

Ultraviolet reflectance in Malagasy chameleons of the genus *Furcifer* (Squamata: Chamaeleonidae)

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Abstract. Chameleons are well known for their colourful appearance and their ability to change colours. Although tetrachromatic colour vision has been proven, UV-reflecting colour patterns have not been studied in chameleons so far. The study presented here provides preliminary data on UV-reflecting colour patterns in chameleons. Three Malagasy chameleon species (*Furcifer pardalis*, *Furcifer lateralis* and *Furcifer oustaleti*) were investigated in terms of UV-reflectance of colour patterns, using a fibre optic spectrophotometer. We show that several body regions reflect in the UV spectrum, i.e. within 300-400 nm. Functions of the reflectance in UV spectrum are briefly discussed.

Key words. Reptilia, Chamaeleonidae, *Furcifer pardalis*, *Furcifer lateralis*, *Furcifer oustaleti*, UV-reflectance, visual communication.

UV-reflectance of body coloration in animals is found in a wide variety of taxonomic groups including arthropods (LYYTINEN et al. 2004), fish (RICK et al. 2004), birds (BENNETT et al. 1996, CUTHILL et al. 2000, SHAWKEY et al. 2003) and reptiles (BLOMBERG et al. 2001, LEAL & FLEISHMAN 2004, MOLINA-BORJA et al. 2006). There is an increasing interest in studying UV-reflecting colour patterns in animals and there is evidence that individuals within these taxonomic groups are able to detect ultraviolet light (JACOBS 1992, FLEISHMAN et al. 1993, BRUNTON & MAJERUS 1995, LOSEY et al. 1999, CUTHILL et al. 2000, BOWMAKER et al. 2005).

Among lizards, there are only a few studies in terms of UV-reflecting body coloration (e.g. FLEISHMAN et al. 1993, LE BAS & MARSHALL 2000, BLOMBERG et al. 2001, MOLINA-BORJA et al. 2006), although many reptile species have a conspicuous colourful appearance or a complex display behaviour with brightly coloured patterns. Chameleons in particular are known for their ability to change colour immediately and to show one of the most complex colour display behaviours in animals.

Chameleons are mainly visually oriented animals with a strong sexual dichromatism and it is well known that coloration plays a decisive role in the social and especially sexual communication of chameleons (e.g. PARCHER 1974, CUADRADO 2000, FERGUSON et al. 2004). BOWMAKER et al. (2005) showed that some chameleon species (*Furcifer lateralis*, *F. pardalis*, *Chamaeleo dilepis*, *C. calyp-*

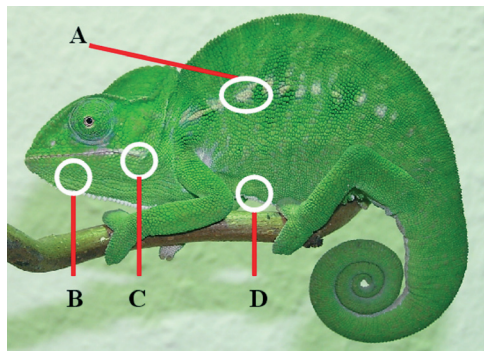


Fig. 1. Male *Furcifer lateralis*. White circles represent body regions where reflectance between 300 and 700 nm was measured. A: midlateral stripe; B: gular region; C: mouth corner; D: ventral ridge. Not to scale.

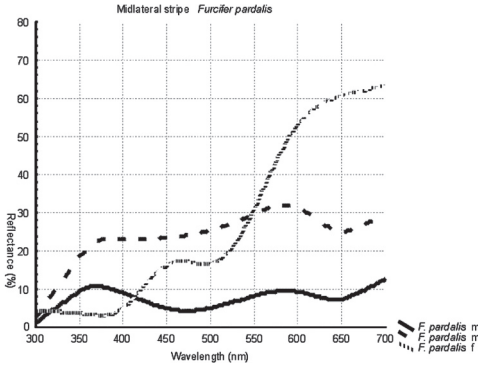


Fig. 2. Ultraviolet reflectance of the midlateral stripe in two males and one female of *Furcifer pardalis*. Reflectance is given in %, wavelength in nm.

tratus) have tetrachromatic colour vision. In the retinas of these species, they found single cones containing visual pigments with a spectral maximum between 375–385 nm. In *C. dilepis*, the spectral maximum reached nearly 350 nm.

Here we provide, for the first time to our knowledge, data on UV-reflectance patterns of body coloration in chameleons.

The genus *Furcifer* is distributed in Madagascar and on some Indian ocean islands (KLAVER & BÖHME 1986, FERGUSON et al. 2004). The following general descriptions are based on GLAW & VENCES (1997) and personal observations. *Furcifer lateralis* is a small (total length: 200–250 mm) chameleon, widely distributed throughout Madagascar. It is characterised by a white medioventral line and three dark circles on the flanks. Colour patterns are highly variable. Specimens from the south-west seem to differ by a brighter green coloration with turquoise eyelids. The *F. lateralis* individuals used in this study are specimens of the latter colour type. *Furcifer oustaleti* is a very large (total length in males: up to 680 mm) chameleon, and widespread throughout Madagascar. Males are generally greyish-brown, while females can have red coloration on head and forelegs and are greenish in some populations. *Furcifer pardalis* is a colourful, large (total length in males:

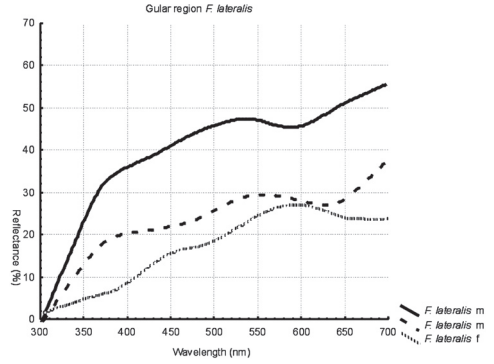


Fig. 3. Ultraviolet reflectance of the gular region in two males and one female of *Furcifer lateralis*. Reflectance is given in %, wavelength in nm.

up to 520 mm) chameleon, common in the lower northern parts (distributed from Ankaramy in the west to Tamatave in the east of the island) of Madagascar. The coloration of males is quite variable, and many local coloration variants can be distinguished.

Altogether, eight adult specimens of the genus *Furcifer*, two male and one female *F. pardalis* and *F. lateralis*, and one male and one female *F. oustaleti*, were investigated in this study. We measured UV-reflectances of the gular region, corner of the mouth, midlateral stripe, ventral ridge and conspicuous patterning (e.g. bright spots) (Fig. 1), using an Avantes AVASPEC - 2048 Fiber Optic spectrometer. A bifurcated 200 micron fibre optic reflection probe, with unidirectional illumination and recording, was held at a 90° angle to the body surface, over an area of 3 mm in diameter. Illumination was given by a Deuterium Halogen light source (AVALIGHT - DHS, 176–1100 nm). The intensity of reflectance over the range of 299–701 nm was recorded relative to a 99% Spectralon white standard. We collected one representative scan from each body region at about 0.5 nm resolution. Data were recorded with AvaSoft 6.2.1 (Avantes, Netherlands) and imported into Microsoft Excel. Analyses were performed with Microsoft Excel and Statistica.

All the regions tested showed reflectance

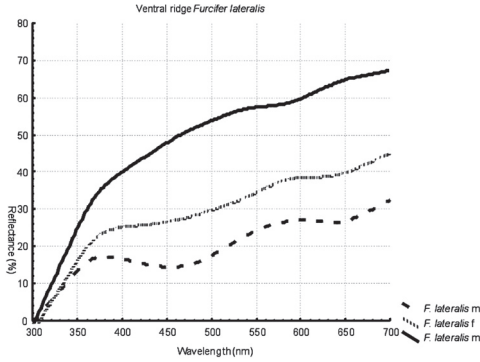


Fig. 4. Ultraviolet reflectance of the ventral ridge in two males and one female of *Furcifer lateralis*. Reflectance is given in %, wavelength in nm.

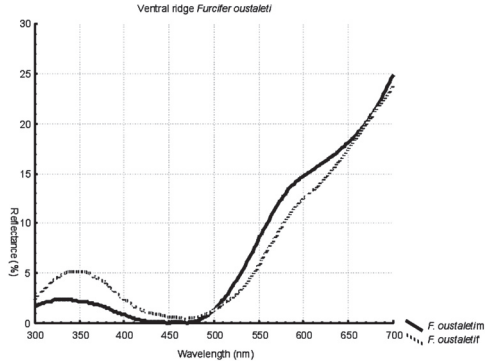


Fig. 5. Ultraviolet reflectance of the ventral ridge in one male and one female of *Furcifer oustaleti*. Reflectance is given in %, wavelength in nm.

in the ultraviolet waveband in all species (see Table 1). For *F. pardalis*, we found a clear reflectance in the ultraviolet waveband between 300 and 400 nm in both sexes. In particular the corner of the mouth and the midlateral stripe (Fig. 1) in males reflected in the UV waveband, with intensities up to 25%.

For the midlateral stripe of *F. lateralis* we measured reflectance intensities of 15% and 10% in males and only 4% in the female (Fig. 2). The gular region (Fig. 3) and the ventral ridge (Fig. 4) showed a high UV-reflecting intensity in *F. lateralis* in males especially, with intensities up to 46% (see Table 1).

Both sexes of *F. oustaleti* showed a lower UV-reflectance intensity in all body regions compared to *F. pardalis* and *F. lateralis*. The UV-reflectance intensity (300–400 nm) reached only 12% at 335 nm in the midlateral stripe in the male *F. oustaleti*, and maximally 10% in the female. Other body regions, e.g. the ventral ridge of *F. oustaleti*, showed an UV-reflectance intensity between 1 and 10% (Fig. 5).

Some conspicuous colour patterns and body parts were also measured, but not in each individual. Males of *F. lateralis* for example showed blue spots on the body flanks, which did not occur in the other species or even in the female. These blue spots had a peak of maximum UV-reflectance intensity

of 12% at 328 nm. The *F. oustaleti* male showed white spots on the body flanks with a peak of 16% at 348 nm. The inside of the hands and limbs in all species and both sexes showed a high UV-reflectance, reaching up to 43% at 362 nm in the *F. lateralis* female.

When comparing the intensity of UV-reflectance in body regions, it seems that each species has a different waveband with a specific maximum of UV-reflectance intensity. Although we could not analyse the differences in UV-reflectance statistically because the number of tested animals was too low, it is obvious that there are some differences in the UV-reflectance intensity between species and between sexes within a species.

The results of our study showed that there are distinct UV-spectra in the coloration of different chameleon species. It seems that there are species- and sex-related differences in the intensity and maximum peaks of these UV-reflectance patterns. In addition to UV-reflecting body regions, DODD (1981) showed that two African chameleon species (*Chamaeleo gracilis* and *Bradypodion fischeri*) also reflect in the infrared spectrum. Thus, the complex colour appearance of chameleons seems to be by far more complex than previously thought, with visual signals not detectable by the human eye.

BOWMAKER et al. (2005) had already re-

ported that chameleons have tetrachromatic colour vision and suggested a role within the context of intraspecific communication. Preliminary data on *F. lateralis* showed that the intensity of UV-reflectance of coloration in a male nearly doubled after seeing a female (pers. obs.). Observations on competing males of *F. pardalis* and *F. lateralis* also showed that UV-reflecting colour patterns (e.g. white midlateral stripe, blue spots around the eyelid, white spots on the body) were more prominent after social interactions than without social interactions (FERGUSON et al. 2004, pers. obs.). There is strong evidence that UV-reflecting colour patterns play a distinct role in the communication and sexual selection of these highly visually oriented lizards. SCHWENK (1995) suggested that UV-reflectance may be an important

component of display behaviour, particularly in lizard species with reduced chemosensory activity. This may be relevant to chameleons as well.

All three tested species are widespread throughout Madagascar and sometimes co-occur in the same habitat. In particular, *F. oustaleti* and *F. pardalis* are sympatric in northern and northwestern Madagascar with very similar structural niches in degraded and suburban habitats (FERGUSON et al. 2004; pers. obs.). Interspecific differences in UV-reflecting colour patterns beside other, more obvious differences in coloration, may be an important pattern in intraspecific recognition. This may be particularly important in degraded habitats with a high UV radiation, like those preferentially inhabited by *F. pardalis*, *F. oustaleti* and *F. lateralis*.

Tab. 1. Summary of the measured reflectance intensities (%) in the Ultraviolet waveband (300-400 nm) in four different body regions of three chameleon species (*Furcifer pardalis*, *F. lateralis* & *F. oustaleti*). R_{\min} gives the minimal measured reflectance intensity; R_{\max} the maximal reflectance intensity. In most cases the reflectance intensities are increasing along with the wavelength (nm), but in some cases exceptions are described as Peaks or as Plateaus. Wavelength (nm) and reflectance intensities are given for these special cases. R_{pl} gives the reflectance intensity at the Plateau, R_p gives the reflectance intensity for a Peak.

Body region	<i>Furcifer pardalis</i>		
	male 1	male 2	female
Midlateral stripe	300-400 nm R_{\min} 2% - R_{\max} 25%	300-400 nm R_{\min} 2% - R_{\max} 12% Peak 370 nm R_p 12%	300-400 nm R_{\min} 3% - R_{\max} 4%
Gular region	300-400 nm R_{\min} 4% - R_{\max} 15% Peak 390 nm R_p 15%	300-400 nm R_{\min} 5% - R_{\max} 10%	300-400 nm R_{\min} 2% - R_{\max} 12% Plateau 332-400 nm R_{pl} 12%
Mouth corner	300-400 nm R_{\min} 9% - R_{\max} 25% Plateau 345-400 nm R_{pl} 25%	300-400 nm R_{\min} 11% - R_{\max} 30% Plateau 340-400 nm R_{pl} 30%	no Data available
Ventral ridge	300-400 nm R_{\min} 6% - R_{\max} 17% Plateau 357-390 nm R_{pl} 15%	no Data available	300-400 nm R_{\max} 8%

Preliminary data for *Rhamphoeleon brevicaudatus*, a small terrestrial chameleon that lives in the leaf litter of African forests, a rather dark photic environment, showed interestingly also UV-reflecting colour patterns on its body surface (pers. obs.).

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	<i>Furcifer lateralis</i>		<i>Furcifer oustaleti</i>	
male 1	male 2	female	male	female
300-400 nm R _{min} 0% - R _{max} 15% Plateau	300-400 nm R _{min} 0% - R _{max} 10% Plateau	300-400 nm R _{max} 5%	300-400 nm R _{min} 6% - R _{max} 12% Plateau	300-400 nm R _{min} 5% - R _{max} 10%
350-380 nm R _{pl} 14%	350-380 nm R _{pl} 10%		330-380 nm R _{pl} 12%	
300-400 nm R _{min} 0% - R _{max} 46%	300-400 nm R _{min} 0% - R _{max} 20%	300-400 nm R _{min} 1% - R _{max} 9%	300-400 nm R _{min} 0% - R _{max} 3%	300-400 nm R _{min} 5% - R _{max} 10% Peak 340 nm R _p 10%
300-400 nm R _{min} 0% - R _{max} 25%	300-400 nm R _{min} 5% - R _{max} 17% Plateau 330-400 nm R _{pl} 17%	300-400 nm R _{min} 3% - R _{max} 9%	300-400 nm R _{min} 0% - R _{max} 7% Peak 330 nm R _p 7%	no Data available
300-400 nm R _{min} 0% - R _{max} 40%	300-400 nm R _{min} 0% - R _{max} 18% Peak 380 nm R _p 18%	300-400 nm R _{min} 0% - R _{max} 25%	300-400 nm R _{min} 1,5% - R _{max} 2,5%	300-400 nm R _{min} 2% - R _{max} 5% Peak 340 nm R _p 5%

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