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Cite this article: Klomp DA, Stuart-Fox D, Das I, Ord TJ. 2014 Marked colour divergence in the gliding membranes of a tropical lizard mirrors population differences in the colour of falling leaves. *Biol. Lett.* **10**: 20140776. <http://dx.doi.org/10.1098/rsbl.2014.0776>

Received: 26 September 2014

Accepted: 2 December 2014

Subject Areas:

evolution

Keywords:

crypsis, antipredator behaviour, geographical variation

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2014.0776> or via <http://rsbl.royalsocietypublishing.org>.

Animal behaviour

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

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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 that the two populations have diverged in gliding membrane coloration to match the colours of their local falling leaves, and that mimicking falling leaves is an adaptation that functions to reduce predation by birds.

1. 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 [1,2]. Patagia are often strikingly coloured when extended, and vary markedly among the 42 described species. Given the apparently conspicuous and diverse coloration of patagia, an obvious hypothesis is that patagial function is associated with social communication [2]. An alternative hypothesis for the coloration of patagia in *Draco* is that it provides camouflage during gliding by resembling falling leaves (electronic supplementary material, figure S1) to reduce the probability of detection by predators. The size of *Draco* lizards, and their shape when gliding with outstretched patagia, are comparable to that of falling leaves. Birds probably constitute the greatest risk for *Draco* while gliding owing to their likely vantage points and mobility [3].

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 coloration 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* (electronic supplementary material, figure S2). 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 coloration in males. By assessing behavioural footage for several species of *Draco*, we first verified that patagia are rarely extended during display

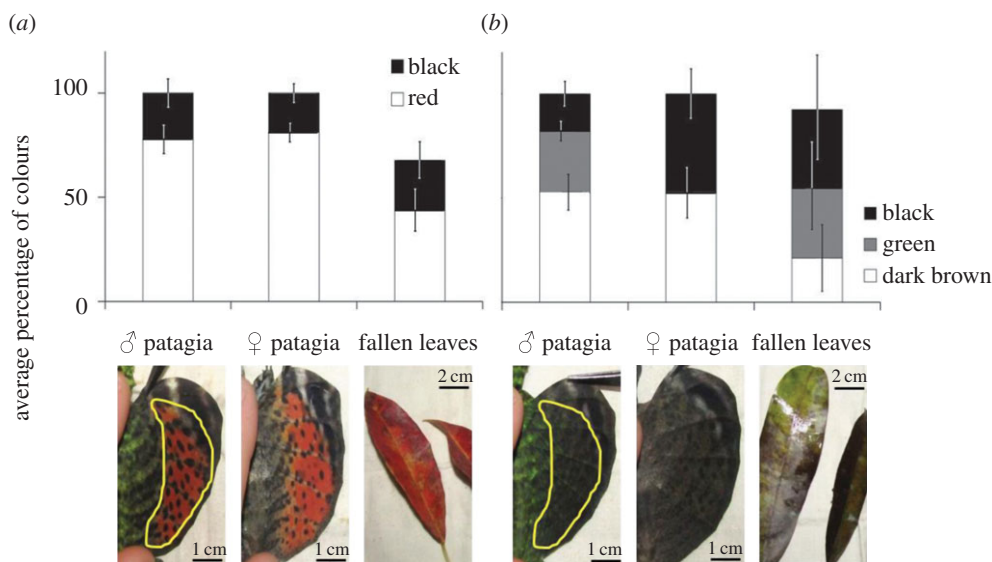


Figure 1. The proportions (and 95% CIs) of colours in the central patagia section for *Draco cornutus* males and females, and the proportions of predominant colours of fallen leaves at (a) Bako National Park and (b) Niah Caves National Park. The falling leaf colours with the smallest proportions are 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.

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 colours of the patagia were from the colours of falling leaves and standing foliage from the point of view of a predatory bird. If selection for resemblance to local falling leaf coloration has driven divergence in patagial coloration in *D. cornutus*, we predicted that the colours of the patagia should closely match 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.

2. Material and methods

Over 32 h of footage was compiled for males of six *Draco* species (table 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 m from the focal lizard and recording continued for 30 min or as long as the lizard remained in view. Footage was analysed for the frequency of patagia extensions.

We captured six male and 10 female *D. 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.* [4], and detailed in the electronic supplementary material, S1. A refuse bag (1.02 × 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 h. 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 cm² 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 (figure 1).

Table 1. Frequency of patagia extension (excluding those involved in gliding) from over 32 h of behavioural footage of *Draco* species.

population	no. patagia extensions min ⁻¹ (median (range))	no. individuals surveyed
<i>D. cornutus</i> (Niah)	0 (0)	17
<i>D. cornutus</i> (Bako)	0 (0–0.15)	14
<i>D. haematopogon</i>	0	1
<i>D. melanopogon</i> (Gombak)	0 (0–0.31)	21
<i>D. melanopogon</i> (Niah)	0 (0)	4
<i>D. obscurus</i>	0 (0)	3
<i>D. quinquefasciatus</i> (Gombak)	0 (0)	3
<i>D. quinquefasciatus</i> (Niah)	0 (0–0.033)	4
<i>D. sumatranus</i>	0 (0)	16

To determine how patagia colours would be perceived by predatory birds we applied the model of Vorobyev & Osorio [5], 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.* [6] and McLean *et al.* [7] and are detailed in the electronic supplementary material, S1.

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

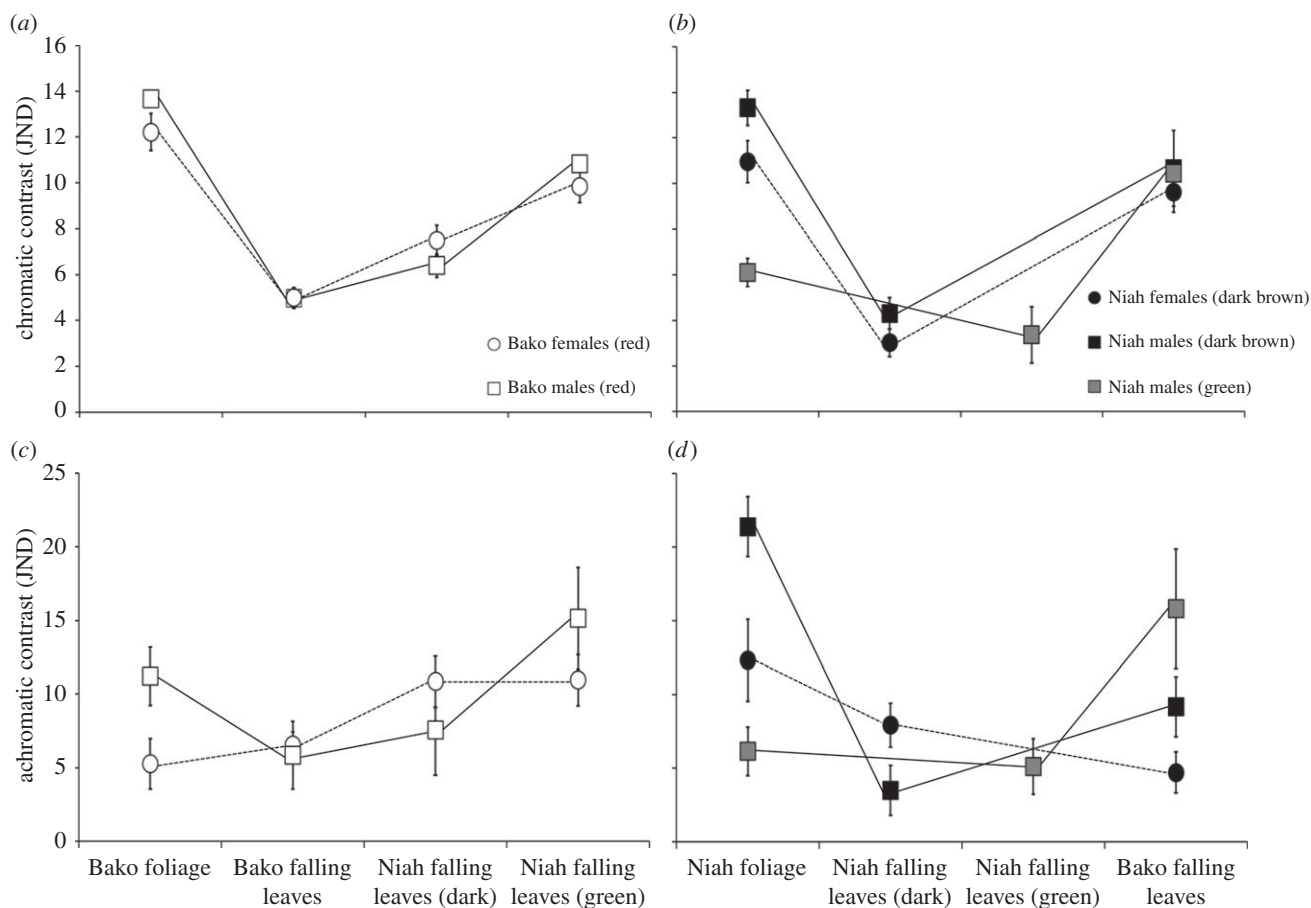


Figure 2. Chromatic contrast for the population at (a) Bako National Park and (b) Niah Caves National Park and achromatic contrast for (c) Bako and (d) Niah populations (means, 95% CIs) in JND. Values represent contrasts between colours of the patagia of *Draco cornutus* at Bako and Niah, colours of the local falling leaves (Bako fallen leaves/Niah fallen leaves (dark)/Niah fallen leaves (green)) and colours of standing foliage (Bako foliage/Niah foliage).

Bako had a single predominant patagia colour (figure 1a), at Niah there were two main colours in male patagia and two main fallen leaf colours: dark grey-brown and green (figure 1b). We therefore contrasted the dark and green male patagia colours against the dark and green parts of local fallen leaves, respectively. Niah females have only dark grey-brown and that was contrasted against the dark of fallen leaves. We used general linear mixed models (SAS v. 9.3 (SAS Institute, Cary, NC, USA); 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.

3. Results

The behavioural observations of six Malaysian *Draco* species indicate that the patagia are very rarely extended during social displays (table 1). We found that the proportions of the colours in the patagia were similar to the proportions of those in the local fallen leaves (figure 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; figure 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 2). Predominant patagia colours matched those of local falling leaves significantly better than local standing foliage (Tukey post-hoc test: $p < 0.0001$) or either falling leaf colour from the other (Niah) population (dark brown: $p = 0.023$; green: $p < 0.0001$; figure 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: $p = 0.75$; figure 2c).

At Niah, there was a significant interaction between sex and background for both chromatic and achromatic contrasts (table 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 ($p = 0.54$; figure 2b). In terms of achromatic contrast, neither the dark brown patagia colour of males nor females matched the dark local falling leaves better 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

Table 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. 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).

	chromatic contrast		achromatic contrast	
	$F_{d.f.}$	p -value	$F_{d.f.}$	p -value
Bako National Park				
sex	0.62 _(1,47)	0.43	1.10 _(1,47)	0.30
background	57.85 _(3,47)	<0.0001	3.86 _(3,47)	0.015
sex × background	1.49 _(3,47)	0.23	2.14 _(3,47)	9.11
Niah Caves National Park				
sex	5.39 _(2,26)	0.011	0.01 _(2,26)	0.99
background	65.12 _(2,26)	<0.0001	6.98 _(2,26)	0.0038
sex × background	5.34 _(4,26)	0.0028	5.54 _(4,26)	0.0023

local standing foliage ($p = 0.0004$), but this was not the case for females ($p = 0.99$) nor for the green patches of the male patagia against the green local falling leaves ($p = 1.00$; figure 2*d*), as the greens of falling leaves and standing foliage are similar.

4. 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 the gliding membranes of *D. cornutus* are rarely used for communication, reinforcing the view that patagia coloration has instead been selected to specifically resemble the colours of falling leaves.

This study recorded an average of six leaves falling onto a 1.24 m² quadrat over 48 h—equivalent to 1008 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 [8,9], suggesting that falling leaves are sufficiently common for mimicry to confer a survival benefit. Additionally, gliding is an integral part of *Draco* ecology [2,10]. Our behavioural observations of these populations recorded a combined average of 3.8 glides per hour, indicating that vulnerability to predation while gliding would constitute a considerable selection pressure. Although motion plays an important role in prey detection by birds [11], 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 [12]. By contrast, the limited or absent sexual dichromatism in the patagia provides further, indirect support for the hypothesis that patagia

coloration functions in camouflage rather than social communication. However, these hypotheses are not mutually exclusive and McGuire & Dudley [2], 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 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 coloration 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 coloration 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 *Draco* species (*D. melanopogon* at Niah, *D. spilopterus* in the Philippines, *D. quinquefasciatus* at Niah and *D. formosus* on the Malay Peninsula; electronic supplementary material, figure S1) 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.

Acknowledgements. We are grateful to Jim McGuire and Lee Grismer for advice on *Draco*. Permits: Malaysian Economic Planning Unit, Sarawak State Planning Unit, Sarawak Forestry Department and Sarawak National Parks and Nature Reserves and the UNSW ACEC protocol #11/33b.

Author contributions. D.K., D.S.F. and T.J.O. conceived the study; D.K., D.S.F. and T.J.O. collected the data; I.D. provided critical support during data collection; D.K. and D.S.F. performed analyses; all authors contributed to writing the manuscript.

Funding statement. Funding was from the National Geographic Society (8875-11). I.D. is supported by a Niche Research Grant Scheme, NRRGS/1087/2-13(01).

Conflict of interest. The authors declare no conflict of interests.

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