



Ultraviolet signals ultra-aggression in a lizard

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Understanding the role of multiple colour signals during sexual signalling is a central theme in animal communication. We quantified the role of multiple colour signals (including ultraviolet, UV), measures of body size and testosterone levels in settling disputes between male rivals in an elaborately ornamented, African lizard, played out in a large 'tournament' in the wild. The hue and brightness (total reflectance) of the UV throat in Augrabies flat lizards, *Platysaurus broadleyi*, as well as body size, were consistent and strong predictors of 'fighting ability'. Males with high fighting ability were larger and displayed a UV throat with low total reflectance. In contrast, males with low fighting ability were smaller and had violet throats with broader spectral reflectance curves (higher total reflectance). As fighting ability is associated with alternative reproductive tactics in this system (territorial versus floater), we also examined the role of colour signals in predicting male reproductive tactic. Territorial males had UV throats with higher chroma but had poorer body condition than floater males, probably because of the energetic costs of maintaining a territory. Although testosterone was not a significant predictor of fighting ability or reproductive tactic, it was correlated with the hue of the UV throat, suggesting that testosterone may impose some constraint on signal expression. Lastly, we show that within the context of the natural signalling environment, UV-reflective throats constitute a conspicuous, effective signal that male Augrabies flat lizards use to advertise their status honestly to rivals.

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Animals use a diverse array of signals to communicate aspects of their social or reproductive status (Andersson 1994; Cuthill et al. 2000). Conspicuous coloration is an important visual sexual signal that has been studied in a wide variety of taxa and contexts, including mate preference, contest competition and species recognition (reviewed in Cooper & Greenberg 1992; Andersson 1994; Losey et al. 1999; Seehausen et al. 1999; Hoffman

& Boulin 2000). However, the majority of studies have focused on a single colour trait such as an ornament or a badge of status (Whiting et al. 2003). In addition, some colour signals, such as ultraviolet (UV) are invisible to the human eye and have therefore received less attention (Bennett et al. 1994; Losey et al. 1999; Cuthill et al. 2000). As a consequence, the relative roles of UV and other conspicuous colour signals in sexual selection have rarely been addressed in the same study. Previous studies have focused on the role of UV signals in female mate choice (Bennett et al. 1996, 1997; Andersson et al. 1998; Hunt et al. 1998; Cuthill et al. 2000; Pearn et al. 2001; Smith et al. 2002). The possibility that UV signals may also function in settling male contests has only recently been considered. Specifically, male eastern bluebirds, *Sialia sialis*, with more intense UV chroma were more successful at acquiring nestboxes than less colourful rivals and fledged more chicks (Siefferman & Hill 2005); blue tits, *Cyanistes caeruleus*, use UV to settle male contests (Alonso-Alvarez et al. 2004); and damselfish, *Pomacentris*

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amboinensis, a coral reef fish, respond to intruding males as a function of their degree of UV reflectance (Siebeck 2004). Our understanding of the extent to which UV signals influence male reproductive success through their role in male–male contests, and how important these signals are in natural systems, therefore remains limited.

In addition to visual traits such as colour badges, features of body size/condition and physiological state (e.g. circulating steroid hormones and immunocompetence) are all potentially important determinants of fighting ability and, therefore, of contest outcome (Anderson & Vitt 1990; Olsson 1992; López et al. 2002; Watt et al. 2003; Perry et al. 2004). For example, in species with intense male rivalry, larger body size frequently predicts contest outcome (reviewed in Andersson 1994). In addition, circulating steroid hormones such as testosterone play a role in both the expression of condition-dependent traits used in male contests and in regulating aggressive behaviour (Cooper et al. 1987; Tokarz 1995; Buchanan et al. 2001, 2003; Hagelin 2002; Watt et al. 2003). More aggressive/dominant males or males with higher fighting ability linked to testosterone levels may be more effective at securing and defending territories and thereby gain greater access to females (Cooper et al. 1987; Brain & Haug 1992; Sinervo et al. 2000; Hagelin 2002; Weiss & Moore 2004). However, high levels of testosterone may serve as an additional constraint on signal expression (as an honest signal) because testosterone can compromise the immune system (Peters 2000; Roberts et al. 2004) and reduce survival (Peters 2000; Sinervo et al. 2000), and may be energetically costly through its effect on metabolic rate (Buchanan et al. 2001; Peters et al. 2004). The relative roles of colour and other morphological traits in predicting contest outcome, and specifically how these relate to testosterone, are not always clear.

Although male contest competition is a key mechanism of sexual selection because winners frequently have access to more females (Andersson 1994), dominance does not always result in higher reproductive success because some individuals may adopt alternative reproductive tactics (Gross 1996; Sinervo & Lively 1996) or females may choose males based on some trait independent of aggression or fighting ability (López et al. 2002). Nevertheless,

the opportunity for sexual selection exists because of variation between males in access to females as a result of relative fighting ability. Most alternative reproductive tactics are condition or frequency dependent (Gross 1996) and often associated with levels of testosterone (Hews et al. 1994; Sinervo et al. 2000; Davis 2002). For example, relative to other morphs of side-blotched lizards, *Uta stansburiana*, orange-throated males have the largest home ranges, the highest endurance and levels of activity, the highest testosterone levels and the greatest access to females. However, compared with other morphs which adopt alternative reproductive tactics, they have the lowest survival (Sinervo et al. 2000). Alternative reproductive tactics need not necessarily be associated with a particular morph, but may occur as a function of resource limitation such that certain individuals adopt a floater or nomadic tactic in lieu of defending a territory. Because being dominant or defending a territory is potentially costly and may require higher levels of testosterone and greater investment in trait expression, the expectation is that floaters will invest less in potentially costly traits (Mateos 2005).

The Augrabies flat lizard, *Platysaurus broadleyi*, represents an excellent system with which to examine the role of multiple male traits in signalling both fighting ability and reproductive tactic. Males have bright orange, yellow or lime-green front legs, a bright orange-yellow ventral colour patch (Whiting et al. 2003) and UV to violet throats (Fig. 1a). Elaborate ornamentation coupled with intense male rivalry make *P. broadleyi* well suited for studies of signalling and sexual selection. During the breeding season, males gain access to females by excluding rivals from their mating territory through signals and chases and by fighting (Whiting 1999; Whiting et al. 2003). To ameliorate the costs of aggression, such as energetic expenditure and risk of injury, males perform a display in which they flash their venter and simultaneously expand their throat (Fig. 1b). Most contests are thus settled quickly through signalling, although they sometimes escalate to physical combat. Male *P. broadleyi* are preferentially territorial, but high male densities at our site (Augrabies) mean that territories are at a premium, resulting in many males adopting a ‘floater’ tactic. Because of this high density, resident males have sharply demarcated

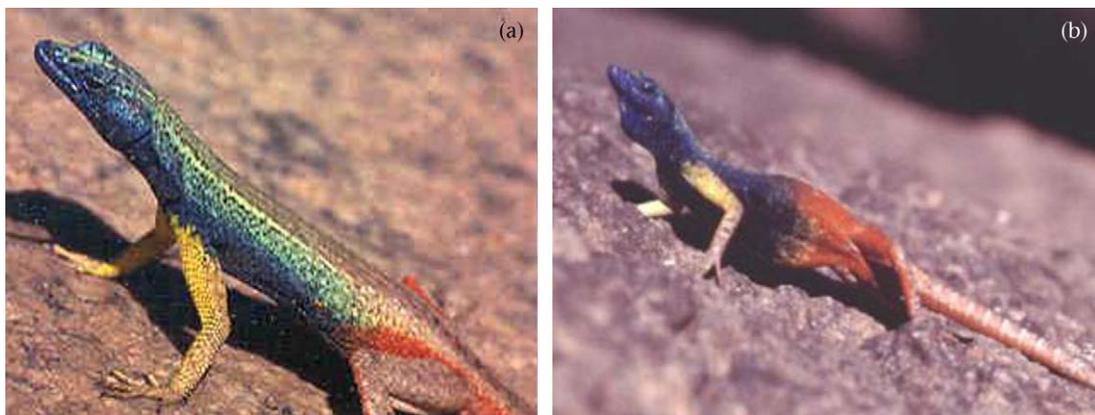


Figure 1. Augrabies flat lizard, *Platysaurus broadleyi*, from northern South Africa. (a) Males have brightly coloured front legs (yellow, orange or lime green); a bright orange or yellow colour patch on the venter and blue-turquoise flanks. (b) Characteristic agonistic display in which males challenge rivals by flashing their venters (Whiting 1999; Whiting et al. 2003) and simultaneously expand their throats, which reflect UV.

territories that share borders with their neighbours and neighbours can be as close as ca. 30 cm. As such, males display throughout the day and contest frequency is high. This system thus provides a rare opportunity to evaluate the role of specific male traits in determining both contest outcome and reproductive tactic.

We examined the relative roles of multiple colour signals, including UV signals, measures of body size and plasma testosterone in settling contests and in determining alternative reproductive tactics in male *P. broadleyi*. We also examined the correlation between signals of fighting ability and testosterone to explore potential constraints on signal expression. Finally, because signal effectiveness is in part a function of the signalling environment (Endler 1992, 1993; Fleishman & Persons 2001), we measured the colour of background rock to examine signal conspicuousness. We discuss how the signals used by *P. broadleyi* in male–male interactions relate to both lizard visual systems and the signalling environment at Augrabies.

METHODS

Study System

Platysaurus broadleyi occurs within close proximity to the Orange River in northern South Africa, from Augrabies Falls National Park in the east to Klein Pella in the west, a distance of ca. 150 km (Branch & Whiting 1997). Although they have a restricted distribution, these lizards are locally abundant. They feed primarily on black flies (*Simulium* spp.) but also eat ripe Namaqua figs when they are available (Whiting & Greeff 1997). We studied a wild population of *P. broadleyi* at Augrabies Falls National Park (28°35'S, 20°20'E) during September–October 2002. Lizards are restricted to rock and the highest densities occur on the granitic banks of the Orange River where large aggregations of their primary prey, black flies, occur in the fast-flowing sections of the river, resulting in discrete feeding areas and spatial clumping of lizards (Whiting et al. 2003). The lizards exist in a xeric environment devoid of vegetation except for the occasional fig tree, *Ficus cordata*. They have relatively small activity ranges. The majority of lizards use communal overnight refuges and normally travel less than 100 m daily to feeding areas close to the river or, in the case of resident males, to their territories. About twice daily, resident males will leave their territories unattended for 15–30 min when they travel to a feeding area. At Augrabies, lizards are habituated to humans and allow close approach, facilitating behavioural observations. We conducted observations in two areas, each about 50 × 80 m, separated by several hundred metres. The lizards in these areas form part of a continuous population.

Lizard Sampling and Testosterone Assays

We sampled 136 male lizards during their peak morning activity period (ca. 0900–1130 hours) over a 5-day period. Upon capture, we immediately took a blood sample from the suborbital sinus using a 150- μ l capillary tube (see Ethical Note below) and stored it on ice. Samples were

centrifuged within 2–3 h of collection at 2500 and the plasma separated for testosterone assays. Lizards were transported back to the laboratory for measurement of morphology and colour and for individual marking. We numbered (see Ethical Note below) each individual on the centre of its back, a location typically not visible to rivals during interactions. All individuals were released at their point of capture the next morning and given 1–2 days of recuperation before behavioural sampling. We assayed testosterone by using DPC Coat-A-Count Total Testosterone kits and validated radioimmunoassays by standard dilution techniques (range 1:1–1:32) and by checking double dilutions against standard curves. We tested for correlations between explanatory variables and testosterone levels to establish potential signalling costs.

Ethical Note

Lizards were captured with Catchmaster (48R) nontoxic glue traps (27 × 13 cm, Atlantic Paste & Glue Co., New York, U.S.A.), which consist of a plastic base with a clear, viscous adhesive that does not run unless subject to high temperatures (Whiting & Alexander 2001). Glue traps were monitored continuously by two people (D.S.F. and D.O.C.) and lizards were removed from the traps as soon as they became stuck. To do this, we used small amounts of vegetable oil on thumb and forefinger to massage the glue gently from the lizard's body (Whiting & Alexander 2001). No other animals were caught on these traps and the glue had no adverse effects on the lizards' skin. We sampled blood for testosterone assays from the suborbital sinus as this is a standard procedure for 'small' lizards (e.g. Woodley & Moore 1999). We have previously used this technique for several hundred lizards (Whiting et al. 2003); none have shown any observable ill effects from this procedure and many individuals display within minutes of release. After blood sampling, lizards were placed in cloth bags in the shade and transported back to the laboratory (for additional measurements) within 2 h of capture. They were stored in a cool room overnight. None of the lizards showed signs of excess stress or injury on release the following morning. As part of a separate study (M. J. Whiting, D. M. Stuart-Fox & D. O'Connor, unpublished data) we monitored lizards for a more extended period after using glue trapping and blood sampling from the suborbital sinus. We maintained 103 males in semi-natural outdoor enclosures (110 × 110 × 100 cm) for 2 weeks. Males were maintained with two to four other individuals and each enclosure contained two separate terracotta tile crevices (20 × 20 cm). Lizards were fed tinned cat food (Whiskas, Mars Inc., Hackettstown, U.S.A.) and had access to large numbers of flies. Food and water were provided daily. There were no fatalities and we observed no permanent injury. We marked lizards with non-toxic xylene-free Pilot paint pens (Pilot Corporation, Tokyo, Japan); paint marks generally lasted 10–14 days. We do not believe that marked individuals were more susceptible to predation because *P. broadleyi* occur in the open on exposed rock and in high densities, where they are

already highly conspicuous. Permission for the study was given by the University of Witwatersrand Animal Ethics Committee.

Spectroradiometry

We measured lizard and background (rock) colours with an Ocean Optics USB2000 spectrometer and deuterium-tungsten DT-1000 mini light source connected to a fibre-optic probe. The probe was mounted within a probe holder that ensured readings were taken from areas 5 mm in diameter at a constant distance from the surface with both illumination and reflectance measurement at a 45° angle to the surface. Measurements were taken in a darkened room with the probe holder flush with the surface of the lizard's throat. Measurements were relative to a 99% WS-1 white reflectance standard. Spectral reflectance was measured at 320–700 nm as this represents the broadest range of wavelengths known to be visible to lizards (Loew et al. 2002). Each measurement used was an average of three consecutive readings, all taken by D.S.F., of three body regions: throat, ventral colour patch (Fig. 1b), and front leg. Measurements of rock were taken from light ($N = 15$) and dark ($N = 15$) patches which occurred in approximately equal proportions (Fig. 2).

We analysed spectral reflectance in two ways. First, we used principal components analysis (PCA), which makes no assumptions about the receiver's visual system (Cuthill et al. 1999). The biological interpretation of the principal components (PCs) was determined by examining the correlations of principal component eigenvectors with wavelength (5-nm intervals), that is, the relation between the PCs and the original reflectance data (Cuthill et al. 1999). In addition, we checked the interpretation by examining the original reflectance curves for males with high and low values of each PC. Second, we also derived traditional measures of hue (spectral location), brightness (spectral intensity) and chroma (spectral purity) (Endler 1990). Hue was calculated as the peak wavelength corresponding to maximum reflectance (320–700 nm). Brightness was calculated as mean reflectance for the interval 320–700 nm. Chroma is a function of slope height and

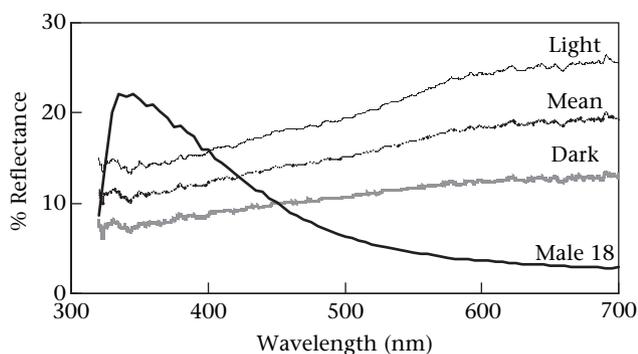


Figure 2. Mean reflectance of the rock background compared to the UV throat of a representative lizard (male 18). Rock backgrounds consist of finely mottled granite with light and dark patches in approximately equal proportions. The mean of these thus represents the background colour as viewed from a distance.

steepness; this variation can be quantified by using the difference between two spectral segments divided by total reflectance. We used $\lambda(R50)$ (the wavelength halfway between minimum and maximum reflectance) as the segment divider, rather than an arbitrary point, to avoid confounding variation in hue with chroma (Pryke et al. 2001). To compute chroma, we used the formula $[R_{320-\lambda(R50)} - R_{\lambda(R50)-700}] / R_{320-700}$ (e.g. Pryke et al. 2001; Andersson et al. 2002), where R = reflectance at a particular wavelength λ , and $R_{320-700}$ is the sum of reflectance from 320 to 700 nm. Although using traditional measures (hue, chroma, brightness) of colour analysis has the advantage that it is simpler to interpret and comparable between studies, it is likely to capture variation in the shape of reflectance curves less accurately than PCA (Grill & Rush 2000). As each method has both advantages and disadvantages, we repeated analyses using both methods and searched for consistency between them.

Morphology

We measured body size (snout–vent length, SVL) as the distance between the tip of the snout and the posterior edge of the cloaca (± 1 mm). Head length (tip of snout to tympanum) and head width (widest point at occiput) were measured with digital callipers (0.01 mm) and mass was measured (± 0.1 g) with a digital scale. All measurements were taken by M.J.W. Head measurements were transformed to a dimension-free variable using residuals from linear regression on body size. For each individual we calculated a standard condition index (residuals of mass/body size). Finally, we scanned the ventral surface of each individual to capture a digital image of the ventral colour patch. Colour patch area was calculated with the graphics software Simple PCI (Compix Incorporated, Sewickley, U.S.A.) and calibrated against known body size.

Statistical Analysis

From scan and focal sampling (Martin & Bateson 1993) of interactions between known individuals, we scored contest outcome (win, loss, draw) based on whether one or both lizards withdrew from the encounter. Draws were not included in analyses. We also scored males as 'resident' (territorial) or 'floater' from repeated sightings (generally > 5) on marked individuals to determine whether they defended exclusive areas or adopted a nomadic tactic.

Contests between males can be viewed as part of a large tournament from which relative 'fighting ability' of individuals can be estimated based on a subset of all possible interactions between 'players'. As interactions involving the same individual are not independent and the number of observations per individual will be variable, we used the Bradley–Terry (BT) model for paired comparisons, a form of generalized linear model which takes proper account of dependency within and between contests and can accommodate an incomplete matrix of possible interactions (Bradley & Terry 1952; Firth 2005).

We fitted BT models to the ‘tournament’ (see Results) of 100 contests involving 77 lizards. The BT model assumes that each lizard has a positive-valued ability, such that the odds for the result of any contest is the ratio of the abilities of the two contestants. For convenience, we refer to this ability as ‘fighting ability’, although contests were often settled without physical contact. The relation between $\ln(\text{ability})$ and a linear combination of the available explanatory variables was explored with maximum-likelihood model fitting and stepwise subset selection. A full description of the structured BT model is provided in Firth (2005; see also Stuart-Fox et al. 2006 for discussion of its application to analysing animal contests). We set the criterion for remaining within the model at $P = 0.1$. To examine the relative magnitudes of effects, we used standardized regression coefficients, equivalent to regression with all predictors scaled to have unit standard deviation. The BT model with individual-specific covariates was run with a freely available package for ‘R’ (Firth 2005; R Development Core Team 2005). Finally, we carried out a separate BT analysis in which we accounted for the potential advantage that a resident may have over a floater. In this analysis, we scored contests as follows: ‘1’ if the winner was a resident and the loser a floater because the winner has a ‘resident advantage’; ‘-1’ if the winner was a floater and the loser a resident because the winner was at a disadvantage; and ‘0’ if both lizards had the same reproductive tactic because neither had an advantage from residency status. We included this ‘resident’ advantage effect as an additional contest-specific predictor in the BT model following procedures in Firth (2005). The results are presented as Supplementary material.

To determine what variables contributed significantly to an alternative male reproductive tactic, we used multiple logistic regression with reproductive tactic (territorial ‘1’ and floater ‘0’) as the response variable. We included in this analysis only the 52 individuals that were observed multiple times over the study period (26 residents, 26 floaters).

In analyses of both fighting ability and alternative reproductive tactics, we ran two models: one using colour variables derived from PCA of reflectance curves and another using colour variables based on traditional measures of hue, chroma and brightness. In addition to variables summarizing reflectance of the three body regions, both models also incorporated morphological variables (SVL, condition, head length and head width) and testosterone levels as covariates.

RESULTS

Colorimetry

The first three PCs accounted for 95, 92 and 87% of variation in throat, ventral colour patch and front leg reflectance, respectively. PC1 describes mean reflectance (typically, variation in brightness; Fig. 3) and was significantly correlated with brightness as measured by the sum of mean reflectance (Pearson correlation: throat:

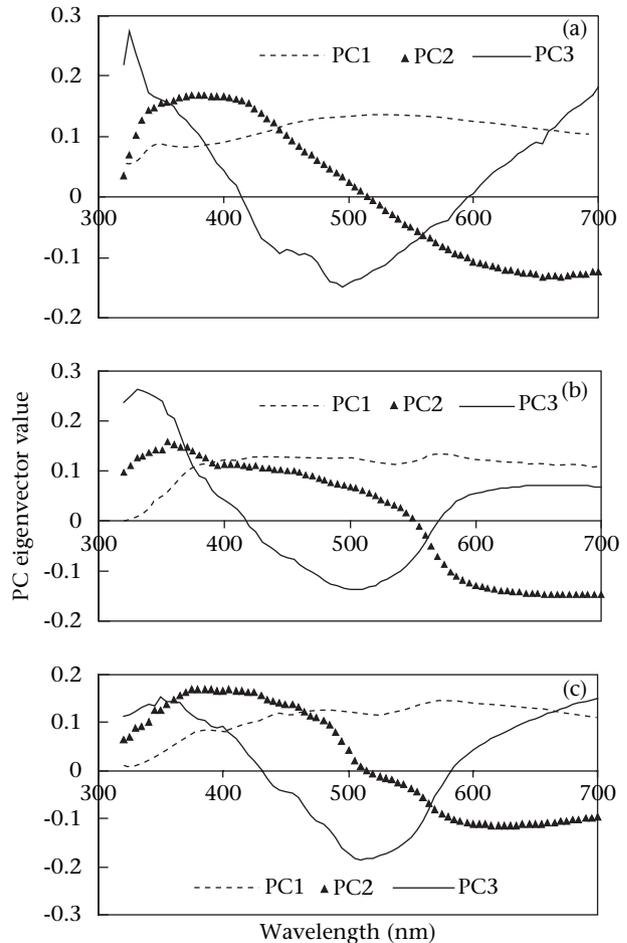


Figure 3. Loadings (eigenvectors) of principal components 1, 2 and 3 of (a) the throat, (b) the ventral colour patch and (c) the front leg of male *Platysaurus broadleyi* against original variables (5-nm wavelength intervals), allowing biological interpretation of PCs (see text).

$r_{72} = 0.82$, $P < 0.0001$; ventral colour patch: $r_{74} = 0.97$, $P < 0.0001$; front leg: $r_{74} = 0.95$, $P < 0.0001$). PC2 represents variation in the amount of short and medium relative to long wavelengths for all three body regions (Fig. 3). From inspection of raw data, this primarily reflects spectral purity for the throat and ventral badge and is significantly correlated with our simpler measure of chroma (throat: $r_{72} = 0.90$, $P < 0.0001$; ventral colour patch: $r_{74} = -0.56$, $P < 0.0001$). In both cases, high positive values for PC2 indicate curves with low chroma. PC2 of the throat was also more weakly correlated with brightness ($r_{72} = 0.51$, $P < 0.0001$), while PC2 of the ventral badge was also more weakly correlated with hue ($r_{74} = -0.38$, $P < 0.001$). For front legs, PC2 was weakly correlated with traditional measures of both hue ($r_{74} = -0.26$, $P = 0.02$) and chroma ($r_{74} = 0.24$, $P = 0.04$). PC3 describes variation in short and long wavelengths relative to medium wavelengths (Fig. 3) and for the throat and front legs corresponded to ‘hue’ (throat: $r_{72} = -0.52$, $P < 0.0001$; front leg: $r_{74} = 0.73$, $P < 0.0001$). Males with high PC3 values for the throat had spectral reflectance curves that peaked in the UV (320–360 nm), whereas

males with low PC3 values had reflectance curves that peaked in the violet part of the spectrum (360–430 nm). In the case of the front legs, high values of PC3 indicate orange legs and low values indicate yellow legs. PC3 of the ventral colour patch correlated only with chroma ($r_{74} = -0.5$, $P < 0.0001$).

Predictors of Fighting Ability

A schematic of how part of the lizard tournament was played out is presented in Fig. 4. Regardless of whether we used variables based on PCA of spectral reflectance curves or traditional measures of hue, chroma and brightness, aspects of the UV throat were consistently the strongest predictors of fighting ability. The single best model using PCs of reflectance for each body region retained several predictor variables (Table 1). The variable that most strongly predicted fighting ability was the third principal component (PC3) of throat reflectance, corresponding to 'hue' (Fig. 3a, b). Throat 'brightness' (PC1) was also a strong predictor of fighting ability although the relation was negative (Table 1). As in other lizards, body and head size (SVL and head length) also influenced fighting ability but were weaker predictors of fighting ability than throat colour. The model based on traditional measures of hue, chroma and brightness similarly retained throat hue, throat brightness and SVL, but not head length, as strong predictors of fighting ability (Table 1). Thus, males with

Table 1. Bradley–Terry 'tournament' model of lizard contests examining variables that predict fighting ability in *Augrabies flat* lizards

Trait	Coefficient	SE	Z	P	Standardized coefficient
PCA*					
Throat PC1	-0.09	0.03	10.3	0.001	-0.68
Throat PC3	0.34	0.11	9.5	0.002	0.80
Head length	-1.13	0.49	5.2	0.02	-0.42
Snout–vent length	0.19	0.1	3.6	0.06	0.45
Traditional†					
Throat brightness	-0.56	0.16	-3.51	0.0005	-1.11
Throat hue	-0.05	0.01	-3.63	0.0003	-1.08
Snout–vent length	0.21	0.11	1.99	0.046	0.50

Note that the positive coefficient estimate for throat PC3 and the negative coefficient estimate for throat hue both indicate that males with throat reflectance peaking at shorter wavelengths have greater fighting ability.

*The single best model based on principal components analysis (PCA) of spectral reflectance.

†The single best model based on traditional measures of hue, chroma and brightness.

high fighting ability were larger and displayed a UV throat with low total reflectance; Fig. 5a). In contrast, males with low fighting ability were smaller and had violet throats with broader spectral reflectance curves (higher total

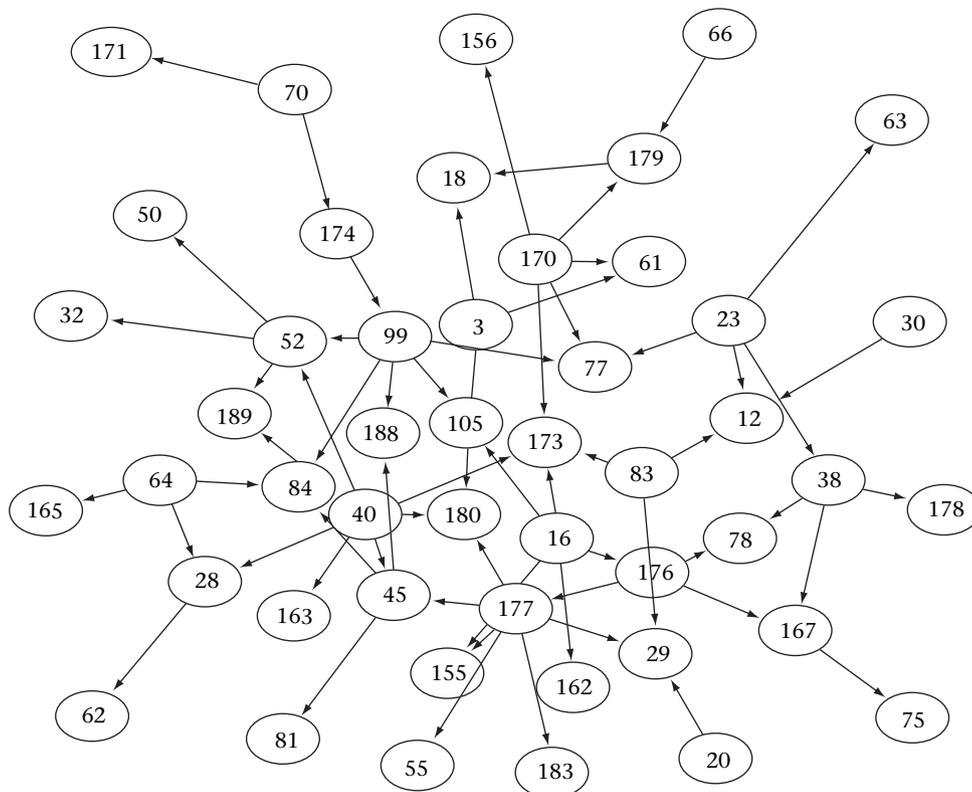


Figure 4. A schematic of a subset of marked individuals which can be viewed and analysed as a 'tournament'. Each numbered circle represents a lizard and all its interactions. An arrow directed away from a circle indicates a win for that lizard, but a loss for the individual receiving the arrow.

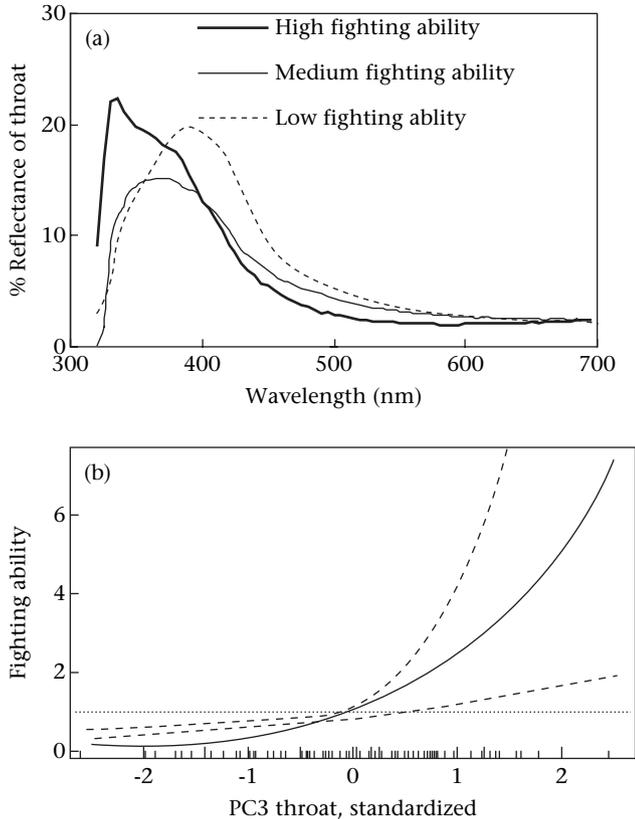


Figure 5. UV signals used in male–male contests in the lizard *Platysaurus broadleyi*, as they relate to fighting ability. (a) Representative spectral reflectance curves of the throats of three males with high, medium and low fighting ability. (b) Relative fighting ability in relation to the ‘hue’ (principal component 3, PC3) of the throat. The Y axis is fighting ability estimated from the Bradley–Terry model, with ability at the mean of PC3 of the throat set to one. The odds on lizard A defeating lizard B is ability A divided by ability B. For example, a lizard at 1 SD above the mean in PC3 of the throat has odds of more than two (i.e. probability > 2/3) of beating a lizard whose PC3 of the throat is at the mean (all else being equal). A lizard at 2 SD above the mean has odds around five (i.e. probability about 5/6) of beating a lizard whose PC3 of the throat value is average, etc. The dashed curves are 95% confidence intervals. The horizontal dotted line is ability = 1, the ability of the ‘mean’ lizard. The ‘rug’ on the abscissa indicates the values of PC3 of the throat for all lizards included in the model.

reflectance; Fig. 5a). As an indication of the potential effect size, we considered two hypothetical lizards with high and low values of throat hue, but equal in all other respects. Based on the more conservative model (with lower standardized coefficient for throat hue, that is, the model using PCs), taking each of the two lizards to be two standard deviations from the mean resulted in estimated odds of $\exp(4 \times 0.801)$, about 25:1, in favour of the lizard with the more UV throat (higher PC3 of throat reflectance) winning the contest. This relation is graphically presented in Fig. 5b.

When we accounted for resident advantage in the BT model, aspects of throat UV (hue and chroma) were still significant predictors of fighting ability, but measures of body size (SVL, head length) were not (Supplementary material).

Although testosterone was not a significant predictor of fighting ability, we tested for a correlation with all aspects of throat colour because testosterone is known to be related to signal expression in other systems. Testosterone was significantly correlated with hue (Pearson correlation: $r_{165} = -0.27$, $P = 0.0003$) but explained only 7.6% of variation: males with UV throats (peaking at shorter wavelengths) tended to have higher testosterone than males with violet throats (peaking at longer wavelengths). Testosterone was not significantly correlated with either throat brightness ($r_{165} = -0.14$, $P = 0.08$) or chroma ($r_{165} = 0.11$, $P = 0.17$).

Predictors of Alternative Reproductive Tactics

Using estimates of fighting ability derived from the BT model, we examined the relation between fighting ability and reproductive tactic. Territorial males had significantly higher fighting ability than floaters ($F_{1,51} \geq 9.30$, $N = 52$, $P < 0.01$ based on estimates of fighting ability from either model). When we examined traits associated with reproductive tactic rather than fighting ability per se, we found that aspects of throat and front leg coloration, in addition to body condition, predicted reproductive tactic, although there was some discrepancy between the model using PCs and the model using traditional measures of hue, chroma and brightness (Table 2). Specifically, the former model indicated that males with more UV throats (high PC3) and higher throat chroma (low PC2), as well as brighter front legs (high PC1), tended to be territorial whereas males with violet throats (low PC3), with lower chroma (high PC2) and duller front legs (low PC1), were generally floaters. The model based on traditional measures of hue, chroma and brightness indicated that males that had throats and front legs with higher chroma, and wider heads tended to be territorial. Thus, throat ‘chroma’ consistently predicted reproductive tactic. In addition, in both models, body condition was negatively associated with reproductive tactic (Table 2): resident males had poorer body condition than floaters.

Table 2. Multiple logistic regression: alternative reproductive tactics

Trait	Coefficient	SE	Wald	P	Standardized coefficient
PCA*					
PC2 (throat)	−0.18	0.09	4.2	0.04	−0.77
PC3 (throat)	0.40	0.17	5.5	0.02	0.92
PC1 (front leg)	0.15	0.07	4.1	0.04	0.84
Body condition	−1.34	0.63	4.5	0.03	−0.88
Traditional†					
Throat chroma	−9.98	4.39	5.18	0.023	−0.95
Front leg chroma	−6.73	3.61	3.48	0.062	−0.66
Body condition	−1.71	0.72	5.7	0.017	−1.12
Head width	2.04	0.79	6.66	0.01	1.17

*The single best model based on principal components analysis (PCA) of spectral reflectance.

†The single best model based on traditional measures of hue, chroma and brightness.

DISCUSSION

Our results suggest that, in addition to functioning in mate choice (Bennett et al. 1996, 1997; Andersson et al. 1998), protection from predators (Losey 2003), and parent–offspring signalling in chicks (Heeb et al. 2003; Jourdie et al. 2004), UV signals may be used to resolve conflict among males competing for females and space. Specifically, we found a consistent link between aspects of UV throat reflectance in male flat lizards and both fighting ability and reproductive tactic. UV-reflective throats in *P. broadleyi* act as an armament (Berglund et al. 1996), honestly signalling a male's fighting ability. (Armaments can be colour patches, vocal signals or physical features such as horns or antlers that signal a male's fighting ability or aggressiveness.) By signalling fighting ability, males are able to avoid the physical and energetic costs associated with fighting, in addition to avoiding any associated increase in predation risk (Zuk & Kolluru 1998). Males with UV throats with higher chroma were also more likely to defend territories. At Augrabies, good territories that encompass resources important to females are heavily contested. For example, food is spatially patchy at Augrabies, resulting in aggregations of lizards in specific areas (Whiting et al. 2003). Males controlling territories in or near these areas have access to more females and may have a reproductive advantage. Therefore, UV signals have the dual function of determining contest outcome and reproductive tactic, both of which are likely to influence fitness. The effects of UV and of reproductive tactic are thus confounded to some degree. When we incorporated a resident advantage into the BT model (see [Supplementary material](#)), aspects of throat UV were still important predictors of fighting ability but a significant amount of the variance was also explained by the 'resident advantage' effect.

Current signalling theory stresses that signal function and evolution must be examined in terms of the interaction between signals, receiver sensory systems and the environment in which signals are transmitted. To be effective, colour signals should be conspicuous to intended receivers, given the visual background and prevailing light conditions (Endler 1992; Fleishman & Persons 2001). Although the visual system of flat lizards is currently unknown, recent phylogenetic work posits that UV perception in all vertebrates is primitive and is likely to have been secondarily lost in groups that lack UV perception, such as primates (Yokoyama & Shi 2000; Shi & Yokoyama 2003). Furthermore, possession of UV-receptive visual pigments among lizards appears to be both pervasive and conservative (Fleishman et al. 1993, 1997; Loew et al. 2002). In anoles (the best known group of lizards), the mean peak sensitivity for ultraviolet-sensitive (UVS) pigments from 13 taxa \pm SD was 365 ± 1 (Loew et al. 2002). This closely matches the mean peak reflectance (363 ± 21 ; $N = 75$) of the throats of *P. broadleyi* males.

The signalling environment of flat lizards is simple, consisting of either exposed bedrock or rocky outcrops of finely mottled grey granite. The UV-reflective throats of *P. broadleyi* males, juxtaposed with the orange-yellow ventral colour patch, are likely to be maximally conspicuous

against the rock background for several reasons. First, the UV throats have sharp peaks (high chroma), whereas the rock background has near-uniform reflectance (low chroma; Fig. 2). Second, the UV throats and orange-yellow ventral colour patch are complementary colours, sharing no wavelengths in common. Combining colours with high and low chroma, or combining complementary colours, are two ways to maximize colour pattern conspicuousness (Endler 1993). Third, UV signals are likely to be easily perceived by UV-sensitive receivers in full sunlight characteristic of open habitats such as Augrabies. Finally, the signalling environment is almost completely devoid of vegetation, with the exception of scattered fig trees, thereby reducing any background 'noise' from reflection off vegetation. The combination of light environment, physical habitat and other colour patches used in male displays probably makes UV-reflective throats an effective, conspicuous signal that males can use to keep rivals at bay.

In addition to aspects of throat colour, body size was a significant predictor of fighting ability. Of two measures of head size, only head length had predictive value and only in the model based on PCs reflectance data (i.e. head length was not a significant predictor of fighting ability in the BT model based on traditional measures of colour). Both head and body size are known to be factors in determining contest outcome in a wide variety of taxa with intense male rivalry (reviewed in Andersson 1994; Olsson & Madsen 1998) including lizards (Anderson & Vitt 1990; Olsson 1992; López et al. 2002; Watt et al. 2003; Perry et al. 2004). Although body condition is also a common predictor of contest outcome, in our study it did not predict fighting ability. Furthermore, resident males (which generally win contests against floaters) had significantly poorer body condition. We suggest that this probably reflects the higher energetic costs associated with territory defence and aggression.

Testosterone did not play an obvious role in determining fighting ability or reproductive tactic. Previous studies of other lizards have shown no difference in testosterone levels between winners and losers (Knapp & Moore 1995, 1996); although fixed morphs associated with alternative reproductive tactics usually have different testosterone profiles (Hews et al. 1994; Sinervo et al. 2000). However, UV throat hue was associated with testosterone levels, suggesting that expression of UV throat coloration may be partially constrained by testosterone. Testosterone and UV hue were only weakly correlated, however, suggesting that UV throat coloration is governed primarily by factors other than circulating hormone levels in adults (although the possibility that testosterone influences UV expression prior to sexual maturity cannot be discounted). Although expression of colour patches used as armaments is frequently regulated by testosterone in other taxa (Buchanan et al. 2001), the relation between UV and hormone levels has rarely been examined. Peters et al. (2004) found that in mallard ducks, *Anas platyrhynchos*, treated with a challenge to their immune system, the resulting increase in antibody production resulted in a decrease in UV reflectance of the bill as well as a decrease in testosterone. However, the relation between testosterone and expression of

the UV signals, even in this system, remains unclear. Uncovering constraints to UV expression promises to be an extremely interesting but challenging area of research.

Although several studies have shown UV signals to be sexually dimorphic traits important for mate choice in birds (Bennett et al. 1996, 1997; Andersson et al. 1998), a role for UV signals in contest competition has only recently been demonstrated in a few taxa (Brunton & Majerus 1995; Bright & Waas 2002; Alonso-Alvarez et al. 2004; Siebeck 2004; Siefferman & Hill 2005). Some previous studies of UV signalling were conducted under artificial conditions in the laboratory, thereby ignoring the environmental context, which is important for effective signal transmission (Leal & Fleishman 2002). Our field study illuminates another aspect of UV-based sexual signalling: animal contests and alternative reproductive tactics in the context of their signalling environment. We showed that males with throats rich in UV were the best fighters and were more likely to be territorial. Furthermore, the strikingly close match between peak UV throat reflectance of *P. broadleyi* and the conservative peak sensitivity of UVS cones in *Anolis* lizards suggests a tight coupling of the signal and the visual system of the intended receiver. This, together with a background and complementary colour patches (the ventral colour patch) that maximize conspicuousness, reinforces the idea that the UV throats of flat lizards constitute an effective signal within their natural signalling context. The throat in *P. broadleyi* is one of a few UV signals shown to act as an armament, honestly signalling a male's status. It is possible that UV is correlated with some other trait that we have not measured. However, a recent study experimentally reduced throat UV reflectance of individuals from this same population and verified that aspects of throat UV signal fighting ability in *P. broadleyi* (Stapley & Whiting, in press). Therefore, UV may play a hitherto unsuspected role in settling disputes among rivals in a wide variety of taxa and function in sexual selection in ways not previously considered.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.anbehav.2005.10.018](https://doi.org/10.1016/j.anbehav.2005.10.018)

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Table S1. Bradley-Terry (BT) ‘tournament’ model of lizard contests examining variables that predict fighting ability in *Augrabies* flat lizards

Trait	Coefficient	SE	Z	P	Standardized coefficient
PCA*					
Throat PC 1	-0.075	0.038	-2.004	0.045	-0.547
Throat PC 3	0.243	0.144	1.697	0.090	0.512
Head length	-1.204	0.695	-1.733	0.083	-0.415
Residency	2.236	0.565	3.957	0.0001	1.326
Traditional+					
Throat brightness	-0.400	0.153	-2.609	0.009	-0.738
Throat hue	-0.045	0.016	-2.702	0.007	-0.952
Residency	2.195	0.569	3.854	0.0001	1.302

We incorporated a contest-specific variable that takes into account the advantage a resident male may have over a floater, which we have termed a ‘resident advantage’ effect (Firth 2005). Compared to the BT model without the ‘resident advantage’ (Table 1), body size and head length are no longer significant. Aspects of throat UV are still significant predictors of fighting ability, but this is reduced in the face of a resident advantage and a smaller sample size.

*The single best model based on principal components analysis (PCA) of spectral reflectance.

+The single best model based on traditional measures of hue, chroma and brightness.