# Hues of a dragon's belly: morphological correlates of ventral coloration in water dragons

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#### Keywords

*Physignathus lesueurii*; Agamidae; ventral coloration; body size; signalling; spectroradiometry.

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### Abstract

Sexual dichromatism is common in lizards, and may play an important role in sex recognition and mating systems. Nonetheless, relatively few published papers provide quantitative analyses of colour, deal with Australian taxa or are based on large-bodied species. Water dragons *Physignathus lesueurii* (Agamidae) from eastern Australia are very large (upto 1 m total length) and sexually dichromatic, with conspicuous red ventral coloration in adult males. We quantified coloration in three ventral regions (throat, chest and abdomen) of males and females using a spectroradiometer and looked for associations of colour with sex and with morphological traits predicted to correlate with fitness (body size, body condition, relative head size and asymmetry of femoral pores). Among adult males, larger individuals showed less red on the abdomen than did smaller animals, and males with relatively large heads had darker, less red abdomens than did males with smaller heads. Among adult females, larger animals had darker chests, and less red on the abdomen and chest, than did smaller females. The similarity in these trends between the sexes, and the location of the sexually dichromatic and size-sensitive colours in an area (under the abdomen) where they presumably are not visible to other lizards cast doubt on their utility as sexual or dominance signals. Hence, although we documented significant sex and body-size effects on ventral coloration, our results suggest that ventral colours in water dragons do not function in sex-specific displays.

## Introduction

Many vertebrates display conspicuous colours that function as signals (Butcher & Rohwer, 1989; Andersson, 1994). Among lizards, body colour can have several functions (Cooper & Greenberg, 1992), with individuals using colour to ascertain the species (Losos, 1985), sex (Cooper & Burns, 1987), reproductive state (Hager, 2001) and/or social dominance (Olsson, 1994; Zucker, 1994) of another individual. In species with pronounced sexual dichromatism (i.e. sex differences in colour), male-specific intense colours typically develop at sexual maturity and hence likely have resulted from sexual selection - probably, male-male competition (Andersson, 1994). Direct colour-based mate choice by females is rare in lizards (Tokarz, 1995; Kwiatkowski & Sullivan, 2002) whereas male-male aggression is common. In some species, males with the largest patch of conspicuous coloration are more likely to win agonistic encounters (Olsson, 1994) and have a higher mating success (Anderholm et al., 2004). Theory predicts that such a correlation between colour and fitness should also generate correlations between colour and fitness-relevant morphological traits such as body size and relative head size. The rationale for this prediction is that for coloration to be an 'honest' signal,

it should be so costly that low-quality individuals cannot afford to display intense colours (Iwasa, Pomiankowski & Nee, 1991). Such costs of nuptial coloration may involve vulnerability to predation (Forsman & Shine, 1995), parasites (Salvador *et al.*, 1996) or male-male aggression (Martín & Forsman, 1999). When carotenoids are the pigments involved in coloration, there may be a trade-off between allocation of carotenoids to signals and to other functions, such as immune system activation (Olson & Owens, 1998). Coloration also affects thermoregulation and camouflage in lizards, and these functions should be important for sexual signals that are located on the dorsal part of the body, although probably of little importance for signals located on the ventral part (Cooper & Greenberg, 1992).

Although lizard coloration has attracted intensive research, most of this work has involved relatively smallbodied species in North America and Europe. Thus, the function of sex-specific colours in many strikingly dichromatic lizard species remains unknown. One such species is the water dragon *Physignathus lesueurii* (Agamidae, Reptilia) from eastern Australia (Cogger, 1986). We studied colour and its morphological correlates in a free-living population of the northern subspecies (*Physignathus lesueurii* lesueurii), a lineage in which males show bright red ventral coloration. The extent of the red patch is highly variable among individual males within a single population, with red restricted to the abdomen in some individuals but extending to the chest, forelimbs and throat in others. Females usually lack red, although a few individuals exhibit a reddish venter (Thompson, 1993). The red colour is probably due to carotenoid and pteridine pigments (Cooper & Greenberg, 1992). Carotenoids must be ingested in the diet and signal phenotypic quality in many vertebrate species (Olson & Owens, 1998). Although pteridines are synthesized de novo in the organism, they might also function as quality indicators because the amounts of pteridine and carotenoid pigments in the tissues are often correlated (Grether, Hudon & Endler, 2001). Water dragons also show sexual size dimorphism, with adult males larger than females. More information about the biology of this species can be found in Thompson (1993) and Harlow (2001).

Does male red ventral coloration constitute a sexual ornament in water dragons? If so, we predict that quantitative measures of colour would confirm the sexual dichromatism perceived by human visual systems, and that the extent or intensity of red ventral coloration would correlate with morphological attributes plausibly linked to fitness (e.g. male body size, condition, relative head size, fluctuating asymmetry (FA): non-directional deviations from perfect symmetry in bilateral traits). Although experimental manipulation would then be needed to ascertain function, the first step is to quantify coloration and look for sex differences and morphological correlates. We have conducted such a study.

Male displays in this species typically involve head-bobbing and forelimb extension (plausibly revealing the colours of the throat and chest: Watt & Joss, 2003), but we have never seen lateral distension of the body in a posture that would reveal significant parts of the animal's belly surface (R. Shine, pers. obs.). Consequently, we assume that these three ventral body areas (throat, chest and abdomen) differ in their visibility to conspecifics: when a lizard is displaying, its throat is likely to be more visible than its chest, which in turn should be more visible than the abdomen. If ventral coloration functions as a sexual signal, we would expect a significant relationship between characters related to fitness and coloration of the most visible ventral areas (throat and maybe chest), while the relationship with abdomen coloration would be less probable.

# **Materials and methods**

#### **Captures and morphological measurements**

We captured 57 water dragons (34 males, 23 females) between 25 and 31 October 2005 in Port Macquarie, New South Wales, in eastern Australia (31°26'S, 152°55'E). These lizards were common in riparian habitats in gardens and parks, and were captured during daylight hours with a noose at the end of a 5-m-long fishing pole. Breeding was in progress: many females were gravid and many males showed recent injuries, probably due to fights with other males. We paint-marked each individual before release so that each

animal is represented only once in our dataset. Immediately after capturing the animal, we measured a series of morphological traits that plausibly correlate with individual fitness (and hence, potentially, with colour): (1) Body size, estimated as snout-vent length (SVL, measured with a tape to the nearest mm). Male body size is strongly correlated with mating success in many lizard species (e.g. Wikelski, Carbone & Trillmich, 1996; Censky, 1997) and female body size is commonly related to clutch size (Fitch, 1970). (2) Body condition, estimated as mass (measured with a spring balance to the nearest 5g) controlled for body size by including SVL as a covariate in statistical analyses (Green, 2001). We also measured additional traits in males only, as follows. (3) Relative head size, based on upper jaw length, maximum mouth width, maximum head width and maximum head height (measured with a digital calliper to the nearest 0.1 mm). From these data, we calculated a head size index by principal component analysis (PCA; high values of this index indicated small heads). Relative head size was estimated as the head size index controlled for body length (from the gular fold to the cloaca, rather than SVL because the latter measure includes head length). Relative head size correlates with male mating success in some lizard species (e.g. Hews, 1990). (4) Femoral pores, epidermal structures on the ventral thighs that produce pheromones. The number of femoral pores and their asymmetry (absolute value of the difference in the number of femoral pores between the right and the left thigh) are related to male sexual attractiveness in at least one lizard species (Martín & López, 2000).

All individuals included in this study were adults based on sizes at sexual maturation in >100 animals dissected from museum collections (J. J. Cuervo, unpubl. data). SVL of males ranged from 21.6 to 28.8 cm, and SVL of females from 17.0 to 23.5 cm. Sexing of individuals was unambiguous based on relative head size (much larger in males than in females; Fig. 1). Ventral redness and blackness were also dichotomous and sex-linked. At least to a human observer, males appeared to have much darker ventral parts than females and males had a reddish tinge to the abdomen whereas females did not (Fig. 1). Many males also everted their hemipenes while they were being measured; in all these cases, our prior sex assignment based on colour or head size was correct.

#### **Colour measurements**

Humans and lizards have different types of photoreceptor cells and pigments in the retina (Yokoyama & Yokoyama, 1996; Barbour *et al.*, 2002). One consequence is that some lizard species can see wavelengths (e.g. UV) that humans cannot (Fleishman, Loew & Leal, 1993). Because human perception of colours can be misleading when studying visual communication in other animals, we need to assess coloration objectively. Spectroradiometry allows quantification of colours in terms of reflectance spectra without relying on human colour vision. Reflectance is defined as the ratio of the total amount of radiation (i.e. light) reflected by a surface to the total amount of radiation incident on the



Figure 1 Ventral parts of (a) male and (b) female water dragons *Physignathus lesueurii*.

surface, and takes values between 0 and 1. We used a Konica Minolta Sensing (Konica, Seoul, South Korea) CM-2600d spectroradiometer measuring reflectances at 10-nm intervals between 360 and 700 nm, and took 10 measurements for each individual on three ventral body areas: abdomen (four measurements, two on the right-hand side and two on the left-hand side), chest (three measurements, right- and lefthand sides and centre) and throat (three measurements, right and left hand sides and centre). These parts of the body probably differ in their visibility to conspecifics (see the 'Introduction'). The measurements were referenced to a standard white (CM-A145, Konica Minolta Sensing) and to a standard dark (CM-A32, Konica Minolta Sensing), with white and dark calibrations made before measuring each lizard. The mean reflectance values for each of the 35 wavelengths were calculated within each body region in every individual. Reflectance spectra at 10-nm intervals for each body area are shown in Fig. 2.

To analyse mean reflectance spectra, we used PCA to summarize reflectances recorded at different wavelengths (Endler, 1990; Cuthill *et al.*, 1999). A different PCA was used for every body area and sex. Only factors with eigenvalues greater than one were retained for analysis (Nie *et al.*, 1975; Table 1). In all cases, the first factor (F1) represented variation in mean reflectance, with positive values indicating dark colours and negative values bright colours (Fig. 3). The second factor (F2) represented variation in red coloration, with positive values indicating less intense redness (more blue) and negative values more intense



**Figure 2** Average ( $\pm$ sɛ) reflectances measured at 10-nm intervals between 360 and 700 nm for the abdomen, chest and throat in (a) male (n=34) and (b) female (n=23) water dragons *Physignathus lesueurii*.

redness (less blue) (Fig. 3). In the only case in which the third factor (F3) had an eigenvalue larger than one (see Table 1), it mainly represented UV, with positive values indicating low reflectance in the UV (and also high reflectance in the green-yellow) and negative values indicating high reflectance in the UV (and low reflectance in the green-yellow) (Fig. 3). Repeatabilities of factors (see Lessells & Boag, 1987) were always highly significant (males: 0.43 < r < 0.75, P < 0.001; females:  $0.34 \le r \le 0.92$ , P < 0.01). Because we measured colour at different points within each individual and body region, these repeatabilities quantify within-versus betweenindividual variability in coloration for each body region. Coloration was patchy rather than uniform; hence our measurement errors were much lower than might be suggested by these repeatability scores. Factors from PCA were used in subsequent analyses.

#### **Statistical analyses**

All variables followed a normal distribution (according to the Kolmogorov–Smirnov test for normality) without

 Table 1 Eigenvalues and percentage of variance explained by each factor after principal component analyses of reflectances between 360 and 700 nm

			Cumulative % variance	
	Eigenvalue	% variance		
Males				
Abdomen				
F1	25.90	73.99	73.99	
F2	7.75	22.14	96.13	
Chest				
F1	26.13	74.67	74.67	
F2	6.88	19.67	94.34	
F3	1.70	4.86	99.20	
Throat				
F1	27.14	77.55	77.55	
F2	7.10	20.30	97.85	
Females				
Abdomen				
F1	26.69	76.25	76.25	
F2	6.95	19.87	96.12	
Chest				
F1	30.25	86.43	86.43	
F2	3.85	11.00	97.43	
Throat				
F1	30.25	86.44	86.44	
F2	4.05	11.57	98.00	



**Figure 3** Loadings of the first three factors from a principal component analysis on reflectances measured at 10-nm intervals between 360 and 700 nm on the chest of male water dragons *Physignathus lesueurii* (n=34). F1 represents variation in mean reflectance, F2 in red coloration and F3 mainly in the UV (see the text for more details). Patterns for females and other body regions (i.e. abdomen and throat) are very similar.

transformation, except for FA of femoral pores, which was impossible to normalize. We used general linear regression models to clarify relationships between coloration and other variables (SVL, head size index, weight or number of femoral pores). Each indicator of phenotypic quality was analysed separately as the dependent variable, with two (or three) colour factors as the independent variables. Body length was included in the model as a covariate when studying relative head size and SVL when studying body condition. We used equivalent non-parametric tests to compare colour factors with FA of femoral pores (i.e. partial Spearman's correlations: Sokal & Rohlf, 1981, pp. 656–661). All statistical analyses were performed with the software Statistica version 6.0. All tests were two-tailed and the level of significance was 0.05.

# Results

### Males

In male water dragons, there was a positive relationship between SVL and F2 (variation in red colour) of the abdomen (i.e. large males showed less reddish abdomens than did small males: Table 2). Relative head size was negatively related to F1 (variation in brightness) and F2 of the abdomen, although the relationship between relative head size and F2 of the abdomen was only marginally significant (i.e. males with relatively large heads had darker and less reddish abdomens than did males with smaller heads: Table 2). None of the relationships between colour factors and condition, number and asymmetry of femoral pores or any other morphological measure was statistically significant.

### Females

In female water dragons, SVL was positively related to F2 of the abdomen and to F1 and F2 of the chest, although the relationship between SVL and F2 of the chest was only marginally significant (Table 2). That is, larger females had darker chests and less reddish abdomens and chests than did smaller females. No other relationships between colour factors and SVL or body condition were statistically significant.

### Discussion

Our analyses of ventral coloration in water dragons confirmed anecdotal reports of sexual dichromatism: as suggested by the human visual system, males and females differ substantially in this respect (Fig. 2). Also, a lizard's coloration shifts with its body size - larger (presumably older) animals of both sexes develop less reddish ventral colours, and larger females develop darker chests. Lastly, relative head size in males correlates with abdominal colour also (Table 2). These sex differences and morphological correlates in coloration suggest the potential for water dragons to utilize ventral colours as sexual signals. However, while in other lizard species throat and ventral coloration certainly appears to serve a signalling function (e.g. Meyers et al., 2006; Whiting et al., 2006), this may not be widely applicable. There are several reasons to doubt that sexually dimorphic ventral colours in water dragons are used to signal an animal's sex, body size and/or head size to conspecifics:

	Phenotype measure	Body region	Full model statistics		Partial regression coefficient (P value)			
			F	d.f.	Р	F1	F2	Body length
Males	SVL	Abdomen	6.38	2,31	0.005	0.275 (0.079)	0.465 (0.004)	-
	HSI	Abdomen	26.13	3,30	< 0.001	-0.276 (0.008)	-0.211 (0.048)	-0.674 (<0.001)
Females	SVL	Abdomen	4.68	2,20	0.021	0.119 (0.53)	0.552 (0.007)	-
	SVL	Chest	10.16	2,20	< 0.001	0.628 (<0.001)	0.330 (0.049)	-

 Table 2
 General linear regression models assessing the relationship between morphological traits (body size, relative head size, condition and number of femoral pores) and colour factors

Only models in which at least one of the colour factors explained a significant portion of the variance have been included. SVL, snout-vent length; HSI, head size index.

(1) The area of the body that shows the most striking sex difference, and is most strongly correlated with body size and head size in males, is the abdomen. It seems unlikely that conspecifics would see the abdomen of another lizard, because male displays in this species (e.g. head-bobbing) would reveal throat (and maybe also chest) colours, but not abdomen coloration (see the 'Introduction').

(2) Large individuals of both sexes exhibited a darker and less reddish chest or abdomen than did smaller conspecifics. Because this pattern was found in both sexes and only in the (less visible) ventral parts of the body, we doubt that this colour change has any signalling utility.

(3) Males with relatively large heads showed a darker and less reddish abdomen than did males with small heads. Although abdominal colour is potentially informative about head size, it seems more likely to be a simple ontogenetic shift in the two traits: that is, as they grow older male water dragons develop relatively larger heads (as in sand lizards: Olsson & Shine, 1996), become darker overall and lose red colour on their ventral surface. Lizards can continue to grow throughout their lives (Haines, 1969). The mechanism producing darkening of ventral parts in this species is unknown, but may involve accumulation of melanin covering other pigments (e.g. pteridines and carotenoids) and thus reducing red coloration.

We have assumed that the visibility of the abdomen is very limited in water dragons; hence it is unlikely that abdomen coloration can work as a signal in this species. However, colour patches on the abdomen are common in many lizard species and may be used for signalling via particular displays that allow exhibition of the abdomen. For example, *Urosaurus ornatus* males laterally compress the body to expose blue belly patches (Meyers *et al.*, 2006), and *Platysaurus broadleyi* males flash their venters to reveal orange-yellow patches to conspecifics (Whiting *et al.*, 2006). We are not aware of any analogous display postures in water dragons, but more studies should be carried out before this possibility is completely dismissed.

We did not find any significant correlations between colour patterns and body condition (mass relative to length). However, we caution that our study population contained several tame individuals that took food from humans, and thus body condition may have been artificially manipulated by this activity because the degree of tameness varied enormously among individuals. Also, mass relative to body length was a poor indicator of condition in females, because our study took place during the breeding season and at least seven out of 23 females were unequivocally gravid (eggs could be felt by palpating the abdomen). Thus, female mass was heavily influenced by reproductive state rather than by underlying energy reserves.

In summary, our study provides the first quantitative information on ventral coloration in a spectacularly dichromatic, very large lizard species. We found considerable variation among individuals in coloration, and significant correlations between specific colour patterns and morphological traits such as body size and relative head size. Nonetheless, in total, our data cast doubt on the hypothesis that water dragons utilize this kind of individual colour variation as a sexual signal. Instead, much of the colour variation may be related to reproductive maturity or to age; we doubt that red ventral coloration functions as a sexual ornament in this species.

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