Sexual dimorphism in conspicuousness and ornamentation in the enigmatic leaf-nosed lizard *Ceratophora tennentii* from Sri Lanka

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Measures of physiological performance capacity, such as bite force, form the functional basis of sexual selection. Information about fighting ability may be conveyed through a structural feature such as a rostrum (i.e. horn) or a colour signal and thereby help reduce costly conflict. We quantified sexual dimorphism in key traits likely to be the targets of sexual selection in Tennent's leaf-nosed lizard (*Ceratophora tennentii*) from Sri Lanka, and examined their relationship to bite force and body condition. We found body length and bite force to be similar for males and females. However, head length was significantly greater in males and they had significantly more conspicuous throats and labials (chromatic contrast and luminance) than females. Males also had a proportionally larger rostrum, which we predicted could be an important source of information about male quality for both sexes. Rostrum length was correlated with throat chromatic contrast in males but not females. Nonetheless, the rostrum and aspects of coloration did not correlate with bite force or body condition as we predicted. We have no information on contest escalation in this species but if they rarely bite, as suggested by a lack of difference in bite force between males and females, then bite force and any associated signals would not be a target of selection. Finally, males and females had similar spectral reflectance of the mouth and tongue and both had a peak in the ultra-violet, and were conspicuous to birds. Lizards only gaped their mouths during capture and not when threatened by a potential predator (hand waving). We hypothesize that conspicuous mouth colour may act as a deimatic signal, startling a potential predator, although this will need careful experimental testing in the future. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **116**, 614–625.

ADDITIONAL KEYWORDS: bite force – colour – deimatic signal – horns – performance capacity – reptile – sexual selection – sexual dimorphism.

INTRODUCTION

Sexual selection acts on multiple traits that signal information about the quality of a signaller to either a rival or a potential mate (Andersson, 1994; Johnstone, 1995; Brooks & Couldridge, 1999; Andersson *et al.*, 2002). These signals may either be static (e.g. armaments, colour) or dynamic (e.g. behaviour, colour) and either act in concert or signal independent sources of information (Johnstone, 1996). Armaments, such as horns, are typically an honest signal of fighting ability and play a key role in determining contest outcome (Whiting, Nagy & Bateman, 2003;

Emlen, 2008; Callander *et al.*, 2013). In some lizard species, these horn-like appendages are pliable and are more appropriately termed a rostrum. A rostrum in these systems does not function as a weapon, but may still act as an arbitrary structure (status signal) signalling information about male dominance (Whiting *et al.*, 2003) or information on male quality to females. Many lizard species with armaments (horns or rostrums) are typically elaborately coloured (e.g. chameleons, Asian agamids; Stuart-Fox & Ord, 2004; Tolley & Herrel, 2013). In these systems, colour may act in concert with ornamentation and provide multiple sources of information to male and female receivers (Johnstone, 1996; Andersson *et al.*, 2002). In cases where the same information is conveyed to a

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receiver in multiple messages, signals are thought to be more reliable and potentially processed more quickly by the receiver (Rowe, 1999).

Many sexually selected traits have a functional basis underpinned by energetics and other measures of physiological or whole-organism performance capacity (Briffa & Elwood, 2001; Lailvaux & Irschick, 2006). Indeed, an animal's state and its energetic capacity underpin a large body of game theory applied to animal contests (Whiting *et al.*, 2003; Lailvaux & Irschick, 2006; Kokko, 2013). Males with higher performance capacity may be able to display more frequently or defend territories for longer. For example, dominant male *Anolis cristatellus* lizards performed more assertion displays in the field and also had higher endurance capacity in the laboratory (Perry *et al.*, 2004). Similarly, males that defend territories or mates may invest more in cranial musculature, horns and head size, thereby gaining an advantage in contests through greater bite force or leverage (Huyghe *et al.*, 2009; Herrel *et al.*, 2010; Vanhooydonck *et al.*, 2010; da Silva *et al.*, 2014). In North American collared lizards (*Crotaphytus collaris*) bite force correlated positively with the number of offspring sired by males suggesting that performance capacity is a target of sexual selection with clear fitness consequences (Husak, Lappin & Van Den Bussche, 2009). Although sexually selected traits may favour fighting ability, fighting is costly in terms of energy expenditure, risk of injury, increased risk of predation and time taken away from other key activities including foraging and courtship (Whiting *et al.*, 2003). Therefore, individuals are predicted to settle conflicts by signalling their intent or their fighting ability, particularly when there is an obvious asymmetry between two rivals. In some of these systems, escalation to fighting may be rare and as a result, status signals such as colour patches may be unrelated to bite force. While a considerable body of literature has been amassed on animal contests (reviewed in Hardy & Briffa, 2013) we still have a poor understanding of the link (if any) between measures of performance capacity, such as bite force, and the nature of animal signals, such as ornaments and armaments, used to convey this information.

A separate class of conspicuous signals function in an anti-predator context and may be aposematic or function as a pursuit-deterrent signal. Classical pursuit-deterrent signals are used at a distance early in an encounter with a predator, to dissuade a potential predator from a costly or fruitless pursuit (Leal & Rodriguez-Robles, 1997; Font *et al.*, 2012). A less well known class of signals are deimatic displays that are concealed and only exposed late in an encounter with a predator, often during subjugation, and are highly conspicuous signals that startle a predator (Umbers,

Lehtonen & Mappes, 2015). Given the diversity of mouth colour across a wide range of species and that lizards typically gape their mouths during capture (pers. observ.), lizards may be a useful system with which to examine the possibility of deimatic signals.

Sri Lankan horned lizards in the genus *Ceratophora* (Family: Agamidae) are known for their spectacular coloration and rostral structure (Somaweera & Somaweera, 2009), which are thought to be the product of both natural and sexual selection (Johnston, Lee & Surasinghe, 2013). We first explore sexual dimorphism in these traits and ask whether aspects of coloration and/or rostrum size are positively associated with bite force or body condition in *Ceratophora tennentii*. Finally, we explored the possibility that mouth colour is a deimatic signal by testing the following predictions: (1) mouth colour is conspicuous to a predator (bird) visual system; and (2) the display (mouth-gape) is only given during the subjugation phase of predation (hand capture).

MATERIAL AND METHODS

STUDY AREA AND STUDY SPECIES

We conducted fieldwork in the Knuckles Forest Reserve (KFR) (7°21′–7°24′N, 80°45′–80°48′E), which spreads across an altitudinal range of 200–1900 m a.s.l. over a 20 km stretch in the central highlands of Sri Lanka (Bambaradeniya & Ekanayake, 2003). The substantial elevational gradient has resulted in a wide range of climates and edaphic conditions that support several forest (e.g. montane, sub-montane, semi-evergreen, riverine, thorny scrubland) and grassland (e.g. savannah, 'patana') vegetation types (Balasubramaniam, 1988; Bambaradeniya & Ekanayake, 2003). The highland areas receive heavy rainfall (>5000 mm year^{-1}) while the lower foothills are drier (<2500 mm year^{-1}). Due to its biological and hydrological value, the area above 1500 m of this forest region was declared a Climatic Reserve in 1873 (Jayasuriya, 2008); a 175 km^2 region was declared as the Knuckles Conservation Area in 1998 and then a National Man and Biosphere (MAB) Reserve in April 2000. More recently, a 313 km^2 section of the range was declared part of UNESCO's Central Highlands World Heritage Site (UNESCO, 2014) including the area where we conducted field work.

Among the reptiles endemic to the Knuckles range is the Critically Endangered Tennent's leaf-nosed lizard, *Ceratophora tennentii*. This slow-moving, arboreal lizard inhabits an array of habitats in the higher altitudes of KFR, including cardamom plantations, mixed cardamom forests with a natural forest canopy as well as pristine montane forests (Somaweera *et al.*, 2015). Males, females and juveniles have a rostrum which is

moveable (Pethiyagoda & Manamendra-Arachchi, 1998) and a recent analysis of 16 male and six female museum specimens did not reveal a significant difference in rostrum size between the sexes although the sample size was small (Johnston *et al.*, 2013).

Anti-predator behaviour, coloration, body size and bite force

Sixty-three lizards (34 males and 29 females) were captured by hand during the day in January 2012, placed in separate cloth bags, and returned to the field station within KFR for processing. At this time of year, females are post-parturient although males are still territorial. Prior to capture, we waved a hand about 10 cm from the lizard for about 5 s, from a stationary position, and scored: (1) if they performed an open-mouthed threat; and (2) if not, did they then perform an open-mouth display when captured by hand and placed into a cloth bag. All lizards were released at their point of capture following processing. We only focused on adults and did not process any juveniles we encountered.

We measured spectral reflectance using an Ocean Optics USB2000 spectrometer and deuterium-tungsten DT-1000 mini light source connected to a fibre-optic probe. We standardized illumination and reflection by taking measurements at a standard angle (45°) and distance and over a standard area (5 mm) using a probe holder. We took a single set of measurements (except throat and labials where we took two in different locations) because this species is capable of dynamic colour change and we wanted to minimize handling time and stress given the need to also take bite force measurements. When lizards were removed from their bags they were in the same colour state as when they were first observed in the field, to a human observer. All measurements were taken relative to a dark and 99% white (WS-1) standard. Each spectral reflectance curve encompassed the range 300–700 nm, comfortably including the 320–700 nm range in which lizards are able to see (Loew *et al.*, 2002). Finally, we quantified background colour by measuring the top and underside of 94 leaves and 49 branches/pieces of bark randomly selected from vegetation where we had collected lizards in the wild. We used an averaged spectral reflectance curve of leaves as the background in visual models because individuals were mainly observed in a leafy visual environment.

We measured body size (snout–vent length, SVL) and tail length to the nearest 1 mm using a plastic ruler and weighed each lizard to the nearest 0.1 g. We used digital calipers to measure rostrum length and width, dewlap depth, crest height, head length, head width and head depth to the nearest 0.01 mm (See Fig. 1). The dewlap was measured by holding the lizard's

head still, in a straight line with the body and gently stretching the dewlap perpendicular to the throat to its maximum 'natural' extent. Bite force was measured three times in succession following measurement of morphology and twice in quick succession after an extended break (>5 h). In each case we measured body temperature using a Miller–Weber quick reading cloacal thermometer. We measured bite force using a Kistler force transducer (Kistler Inc.), connected to a Kistler charge amplifier (Model 5995; Kistler Inc.). Lizards were induced to bite two plastic plates by gently pinching the sides of their mouth. We used only the single highest reading of bite force (maximal performance capacity) because lizards vary in their motivational state (Losos, Creer & Schulte, 2002).
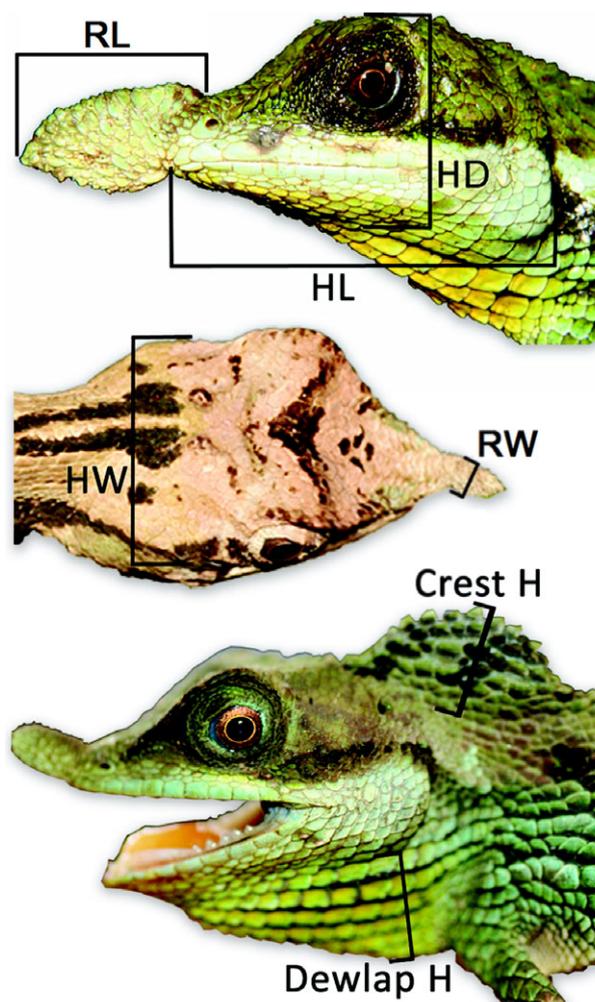

Figure 1. Landmarks for morphological measurements used to test for sexual dimorphism and for examining links to condition, colour and bite force. RL = rostrum length, RW = rostrum width, HD = head depth, HL = head length, HW = head width, H (by itself) = height. See text for details.

VISUAL MODELLING

We estimated the visual contrast of throat and labial patches against background (i.e. leaves) to assess sexual dichromatism using the lizard visual system. We also modelled the chromatic contrast of the roof of mouth and tongue using an avian visual system following Stuart-Fox, Moussalli & Whiting (2008). Prior to analysis each individual's spectra (1–2 spectra per patch – throat and labial; 1 spectra per patch – roof of mouth and tongue) were averaged and smoothed (LOESS smoothing parameter = 0.2) to remove electrical noise. We applied the model of Vorobyev & Osorio (1998) to calculate chromatic (ΔS) and achromatic (ΔL) contrast as discrimination thresholds in 'just noticeable differences' (JNDs) for each colour patch and for each individual against a background. Chromatic thresholds are calculated using spectral sensitivities of single cones in the UV, short, medium and long wavelengths, whereas achromatic thresholds are calculated using the long-wavelength photo pigments in the double cones. This model therefore requires data on maximal spectral sensitivities for cone pigments, along with environmental irradiance and the spectral curves for each of the colour patches of interest. We used 'forest shade' as our irradiance and leaves as our background given that this best characterises the visual environment that these lizards occupy (pers. observ.). Spectral sensitivities for *C. tennentii* cone pigments are not available so we used sensitivities from another agamid, *Ctenophorus ornatus* (Barbour *et al.*, 2002), which is the only agamid species with published sensitivities. Barbour *et al.* (2002) did not find UV wavelength sensitive pigments in *C. ornatus*, but these have been found in all other lizard species (Loew *et al.*, 2002; Bowmaker, Loew & Ott, 2005; Fleishman, Loew & Whiting, 2011) and visual systems in lizards are considered conserved (Fleishman *et al.*, 2011). Therefore, in addition to the short (SWS: λ_{max} = 440 nm), medium (MWS: λ_{max} = 493 nm) and long-wavelength sensitive pigments (LWS: λ_{max} = 571 nm), we assumed that *C. tennentii* also contains UV sensitive wavelength pigments (UVS: λ_{max} = 360 nm) in our visual models. We derived receptor quantum catches between the 300–700 nm wavelength range and applied a von Kries transformation to the spectral curves for each of the colour patches of interest and assumed that colour discrimination is limited by photoreceptor noise. We also assumed a signal-to-noise ratio (v) of 0.10 based on empirical measures from the Pekin robin (Vorobyev & Osorio, 1998), and relative photoreceptor class densities of 1:1:3.5:6 (UVS: SWS: MWS: LWS) for the lizard visual system and 1:2:3:3 (UVS: SWS: MWS: LWS) for the avian photoreceptor classes. We used average avian spectral sensitivities (UVS species) for the four bird pigments (λ_{max}: UVS = 372 nm; SWS = 456 nm; MWS = 544 nm and LWS = 609) and also used a signal-to-nose ratio of 0.10. All spectral processing and visual modelling was done using 'pavo' (Maia *et al.*, 2013) in R ver. 3.0.2 (R-Core-Team, 2014).

STATISTICAL ANALYSIS

All statistical analyses were conducted in R ver. 3.0.2 (R-Core-Team, 2014). We used multiple linear regression to test whether *C. tennentii* are sexually dimorphic in morphological traits. In models with mass and snout–vent length (SVL) as response variables we included 'sex' as a two-level categorical predictor and evaluated the significance of sex using *F*-tests. To understand how head dimensions (head width, depth and length), rostrum length, crest height and dewlap height were different between the sexes we log transformed each response variable and included log transformed SVL, sex and their interaction in our full models. If interaction parameters were not significant, as assessed using an *F*-test between the full model and a reduced model (without the interaction), we excluded the interaction and present the reduced model with all main effects (log SVL and Sex).

We compared the labial and throat JNDs, taken from a lizard visual system, between males and females using a Wilcoxon rank sum test owing to the highly skewed nature of these variables. We further tested whether males and females differed significantly in their chromatic and achromatic contrast, computed using an avian visual system, in roof and tongue mouth patches using a Wilcoxon rank sum test.

We tested whether rostrum length and chromatic discrimination scores (i.e. JNDs; ΔS) signalled biting performance and body condition (i.e. residuals from a regression between log transformed body mass and SVL) using multiple linear regression. We modelled log transformed maximal bite force (response variable) as a function of SVL, temperature, sex, rostrum length, head length, ΔS, and interactions between SVL, head length, rostrum length, ΔS and sex because the sexes were predicted to scale differently in their relationships between these variables and bite force. We used head length only as opposed to head width and depth because these variables were correlated in any case and because head length explained the most variance in biting force. In contrast, we modelled body condition (response variable) as a function of sex, ΔS, rostrum length and interactions between sex and ΔS and rostrum length. Again, we simplified all models by excluding any nonsignificant interactions using *F*-tests between the full

model and the model without the interaction. We present models using chromatic contrast in the results and achromatic contrast in Table S1 given that inferences from models were very similar.

We assessed model assumptions (normality, homogeneity of variance in groups and covariates) and tested for outlying data points by evaluating residual plots, Cooks D and hat values. Studentized residuals greater than three standard deviations from the fitted values may have strong effects on model parameters. When outlying data points were identified or the assumption of homogeneity of variance was questionable we used robust regression with a Huber estimator. Robust regression is done with iterative re-weighted least squares, where residuals are re-weighted by their deviation from the predicted values with larger deviations contributing less to parameter estimation in the next iteration. This is done repeatedly until models converge. Given that asymptotic estimates for standard errors can be biased in robust regression (Fox & Weisberg, 2011), to generate 95% confidence intervals around coefficients we used bootstrap methods, re-sampling the data with replacement 1000 times using the 'boot' package (Canty & Ripley, 2014). This allowed us to construct confidence intervals around estimates using normal approximation theory. In crest height models, the interaction parameter estimate was large, but marginally nonsignificant. To avoid missing important scaling differences between the sexes we retained this interaction in the model. There were few differences between robust regression and ordinary least square regression methods for rostrum length models and we retained estimates and standard errors from OLS estimates. In all models, we present the main effects regardless of significance as these were of direct interest while only significant interactions are presented. We present standardized effect sizes from final models [$x - mean(x)/2*sd(x)$] throughout given that standardizing main effects makes them directly comparable and they can be interpreted in the presence of interactions. Sample sizes varied slightly between analyses owing to missing data in one or more of the variables, therefore, these are reported throughout. Data and code used for all analyses can be found at: http://dx.doi.org/10.6084/m9.figshare.1452908.

RESULTS

SEXUAL DIMORPHISM AND DICHROMATISM

Males did not differ significantly from females in SVL (Sex: $F = 0$, d.f. = 1, $P = 0.99$, $N = 63$) and mass (Sex: $F = 1.56$, d.f. = 1, $P = 0.22$, $N = 63$). Males had significantly longer rostrum length compared with females

Table 1. Mean and standard deviation (SD) for male and female head length, width, and depth, rostrum length, dewlap height, total length, snout–vent length (SVL), mass and crest height. Sample sizes for females, $N = 29$ and males, $N = 34$. Bold estimates indicate males and females differ significantly in these traits when accounting for scaling effects with body size. Effect sizes and significance can be found in Tables 2 and 3.

	Sex	
	Female	Male
Head length (mm)	**18.95**	**19.59**
SD	**1.97**	**2.22**
Head width (mm)	11.10	11.18
SD	1.13	1.48
Head depth (mm)	10.57	10.64
SD	1.50	1.36
Rostrum length (mm)	**6.69**	**8.42**
SD	**1.81**	**1.84**
Dewlap height (mm)	11.06	11.89
SD	2.20	2.48
SVL (mm)	6.64	6.64
SD	0.74	0.75
Total length (mm)	17.89	18.82
SD	1.97	2.15
Mass (g)	8.59	7.76
SD	3.04	2.22
Crest height (mm)	4.41	4.40
SD	1.28	0.99

Table 2. Standardized [$x - mean(x)/2*sd(x)$] model coefficients (Est.) and standard errors (SE) for models testing for sexual dimorphism in log transformed rostrum length, crest height and dewlap height as a function of log transformed snout–vent length (SVL). Outliers affected estimates in crest and dewlap height models so estimates are presented using robust regression fitting procedures. Confidence intervals for estimates from robust regression were derived from normal approximation theory after 1000 bootstrap samples. There was no evidence for a significant interaction between sex and log SVL in dewlap height models. Bolded estimates and standard errors indicate significance at $P < 0.05$. '*' Indicates that confidence intervals marginally overlapped zero.

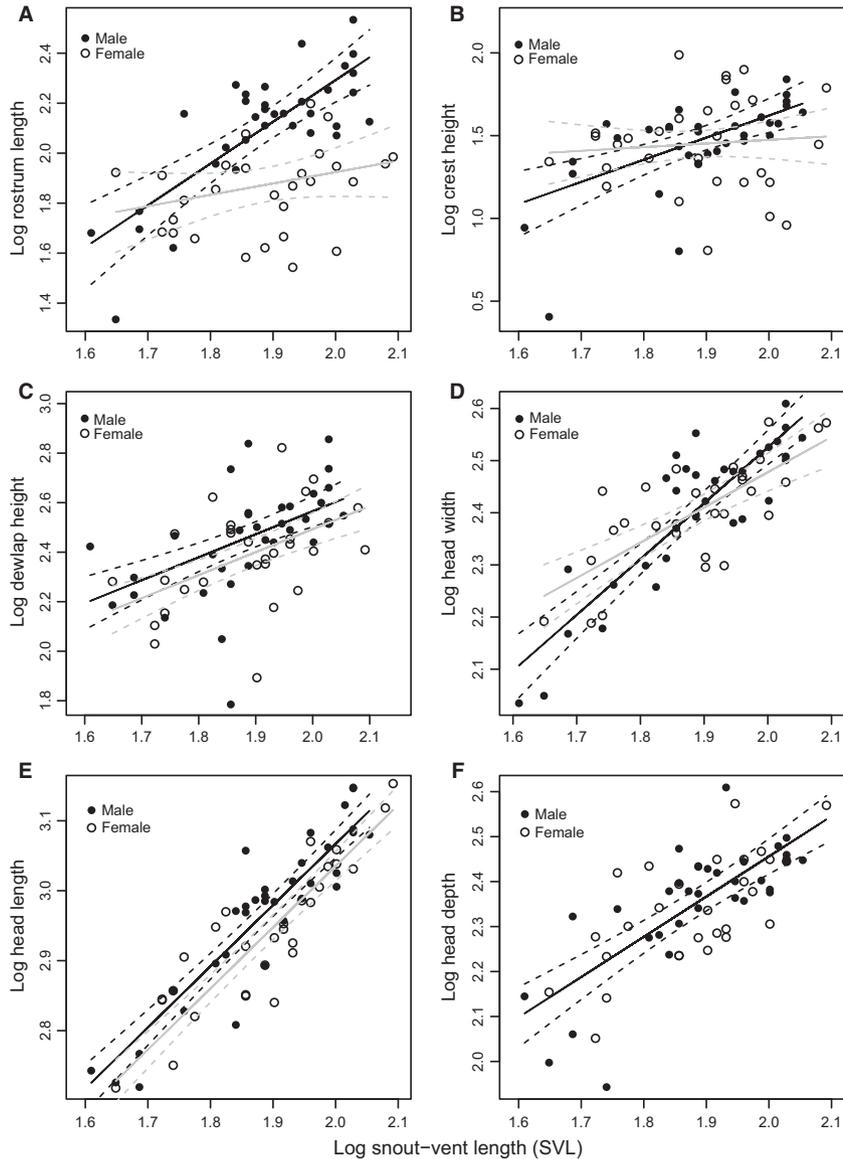|	Log rostrum length		Log crest height		Log dewlap height	
Predictors	Est.	SE	Est.	SE	Est.	SE
Intercept	**2.00**	**0.024**	**1.46**	**0.029**	**2.42**	**0.020**
Log (SVL)	**0.25**	**0.048**	**0.18**	**0.058**	**0.21**	**0.041**
Sex (m)	**0.23**	**0.047**	0.02	0.057	0.07	0.041
Log (SVL) *Sex (m)	**0.28**	**0.096**	0.26	0.116*	–	–

Figure 2. Relationship between log snout–vent length (SVL) and (A) log rostrum length; (B) log crest height; (C) log dewlap height; (D) log head width; (E) log head length; (F) log head depth for males (black dots: solid line) and females (open dots: grey line). See Tables 2 and 3 for coefficients used to make model predictions.

and they scaled differently with log SVL between the sexes (Tables 1 and 2 & Fig. 2A). There appeared to be a stronger relationship between log SVL and log crest height in males but not females, although this was marginally significant (Tables 1 and 2 and Fig. 2B). The relationship between log SVL and log dewlap height was not significantly different between the sexes (Tables 1 and 2 and Fig. 2C). The relationships between log head width and log SVL differed significantly between the sexes (Table 3 and Fig. 2D), whereas there was no heterogeneity of slopes for head length and depth between the sexes (Table 3 and Fig. 2E, F). Although a weak effect, males had significantly

longer head length than females whereas the sexes did not differ in head width or depth after controlling for body size (SVL) (See estimates of Sex in Table 3).

Males had higher total reflectance for both the throat and labial patches (Fig. 3A, B), whereas reflectance of mouth areas did not differ between the sexes (Fig. 3C, D). Under a lizard visual system, males and females differed significantly in throat and labial chromatic contrast scores (ΔS) (Wilcoxon rank sum test: Labial: W = 293, P = 0.04; Throat: W = 212, P < 0.001) and achromatic contrast (ΔL) against the background (Wilcoxon rank sum test: Labial: W = 159, P < 0.001; Throat: W = 197, P < 0.001).

Table 3. Standardized $[x - \text{mean}(x)/2*\text{sd}(x)]$ model coefficients (Est.) and standard errors (SE) for models testing for sexual dimorphism in log transformed head width, depth and length as a function of log transformed snout–vent length (SVL). Bolded estimates and standard errors indicate significance at $P < 0.05$. Sample sizes: $N = 63$, $N = 29$ females and $N = 34$ males.

Predictors	Log head width		Log head length		Log head depth	
	Est.	SE	Est.	SE	Est.	SE
Intercept	**2.40**	**0.009**	**2.95**	**0.006**	**2.35**	**0.012**
Log (SVL)	**0.20**	**0.018**	**0.20**	**0.012**	**0.20**	**0.024**
Sex (m)	0.00	0.018	**0.03**	**0.012**	0.01	0.024
Log (SVL) *Sex (m)	**0.09**	**0.036**	–	–	–	–

DO COLOUR AND ROSTRUM SIZE SIGNAL INDIVIDUAL QUALITY TO CONSPECIFICS?

Males and females did not differ significantly in log bite force (Welch's t-test: $t = 0.60$, d.f. $= 54.80$, $P = 0.55$; see also Table 4) but males were in poorer condition compared to females (Welch's t-test: $t = 2.65$, d.f. $= 55.22$, $P = 0.01$; see also Table 4).

Rostrum length was correlated with log transformed chromatic contrast for the throat (Spearman rho $(r_s) = 0.36$, $S = 19674.46$, $P = 0.01$) but not for labial patch ($r_s = 0.05$, $S = 27845.93$, $P = 0.72$). The correlation between log transformed throat chromatic contrast and rostrum length was only positive for males ($r_s = 0.37$, $S = 2848$, $P = 0.047$), whereas this relationship did not exist in females ($r_s = 0.02$, $S = 3224$, $P = 0.94$). There was no evidence that the relationship between rostrum length and maximal bite force (Throat colour model: Sex*Rostrum length:
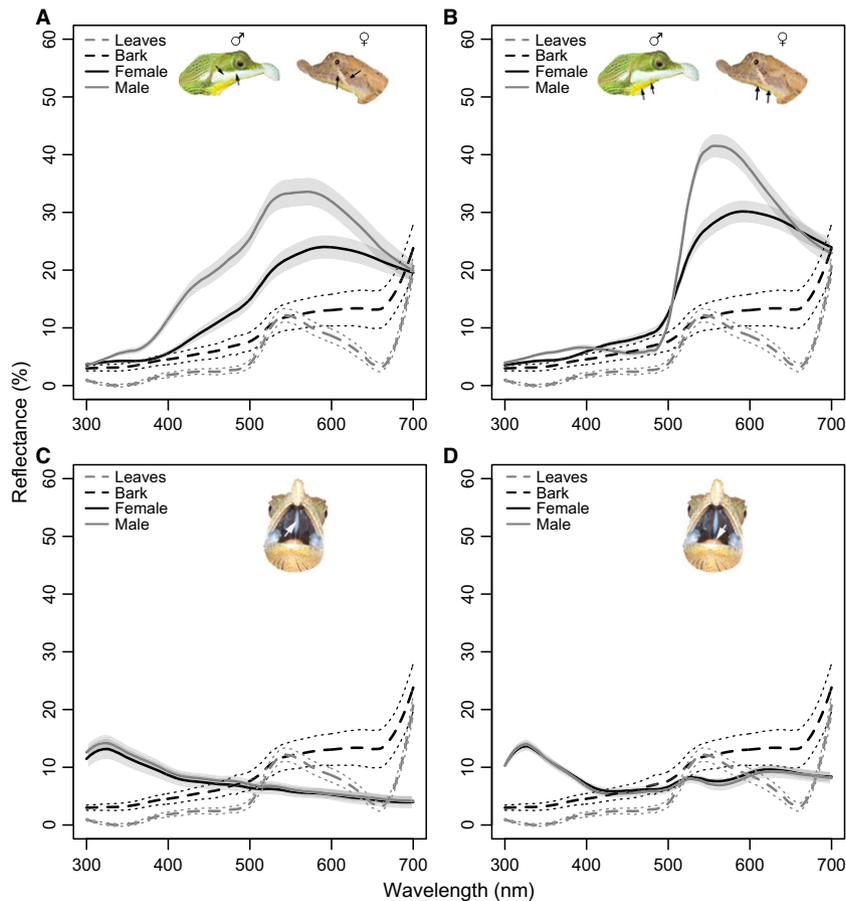

Figure 3. Mean ($\pm 95\%$ confidence intervals) spectral reflectance curves for male and female *Ceratophora tennentii* as well as their background (leaves and bark) for (A) the labials (females: $N = 27$; males: $N = 29$); (B) the throat patch (females: $N = 27$; males: $N = 30$); (C) the roof of the mouth (females: $N = 27$; males: $N = 30$ and (D) the tongue of the mouth (females: $N = 27$; males: $N = 33$). Arrows in pictures indicate the locations of the reflectance measurements.

Table 4. Standardized $[x - \text{mean}(x)/2*\text{sd}(x)]$ model coefficients (Est.) and standard errors (SE) for log maximal bite force and body condition as a function of rostrum length and chromatic contrast values. Bolded estimates and standard errors indicate significance at $P < 0.05$. Sample sizes are indicted. Interactions not included in the table were not significant and were excluded from the model.

	Log maximum bite force		Body condition	
(a) Throat colour				
N = 57	Est.	SE	Est.	SE
Intercept	**1.90**	**0.02**	0.05	0.03
Sex (m)	0.04	0.05	**−0.10**	**0.04**
ΔS (JNDs)	−0.08	0.05	−0.02	0.04
Rostrum length	−0.07	0.07	0.01	0.04
SVL	**0.43**	**0.10**	–	–
Head length	0.12	0.10	–	–
Temperature	**−0.13**	**0.05**	–	–
Sex*Head length	**1.01**	**0.23**	–	–
Sex*SVL	**−0.63**	**0.20**	–	–
(b) Labial colour				
N = 56	Est.	SE	Est.	SE
Intercept	1.89	0.02	0.05	0.03
Sex (m)	0.06	0.05	**−0.10**	**0.04**
ΔS (JNDs)	**−0.12**	**0.04**	−0.01	0.04
Rostrum length	−0.07	0.06	0.01	0.04
SVL	**0.41**	**0.10**	–	–
Head length	**0.12**	**0.10**	–	–
Temperature	−0.09	0.06	–	–
Sex*Head length	**0.97**	**0.22**	–	–
Sex*SVL	**−0.63**	**0.19**	–	–

$F = 0.62$, $P = 0.44$; Labial colour model: Sex*Rostrum length: $F = 0.61$, $P = 0.44$) or body condition (Throat colour: Sex*Rostrum length: $F = 0.01$, $P = 0.94$; Labial colour: Sex*Rostrum length: $F = 0.02$, $P = 0.90$) varied between the sexes. Rostrum length was more generally not a predictor of bite force or body condition when controlling for temperature, SVL, head length and chromatic contrast (main effects – Table 4).

The relationship between throat and labial chromatic contrast and maximal bite force did not differ between the sexes (Fig. 4; Throat: Sex*ΔS: $F = 1.34$, $P = 0.25$; Labial: Sex*ΔS: $F = 1.12$, $P = 29$). Throat chromatic contrast did not predict maximal bite force (Table 4) whereas labial chromatic contrast was negatively related to maximal bite force (Fig. 4 and Table 4). Neither throat nor labial chromatic contrasts were related to body condition (Table 4). We found
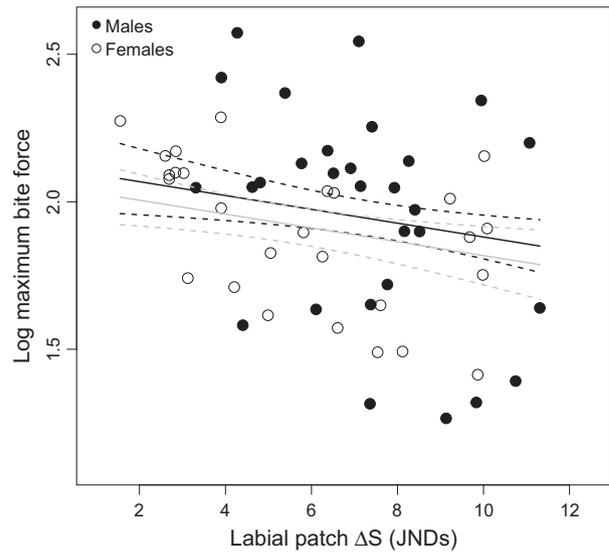

Figure 4. Relationship between predicted log maximum bite force and labial patch chromatic contrast (ΔS: JNDs) for males (black) and females (grey). Predictions and 95% confidence intervals are based on the model presented in Table 4(b) where all other variables are held at their mean values.

largely similar results for achromatic contrast and present these in Table S1.

OPEN-MOUTH DISPLAYS AS A POTENTIAL DEIMATIC SIGNAL

Male and female mouth reflectance did not differ in chromatic (ΔS) (Fig. 5; Wilcoxon rank sum test; Roof: $W = 435$, $P = 0.64$; Tongue: $W = 413$, $P = 0.63$) or achromatic (ΔL) contrast (Fig. 5: Wilcoxon rank sum test; Roof: $W = 460$, $P = 0.38$; Tongue: $W = 335$, $P = 0.10$) under a bird visual system, but were mostly highly conspicuous to birds (JNDs > 10). No lizards performed an open-mouth threat when exposed to a waving hand at 10 cm ($N = 51$). Upon capture, 92% (47/51) of lizards performed an open-mouth display.

DISCUSSION

We found no differences in body length (SVL) or mass between males and females. When body size was controlled for, males had significantly longer heads than females, but neither head width or depth was significantly dimorphic. Furthermore, the significant difference in head length was not strong. Males and females had similar dewlap and crest heights and the greatest level of sexual dimorphism occurred in rostrum length: males had significantly longer rostrums
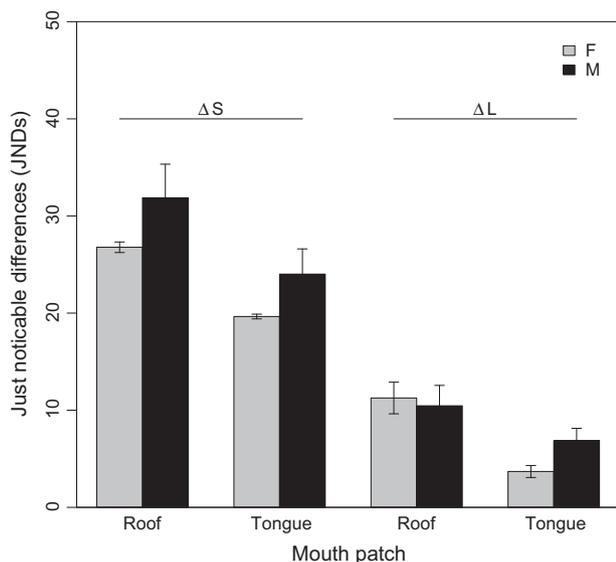
Figure 5. Mean (±standard error) chromatic (ΔS) and achromatic (ΔL) contrast of the roof and tongue of the mouth for males (black) and females (grey) viewed from a bird visual system. Sexes did not differ significantly on any of the comparisons. See Results for more details.

than females for a given body size. In addition, males are sexually dichromatic, having brighter yellow throats and labials than females. Neither rostrum length nor throat coloration signalled bite force or body condition in either sex. However, there was a negative relationship between labial chromatic contrast and bite force.

Our primary hypothesis that rostrum and colour traits signal male quality was not supported. Specifically, we found no support for our predictions that these traits should be positively associated with stronger bite force and higher body condition. Rostrum length was not a predictor of body condition, and as such, cannot be considered a condition-dependent signal. Having said that, it is important to remember that our study represents a snapshot of this system and we have no knowledge of the long-term relationship between rostrum length and body condition. That is, the rostrum is unlikely to reflect any short-term changes in condition experienced by a male. Males and females also did not differ in bite force and bite force was not associated with rostrum length. While rostrum length is clearly greater in males than females, it is unlikely to be used as a weapon in male contests because the rostrum is pliable (unlike a true horn), although an alternative hypothesis is that it could still act as a status signal to other males. However, our data suggest that it does not provide information on male bite force, which may be used by conspecific males to assess male rivals prior to escalated contests. While rostrum length may convey

other information to males, behavioural tests are also needed to determine whether contests escalate in this species, what the predictors of contest outcome are, and whether status signals help ameliorate conflict.

Males and females were obviously dichromatic, suggesting sex-specific differences in selection. Furthermore, many lizards were collected from the trunks of trees, against which females appear to be more cryptic. Males may therefore be more conspicuousness as a consequence of sexual selection although the mechanism is unclear. The most conspicuous difference was in labial and throat chromatic contrast and luminance. Male throat coloration was not strongly associated with bite force or body condition, although we found a negative relationship between bite force and labial chromatic contrast that did not appear to be sex-dependent. While this relationship was weak, it was not in line with our predictions. While we cannot provide a satisfactory explanation for this given the limited data, it maybe the result of correlated effects of aging (i.e. decreased contrast with increased age given large males bite harder). However, testing this hypothesis would require a more longitudinal approach to colour quantification than was possible in our study. Overall, we did not find convincing evidence that chromatic contrast predicted body condition but we cannot exclude the possibility that it signals some other aspect of male quality, such as immunocompetence. Interestingly, rostrum length in males correlated with throat chromatic contrast. These two independent sources of information may either signal different information to a male or female receiver, about male quality, or reinforce the same message. Future work will be necessary to test this hypothesis.

A recent comparative study of rostral appendages in *Ceratophora* failed to detect sexual dimorphism in rostrum length in *C. tennentii* but was constrained by moderate sample size, although the trend was in the predicted direction (male + dimorphism) (Johnston *et al.*, 2013). Nevertheless, the strength of this dimorphic relationship does suggest that rostrum length is a target of sexual selection and may be a cue used by females to assess some aspect of male quality other than condition or likewise, used by males to assess rivals in other traits we were unable to measure. An interesting species for comparison is the horned anole of Ecuador, *Anolis proboscis*. Males of this species also have a pliable horn, but unlike *C. tennentii*, females are hornless. The function of the horn is unknown but thought to either act as a signal of male status, or a cue to females (Losos *et al.*, 2012). While female mate choice appears to be rare in lizards (Tokarz, 1995) these two species may be ideal model systems to explore the possibility of female mate choice.

Sex differences in bite force are relatively common in lizard species with male contest competition and typically, but not always (Husak *et al.*, 2006, 2009; Noble, Fanson & Whiting, 2014), reflect selection on head size (Lailvaux *et al.*, 2004; Vanhooydonck *et al.*, 2010). Head size and bite force can be the product of both natural and sexual selection such that diet may best explain head morphology in females (natural selection), while contest competition may drive head size and shape in males (sexual selection) (Vanhooydonck *et al.*, 2010). Disentangling these effects can be difficult, particularly in the absence of detailed dietary data. However, these lizards appear to have a broad diet including caterpillars, cockroaches, bees, moths, large ants and rarely, their own young (Rodrigo & Jayantha, 2004; de Silva *et al.*, 2005). We think it is unlikely that there are any major differences in diet between males and females given their overlap in body size and habitat use, but more detailed studies are necessary to unequivocally answer this question. Importantly, we did not find any link between male bite force and armament/ornament expression despite the sexes varying in head length. Males may therefore be assessing rivals using behavioural cues alone, or they may use simple size assessment in isolation. We need a controlled study of contest competition to better understand signals of dominance and whether contests actually escalate to fights.

We measured mouth colour because a wide range of lizard species have colourful mouths and many species use open-mouth threats as a defensive behaviour during capture (pers. observ.). Signals that are normally concealed but highly conspicuous when exposed (by choice), are termed deimatic signals, and are designed to startle a predator (Umbers *et al.*, 2015). These signals are also generally deployed during the subjugation phase of predation, as a last resort, as opposed to a pursuit-deterrent signal, which is used in the early stages of an encounter with a predator. While we did not witness any interactions between lizards and predators, 92% of lizards used an open-mouth threat during capture and handling but none responded to a predatory threat (hand waving). Also, we found no sexual differences in tongue or mouth colour. Both regions of the mouth had UV that was highly conspicuous (mostly >10 JNDs) to a bird predator. These behavioural and chromatic/achromatic data suggest that mouth colour in this species and possibly many other lizard species, may act as a potential deimatic signal during predatory encounters. This hypothesis will no doubt require detailed data on receiver psychology, predator handling behaviour, and their responses to these displays, however, our data support predictions that are consistent with this hypothesis.

In summary, we did not find a link between bite force, a functional measurement of performance capacity typically important in lizard systems experiencing classical sexual selection, and ornamentation. Rostrum size and aspects of coloration were also not associated with body condition. However, throat chromatic contrast and rostrum size were correlated and may act as multiple signals to either male and/or female receivers. Finally, the use of open-mouthed threat displays is consistent with predictions associated with deimatic signalling but requires experimental testing from the receiver's perspective. This system, like so many others, retains very much an air of mystery and will require carefully planned experiments to further elucidate signal structure and the nature of the information conveyed to rivals, potential mates, and predators.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Standardized $[x - \text{mean}(x)/2*\text{sd}(x)]$ model coefficients (Est.) and standard errors (SE) for log maximal bite force and body condition as a function of rostrum length and achromatic contrast values (ΔL; JNDs). Bolded estimates and standard errors indicate significance at $P < 0.05$. Sample sizes are indicted. Interactions not included in the table were not significant and were excluded from the model.