

# Individual quality and nuptial throat colour in male European green lizards

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## Keywords

condition-dependence; lizard; multiple signalling system; signalling; sexual selection.

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## Abstract

Nuptial traits signalling individual quality are common in numerous animal taxa, and play a significant role in sexual selection. Detecting female mate choice based on visual cues is notoriously hard in lizards. Previously, we found that female European green lizards (*Lacerta viridis*) preferred to associate with males with high ultraviolet (UV) throat reflectance. Here, we investigated if different components of nuptial throat colour of male European green lizards were correlated to other fitness-related traits, and thus could signal male quality. We found that (1) high UV chroma correlates positively with directional asymmetry and shows a negative trend with body condition; (2) blue chroma is not related to any individual traits; and (3) total throat brightness correlates positively with body size and relative head size, and negatively with ectoparasite load. Our results suggest that having high throat UV reflectance is costly for male European green lizards, so probably only high-quality individuals can afford it, while total brightness of the throat colour signals age, relative head size and health status. Hence, throat colour in male European green lizards is a multiple honest signal.

## Introduction

Information about individual quality provided by different signals varies in reliability, with the main attributes determining female preference being honesty and detectability (Schluter & Price, 1993). Considering that female mate choice can have negative effects on the females' reproductive success, female mate preference is expected to increase with increasing honesty of male traits (Iwasa & Pomiankowski, 1991; Schluter & Price, 1993). Conditional handicap models (Zahavi, 1977; Iwasa & Pomiankowski, 1991) predict that (1) the expression of selected male traits are to be related to male body condition; (2) the expression of these secondary sexual traits are to have a cost for the possessor; and (3) males of better body condition are to have lower cost of expression than those of worse condition. However, male quality can involve other aspects than body condition, as males can also assure access to high quality and/or quantity resources for the female by defending a good territory (Kotiaho, 2000). A number of traits can work as honest signals at the same time and act in multiple signalling systems, whereas receivers should take numerous attributes into account in order to estimate the signaller's quality with high precision (Calsbeek & Sinervo, 2002; Candolin, 2003).

Colour, morphological and chemosensory traits of lizards all play a role in mate choice and intrasexual competition, thus representing signals under sexual selection (Gvozdk & Van

Damme 2003; Stapley & Keogh, 2006; Kopena *et al.*, 2011). Colour traits signal social status (Healey, Uller & Olsson, 2007), fighting ability (Stapley & Whiting, 2006; Whiting *et al.*, 2006), bite force (Huyghe *et al.*, 2009), and are used as cues in male and female mate choice in lizards (Bajer *et al.*, 2010), and are often correlated to body condition (Healey & Olsson, 2009). Recent studies on signalling focused on the possibility of several traits acting together to signal an individual's quality (e.g. Candolin, 2003), with different components often signalling different aspects of the signaller (Badyaev *et al.*, 2001). Females consider multiple male traits in parallel (Calsbeek & Sinervo, 2002; Lopez, Aragon & Martin, 2003; Hamilton & Sullivan, 2005), even considering their offspring's survival while making mating decisions (Lancaster, Hipsley & Sinervo, 2009). However, the fact that a trait represents an important signal in one context, for instance in intrasexual selection, does not necessarily mean that it is also important in another context, for instance in intersexual selection, as well (e.g. Lebas & Marshall, 2001; Lopez, Munoz & Martin, 2002).

The European green lizard (*Lacerta viridis*) is a wide-spread lacertid species in Central and Eastern Europe. Males develop a blue nuptial throat patch, which shows high reflectance in the ultraviolet (UV) range (see Bajer *et al.*, 2010). The role of this male ornament in sexual selection is particularly interesting as both UV and blue colours represent structural colours,

hence their developmental costs and the environmental factors influencing them are less straightforward than in the much better studied pigment-based colours (Prum, 2006). UV colour has been demonstrated to function as an honest signal of weapon size in the collared lizard (*Crotaphytus collaris*) (Lappin *et al.*, 2006), determine outcome of male contests in the *Platysaurus broadleyi* (Stapley & Whiting, 2006; Whiting *et al.*, 2006) and affect male mate choice in *Ctenophorus ornatus* (LeBas & Marshall, 2000). In manipulative experiments, we showed that female *L. viridis* prefer males with high UV chroma on their throat patch (Bajer *et al.*, 2010) and males with high UV chroma are more successful in male contests (Bajer *et al.*, 2011), hence throat colour of male European green lizards is likely to be under sexual selection and to hold information of male quality.

Here we tested the hypotheses that (1) UV colour in male European green lizard is an honest signal, and (2) different components of the throat colour signal different aspects of male quality. Namely, we investigated the relationships between (1) UV chroma, as it affects female mate choice and male competition in the species (Bajer *et al.*, 2010); (2) blue chroma, as it is connected to parasite load in the species (Václav, Prokop & Fekiác, 2007); (3) total brightness as it is an important signal in other species (LeBas & Marshall, 2000; Martin & Lopez, 2009) and body size, body condition, ectoparasite load, relative head size, number of femoral pores, and asymmetry, as these traits are all known to affect fitness of lizards (Dunlap, 1993; Lopez *et al.*, 2002; Hamilton & Sullivan, 2005; Hofmann & Henle, 2006). We expected that lizards of more intense coloration would also be those of better quality.

## Materials and methods

### Data collection

Fieldwork was conducted from 2007 to 2009 during the mating seasons (May–early June). Yearly samplings were conducted for no more than 10 days during the first part of the annual mating period. The sample site was a forest-scrub-grassland near Tápíószentmárton, Hungary; 47°20'25" N, 19°47'11" E. Altogether, 68 adult males were caught during the 3 years (27, 26, 15; in the three years respectively). In order to prevent repeated sampling, captured males were marked by clipping throat scales (collar) in unique sequences. Lizards spent no more than 1 hour in captivity, during which all measurements were taken. Snout-vent-length (SVL), tail length (TL), head height, head length and head width were recorded with digital callipers (Mitutoyo, Kawasaki, Japan) to the nearest 0.01 cm. Animals with tails shorter than 40 mm were excluded from all further analyses. Body weight (BW) was measured with an analytical balance (pm 4800, Mettler Toledo, Greifensee, Switzerland) to the nearest 0.01 g. Number of femoral pores and their bilateral asymmetry is related to pheromone-based female mate choice and male immune response in *Lacerta monticola* (Martin & Lopez, 2000; Lopez, Amo & Martin, 2006). Hence, we also counted the number of femoral pores (FP) on both sides of the indi-

vidual. Generally, three types of asymmetry can be distinguished: directional asymmetry (a consistent bias towards one side), antisymmetry (consistent bias towards a random side) and fluctuating asymmetry (small nondirectional departures from perfect symmetry) (van Valen, 1962; Palmer & Strobeck, 1986). While the first two are usually part of normal development and probably result from adaptive evolution, the latter is a result of disturbed development and an indicator of developmental instability (van Valen, 1962; Palmer & Strobeck, 1986; van Dongen, 2006). To reveal which type of asymmetry we are dealing with, we tested the distribution of the signed asymmetries (right side – left side) and their mean's deviation from zero. The distribution was not normal (Kolmogorov–Smirnov test:  $d_{68} = 0.226$ ,  $P < 0.001$ ) and the mean differed significantly from zero (one sample  $t$ -test:  $t_{67} = 3.992$ ,  $P < 0.001$ ), hence the asymmetry could not be explained by fluctuating asymmetry. Because the mean was negative (mean =  $-0.41$ ), and there was no sign of more than one peak of the distribution, we believe that we detected directional asymmetry. In our analyses (see below), we used the signed asymmetries as a proxy for directional asymmetry (DA). However, because directional and fluctuating asymmetry are not easy to separate, and both can be a sign of stress and developmental instability in some cases (Lens & Van Dongen 2000), we also run our models (see below) with the absolute values of the differences between right and left femoral pore numbers. Finally, the number of ectoparasites (*Ixodes* sp., Ixodidae) was counted for each individual (ticks are easily detected on the body surface).

Colour variables of the throat were measured with an Ocean Optics USB4000 spectrometer, using a DT-Mini-2-GS light-source and a QR400-7-SR/BX reflection probe, single end fixed in an RHPI holder (Ocean Optics Inc, Dunedin, FL, USA), explained in detail earlier by Bajer *et al.* (2010, 2011). Briefly, three independent measurements on different, randomly chosen spots of the throat were recorded for every lizard, using a separate probe contact per measurement, and the average was calculated for each individual. Throat reflectance was characterized by total brightness ( $R_{320-700}$ ), UV chroma ( $R_{320-400}/R_{320-700}$ ) and blue chroma ( $R_{400-490}/R_{320-700}$ ) (Whiting *et al.*, 2006).

### Statistical analyses

Principal components analysis was performed on the three head variables. The first principal component (Head PC) described 90% of the total variation (eigenvalue = 2.69), and showed positive correlation with all original variables (factor loadings: head height = 0.94; head length = 0.95; head width = 0.96). The Head PC scores were used in the subsequent statistical analyses. The number of ectoparasites were  $\log_{10}$  transformed ( $\text{Log}_{10}\text{Par}$ ) for better distribution.

We used general linear models (GLMs) to test for correlations between different throat colour traits (UV chroma, blue chroma, total brightness) and other individual characteristics. We are aware of the problem imposed by the non-independence of these colour variables, but because both UV and blue chroma are calculated from brightness, we decided to

analyse them separately. Each GLM was run with identical predictor variables (SVL, BW, Head PC, TL, FP, DA and Log<sub>10</sub>Par) and year of capture as random factor. We applied backward stepwise model selection. Non-significant explanatory variables were deleted one by one in decreasing order of *P*, and final models included only the significant main effects. SVL and year of capture was never removed from the models in order to keep them for correction. Model selection based on the *P*-value is considered conservative in comparison with, for example, the selection methods based on Akaike's or Bayesian information criteria, and differs very little from the others in its predictive ability (Murtaugh, 2009). DA in all these models was represented as the signed differences between right and left femoral pore numbers. However, because of the problem of separating directional and fluctuating asymmetry and the information content of directional asymmetry (see above), we also ran these models with the absolute difference between sides. Whenever the results differed qualitatively, we report them in addition to the original models. All analyses were performed using the SPSS 17 (SPSS Inc., Chicago, IL, USA) software.

## Results

We found a positive relationship between directional asymmetry and UV chroma, and a negative (marginally significant) trend between body condition (BW corrected for SVL) and UV chroma (Table 1, Fig. 1a,b). When the absolute value of asymmetry was used in our analyses instead of the signed differences, the UV chroma – body condition correlation became significant (*P* = 0.049). In short, individuals with higher throat UV chroma showed higher levels of left-biased directional asymmetry and were of worse body condition. We found no relationship between blue chroma and the explanatory variables (Table 1). Finally, total brightness was positively associated with relative head size (Head PC corrected for SVL) and SVL, and negatively with ectoparasite load (Table 1, Fig. 1c–e). Individuals with brighter throats were larger with relatively larger heads and had lower ectoparasite load than their conspecifics with duller throats. The year effect was significant in all three colour variables (all *P* < 0.011).

## Discussion

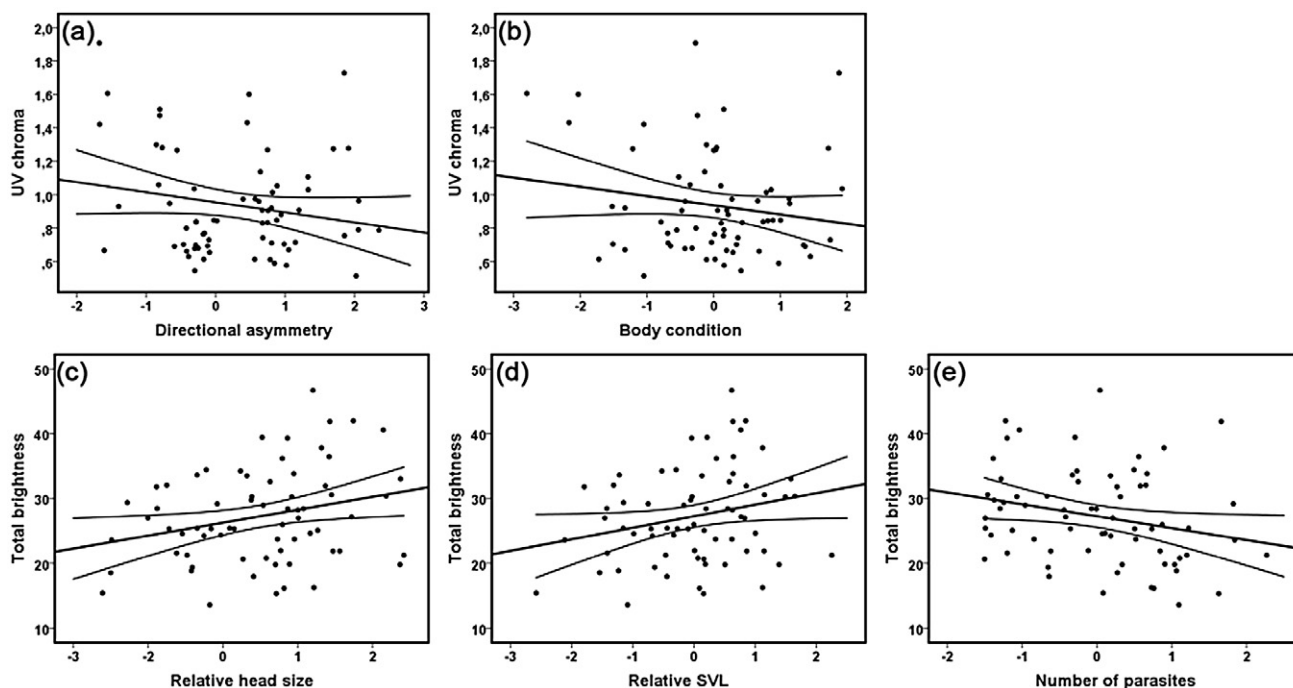
We showed that different components of the throat coloration of male European green lizards are indeed connected to different individual traits. Males with high UV reflectance exhibited high level of directional asymmetry in their femoral pores and tended to have lower body condition. Individuals with high total brightness were larger, had relatively large heads and a lower ectoparasite load. Blue chroma was not related to any of the studied explanatory variables. All colour traits showed significant annual variation. As such, our results suggest that the nuptial throat colour of male European green lizards is a complex multiple trait with different components signalling different information, and is most likely influenced by the environment.

**Table 1** Results from the general linear models on the throat colour variables of male European green lizards. Non-significant effects are shown as seen at the time of removal during the stepwise backwards model selection. R<sup>2</sup>, parameter estimates and their standard errors are shown. For the abbreviations and descriptions of the models, see Materials and Methods

Colour variable	Effect	R <sup>2</sup>	<i>B</i>	<i>SE</i>	<i>P</i>
UV chroma	SVL	0.023	0.012	0.01	0.234
	Head PC	<0.001	−0.01	0.085	0.903
	BW	0.053	−0.032	0.017	0.068
	TL	0.008	−0.001	0.001	0.488
	FP	0.002	0.004	0.012	0.722
	DA	0.065	−0.066	0.032	0.042
Blue chroma	SVL	<0.001	0.008	0.095	0.933
	Head PC	0.031	0.004	0.003	0.156
	BW	0.048	−0.098	0.054	0.078
	BW	0.003	−0.005	0.013	0.696
	TL	0.002	<0.001	0.001	0.759
	FP	0.001	−0.002	0.009	0.803
Brightness	DA	0.007	−0.015	0.023	0.503
	Log <sub>10</sub> Par	0.019	0.066	0.061	0.28
	SVL	0.068	0.742	0.35	0.038
	Head PC	0.076	5.518	2.443	0.027
	BW	0.001	−0.113	0.619	0.855
	TL	0.01	0.029	0.037	0.429
	FP	0.005	0.207	0.39	0.596
	DA	<0.001	0.081	1.069	0.94
	Log <sub>10</sub> Par	0.064	−5.641	2.736	0.043

SVL, snout-vent-length; Head PC, first principal component; BW, body weight; TL, tail length; FP, femoral pores; DA, directional asymmetry; Log<sub>10</sub>Par, number of ectoparasites log<sub>10</sub> transformed.

In previous studies, we demonstrated that female European green lizards prefer males with high UV chroma (Bajer *et al.*, 2010) and males with high UV chroma are likely to win aggressive encounters (Bajer *et al.*, 2011). Hence, UV chroma is a sexually selected trait. We found a positive correlation between directional asymmetry in femoral pores and UV chroma. The evolutionary and developmental background of directional asymmetry is hard to understand without targeted experiments; it is usually interpreted as an adaptive trait (e.g. Palmer, 2004), but it can also be a result of stress (Lens & Van Dongen 2000) or a by-product of genetic change (Bell, Khalef & Travis, 2007). In our case, where we found that femoral pore directional asymmetry is positively correlated to UV chroma – which is under positive sexual selection (Bajer *et al.*, 2010, 2011) – we think that femoral pore directional asymmetry is adaptive. For instance, it can be a sign of 'handedness' during depositing femoral secretions, which transfer important information in our species (Kopena *et al.*, 2011), similarly to what is observed in snake hemipenis use (Shine *et al.*, 2000). However, it has been shown in other lacertids that females prefer secretion of males with symmetric femoral pores (Martin & Lopez, 2000), so the information content of femoral pore asymmetry in male *L. viridis* surely warrants further investigations.



**Figure 1** Correlations between (a) UV chroma and directional asymmetry, (b) UV chroma and body condition, (c) total brightness and relative head size, (d) total brightness and relative SVL, and (e) total brightness and number of parasites. SVL is corrected for year of capture, while the other predictors are corrected for both year of capture and SVL. SVL, snout-vent-length; UV, ultraviolet.

Body condition showed a negative trend with UV chroma. Such sexually selected signals can be related to condition in opposite ways: (1) individuals with better body condition can afford high costs with relatively low effects, unlike those of poor condition, therefore individuals in better condition develop stronger signals (positive correlation); or (2) because development, maintenance and even wearing the signal can be costly, only the best individuals can afford it but still at the cost of decreased body condition (negative correlation). There is support for both scenarios, for instance individuals of the striped plateau lizard (*Sceloporus virgatus*) with better body condition developed brighter colours (Weiss, 2006), while those of the collared lizard (*C. collaris*) faced a growth cost of conspicuous coloration (Baird, 2008). We found a negative trend between UV chroma and body condition, suggesting a cost of high UV chroma. Several costs of the expression of sexually selected signals have been shown, including developmental (Baird, 2008), social (Martin & Forsman, 1999), physiological (Cox *et al.*, 2010) and predatory costs (Stuart-Fox *et al.*, 2003). In a manipulative factorial experiment (Bajer *et al.*, 2012), we found that UV colour development before mating season was unaffected by food manipulations (even though body condition was affected) but was significantly influenced by ambient temperature (even though it did not affect body condition). Hence, direct developmental costs are unlikely, but indirect costs are possible due to the need of extended periods of high body temperature, which requires accurate behavioural thermoregulation

that comes with many costs (e.g. Huey & Slatkin, 1976). Predatory costs are to be considered in species with a bright dorsal coloration conspicuous to avian predators (Stuart-Fox *et al.*, 2003). Hence, direct predatory costs are also unlikely in male *L. viridis*, as the nuptial coloration is maintained on the throat. Social costs are, however, quite likely as more active males might lose their initial condition through social interactions, such as territory defence and fighting (Martin & Forsman, 1999).

Large body and head size seem to be beneficial in sexual selection of lizards (Bull & Pamula, 1996; Hamilton & Sullivan, 2005; Hofmann & Henle, 2006); hence, it is not surprising that larger male European green lizards with relatively larger heads also had generally brighter throats. For instance, if females prefer or if other males avoid those with larger heads, signalling this characteristic can be advantageous for the owner. Alternatively, throat brightness can act as an amplifier of head size, as previously suggested in a closely related species, *Lacerta schreiberi* (Martin & Lopez, 2009) and in *C. collaris* (Lappin *et al.*, 2006). As head size was often found to determine social status and reproductive success, making the trait easier to estimate can be advantageous for animals of better quality. In the case of body size, total brightness may act as a signal informing conspecifics about the size and age of the owner, which might be good proxies for individual success. Mate choice experiments revealed female preference towards larger/older males in *L. monticola* (Lopez *et al.*, 2003).

The fact that high ectoparasite (tick) load was connected with low total brightness suggests that brightness can also be an honest signal of high parasite resistance. Of course, our study is correlative; hence, we cannot exclude the possibility that ectoparasites cause a loss of brightness directly. However, throat brightness can still honestly signal actual health status in the latter case. Numerous studies have demonstrated endo- and ectoparasites being costly for the host (Klukowski & Nelson, 2001; Bouma *et al.*, 2007). Ticks have been demonstrated to act as vectors of lizard blood parasites, *Haemolivia stellate* (Haemogregarinidae) (Lainson, De Souza & Franco, 2007) and to decrease their hosts' body condition (Dunlap, 1993), while parasite resistance was also shown to be costly (Olsson *et al.*, 2005) and in trade-off with male reproductive success (Uller & Olsson, 2003). Thus, an individual with the ability to avoid such detrimental effects is possibly of better quality. The Hamilton & Zuk (1982) hypothesis assumes that males may develop bright colours fully only if they possess resistance genes to parasites, and thus females should mate with brightly coloured males to associate their genes with 'good genes', giving their offspring the best chance of survival. One intraspecific prediction of this hypothesis is that males with brighter colours are less parasitized, and our data support this prediction.

We found no connection between blue chroma and the measured individual traits, which suggests that blue chroma does not play a role in signalling any characteristics, at least not in this studied population. We note that blue colour is not necessarily a pure structural colour. In some cases, blue colour is a by-product of the melanin layer beneath the structural layer, which absorbs all non-blue radiation (Quinn & Hews, 2003). If such mechanism was present in *L. viridis*, blue colour might be a melanin-based signal, signalling aspects of individual quality we did not grasp with our morphological traits. Unfortunately, structure of skin layers has not yet been examined in our species yet.

All three studied throat colour components (UV chroma, blue chroma and total brightness) varied significantly between years. Considering that male throat nuptial colouration is developing after hibernation and before the onset of the mating season in our species, the significant year effect is suggestive of a strong environmental component in colour development. Indeed, our manipulative experiment showing the importance of ambient temperature in colour development in *L. viridis* (Bajer *et al.*, 2012), along with our observations of great yearly variation in precipitation and temperature during spring in the three study years, supports this scenario. At any rate, if colour development is affected by environmental conditions, the ability to occupy and defend territories with high thermal quality can also be viewed as an aspect of individual quality, hence the environmental effect further supports our view that the studied colour signals transfer relevant information about their holder.

Taken together, we found that the nuptial throat patch colour of male European green lizard is a complex, multiple signal. All colour components varied between years, suggesting an environmental factor in colour development. Both UV chroma and total brightness can be honest signals advertising

different qualities of the owner, as previously demonstrated not only in lizards, but in birds as well (Doucet & Montgomerie, 2003; Lopez, Figuerola & Soriguer, 2008). With respect to possible information gathered from males' nuptial coloration, it is reasonable to assume that the same trait can be used in intersexual (female choice) and in intrasexual (male–male competition) selection (Stapley & Keogh, 2006; Fitz *et al.*, 2008). However, it is also possible that different components are relevant in each process, and different characteristics are assessed by males and females (Lebas & Marshall, 2001; Lopez *et al.*, 2002). Rigorous assessment of the separate and/or common roles of UV chroma and total brightness of male European green lizards' nuptial throat colour warrants further study.

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## Conflict of interest

The authors declare that they have no conflict of interest.

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