in the colours of falling leaves (red in the mangroves and green in the forest), and the gliding membranes of the *D. cornutus* populations match the colours of falling leaves in their respective habitats to many predatory birds. The achromatic colour match is convincing, but the chromatic match between patagia and falling leaves is especially close. This is a good example of how when viewed out of the natural context, body colouration may appear conspicuous but in reality functions as camouflage. It also highlights the strong influence of predation on body colouration in *Draco* given it appears to have resulted in divergence between populations of the same species (and perhaps other species as well; see Chapter four).

Chapter five of this thesis found that *D. sumatranus* lizards orientate themselves when displaying, so that their dewlaps are perpendicular to the sun, probably increasing the effectiveness of the dewlap signal. These results are consistent with recent studies showing that certain animals are sufficiently aware of their surroundings to exploit environmental variation to increase the effectiveness of visual signals (Endler and Thery 1996; Doucet and Montgomerie 2003; Penteriani and Delgado 2009; Ord et al. 2011). Studies of a broad range of taxa show that this awareness not only results in behavioural modifications to enhance signal conspicuousness, but also to enhance camouflage. For

example, in times when the perceived risk of predation is heightened, animals may modulate display so that it is less likely to elicit predator attention (e.g. Steinberg *et al*. 2014), and animals that signal with otherwise concealed ornaments, like the dewlap, can avoid signalling altogether (until the risk of predation is reduced). Adapting the behaviour associated with signalling means that these species are less constrained by their signalling environments (and potentially population variation in those environments), and thus the pressure for signals to diverge in different habitats may be reduced.

The results of chapter five also highlight how differences in the appearance of the signal arise from relatively minor changes in the position of the receiver and signaller in heterogenous and complex environments. Visual ecologists model the conspicuousness of colours given the spectral sensitivities of the receiver, but results of these models are highly dependent on the context in which the signal is viewed (Renoult et al. 2015). For instance, the position of the receiver and the signaller relative to each other and to the sun can have a large impact on the illumination of the signal and therefore how much light is reflected (or in some cases transmitted) and of which wavelengths (Endler 2000; Fleishman et al. 2006). In addition, ambient lighting conditions change temporally – over the day and year, and with the weather – and are spatially heterogeneous – depending on habitat structure (Endler and Thery 1996; Bro-Jørgensen 2010). The background colours also influence the conspicuousness of signal colours, but what constitutes the relevant signal background changes with receiver distance and signallers also have the potential to behaviourally control the immediate signal background through microhabitat selection (Endler 1993b; Leal and Fleishman 2004; Uy and Endler 2004). All of these factors can lead to changes in the appearance of a visual signal, but are rarely all modelled.

Our current understanding of the perception of signals by receivers is rudimentary and uncertainty surrounding estimations of signal appearance is one of the main issues in the field of visual ecology today (Kemp et al. 2015; Renoult et al. 2015). To determine the conspicuousness of colour signals we largely use models that incorporate the spectral sensitivities of receivers, but this is often limited by the availability of photoreceptor data, which is species specific. Nevertheless, spectral sensitivities, at least within major groups of terrestrial vertebrates, tend to be highly conserved (Fleishman et al. 1997; Osorio and Vorobyev 2005; Hart and Hunt 2007; Hunt et al. 2009). The visual acuity of receivers is also rarely known, though this can have a large impact on signal appearance (specifically whether individual colour patches can be resolved or appear as a 'blended average'), as was seen in chapter two of this thesis. But regardless of our knowledge of the visual physiology of a species, it is still not well understood how specific physiology relates to the neural processes underlying perception (Kemp et al. 2015).

Visual models based on photoreceptor noise, such as I have employed throughout this thesis, are able to accurately predict colour discrimination thresholds ('just noticeable differences' - JNDs) that have been behaviourally determined (Kelber et al. 2003). This is excellent for estimating whether two very similar colours can be distinguished (at least 75% of the time) by a given receiver under ideal conditions, but whether these models are also appropriate for modelling how very different colours are perceived (e.g. a red dewlap against a green vegetation background) under variable viewing conditions is currently a topic of much discussion (Kemp et al. 2015; Renoult et al. 2015). That is, we have little understanding of how perceptual differences scale with JNDs (e.g. whether they scale linearly). Scaling of perceptual differences with JNDs can only be determined

by testing receiver behaviour, and few of these experiments have been undertaken to date. To this end, Fleishman *et al.* (2016) conducted behavioural assays testing the relative conspicuousness of different signal and background colour combination in *Anolis sagrei* lizards, and found visual models based on photoreceptor noise are able to make behaviourally relevant predictions of the 'perceptual distance' between conspicuous colours and their backgrounds. This is encouraging, but this work needs to be replicated, and across multiple taxa, in order to verify the generality of these results.

This thesis has presented the results of experimental and observational studies that confirm the centrality of sexual selection, species recognition and predation as primary factors influencing signal design in *Draco*. By investigating the physical and behavioural factors influencing the evolution of different signal components, this thesis furthers our understanding of signal divergence in *Draco*. Still, a great deal more research is required to fully understand the role of the dewlap, or any visual signal, in speciation. Specifically, evaluating relevant selection pressures based on the function and processes of complex and dynamic signals, and better understanding the appearance of signals to both intended and unintended receivers, will facilitate our understanding of how visual communication has led to signal (and ultimately species) diversity in *Draco*, as well as our understanding of the evolution of colour and ornament diversity throughout the animal kingdom.

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