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Negative correlation between nuptial throat colour and blood parasite load in male European green lizards supports the Hamilton–Zuk hypothesis

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Abstract During female mate choice, conspicuous male sexual signals are used to infer male quality and choose the best sire for the offspring. The theory of parasite-mediated sexual selection (Hamilton–Zuk hypothesis) presumes that parasite infection can influence the elaboration of sexual signals: resistant individuals can invest more energy into signal expression and thus advertise their individual quality through signal intensity. By preferring these males, females can provide resistance genes for their offspring. Previous research showed that nuptial throat colour of male European green lizard, *Lacerta viridis*, plays a role in both inter- and intrasexual selections as a condition-dependent multiple signalling system. The aim of this study was to test the predictions of the Hamilton–Zuk hypothesis on male European green lizards. By blood sampling 30 adult males during the reproductive season, we found members of the Haemogregarinidae family in all but one individual (prevalence=96 %). The infection intensity showed strong negative correlation with the throat and belly colour brightness in line with the predictions of the Hamilton–Zuk hypothesis. In addition, we found other correlations between infection intensity and other fitness-related traits, suggesting that parasite load has a remarkable effect on individual fitness. This study shows that throat patch colour of the European green lizards not only is a multiple signalling system but also possibly acts as an honest sexual signal of health state in accordance with the Hamilton–Zuk hypothesis.

Keywords Hamilton–Zuk hypothesis · Nuptial coloration · Blood parasite · Haemogregarinidae · Lizard

Introduction

Sexual selection results in the elaboration of conspicuous, intense sexual signals advertising different aspects of individual quality (Andersson 1994). For example, sexual signals can be used to advertise body size (Lebas and Marshall 2001), body condition (Weiss 2006), fighting ability (Stapley and Whiting 2006), aggression (Whiting et al. 2006) or health state (McGraw and Hill 2000). Sexual signals can be acoustic, chemical or visual traits; behavioural displays or combinations of these acting as multiple signalling systems (Candolin 2003). Colour signals can be further divided into structural and pigment-based coloration. Structural colours (e.g. ultraviolet (UV) and blue) are created by different light-reflecting and light-scattering ultrastructures, while pigment-based colours (e.g. yellow, red and brown) are produced by light-absorbing pigment molecules of the integument (Grether et al. 2004). Although the two mechanisms of colour expression have different physiological backgrounds, certain processes can affect elaboration of both colour types (Peters et al. 2007). Colour traits

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have been demonstrated to be honest signals of fighting ability (Stapley and Whiting 2006; Bajer et al. 2011), bite force (Huyghe et al. 2009) and social status (Healey et al. 2007) in lizards.

There are numerous theories explaining how sexual signals become widespread in populations. The good genes hypothesis (Trivers 1972) suggests that signals provide information about the signaller's genetic quality. Thus, positive mate choice towards the trait is beneficial. The handicap hypothesis (Zahavi 1975, 1977) states that intense sexual signals incur developmental or maintenance costs, and only high-quality individuals can afford such costs. An important trait determining individual quality is the individual's health state or immunocompetence, and this can deteriorate significantly as a cost of the ontogenetic development of the signal (Olsson et al. 2005). For example, infections can decrease the haematocrit value of the blood (Dunlap 1993) or quality of the ejaculate (Charge et al. 2010), and susceptibility to infections is inherited by progeny (Boulinier et al. 1997). Hence, infections can significantly reduce individuals' fitness, and thus, parasite load can have a strong effect on the evolution of reproductive systems and strategies.

The Hamilton–Zuk hypothesis (Hamilton and Zuk 1982) states that parasite load affects relative fitness of individuals within a population, and the intensity of sexual signals is correlated with parasite prevalence among populations. The theory presumes that genetic variance is maintained by host–parasite co-adaptive cycles and contains three associated assumptions: (1) the parasite should be costly for the owner, affecting survival and/or reproductive ability negatively, (2) the infection should affect the evolution of male sexual colour signals and (3) females should prefer less parasitized males (Clayton 1991). The Hamilton–Zuk hypothesis's predictions differ between species with low vs. high parasite prevalence and are evaluated on both intra- and interspecific scales. Among species, Hamilton and Zuk (1982) predict that those more susceptible to pathogens are likely to display highly ornamented colour signals to provide more precise information about their health state. When examining species showing high parasite prevalence, the intraspecific prediction of the model assumes that resistant males need to allocate less energy into defence against parasites and thus have more to invest into their sexual signals. Hence, individuals with more intense signals are thought to be less infected and that this resistance capacity is heritable. Females can therefore increase their fitness by choosing to mate with more elaborately ornamented males.

The Hamilton–Zuk hypothesis has been tested in numerous vertebrates, with contradictory results. Carotenoid coloration in house finches (*Carpodacus mexicanus*) and blue tits (*Cyanistes caeruleus*) is negatively correlated with endoparasite load (Brawner et al. 2000; del Cerro et al. 2010; Saks et al. 2003). Similarly, rock dove (*Columba livia*)

females preferred males with less ectoparasites (Clayton 1990). Conversely, blue bowerbirds (*Ptilonorhynchus violaceus*) with lower parasite loads had lower reproductive success and there was no relationship between coloration and rate of infection (Borgia 1986; Borgia and Collis 1990). In lizards, both sexual dichromatism and conspicuous colour signals are common (including pigment-based and structural colours) (Sinervo and Lively 1996; Hamilton and Sullivan 2005). Additionally, numerous species have been shown to carry one or more species of blood parasite closely related to those that have been used to test the Hamilton–Zuk hypothesis in the past (Telford 2009; Hamilton and Zuk 1982). However, in reptiles, very few studies have supported the predictions of the Hamilton–Zuk hypothesis to date (Martin et al. 2008). Moreover, none of these examine structural coloration (see Moller 1990; Lefcort and Blaustein 1991; Schall and Staats 1997; Ressel and Schall 1989; Schall and Dearing 1987).

The European green lizard (*Lacerta viridis*) is a medium-sized lacertid lizard widely distributed across central and eastern Europe. During the mating season, males enhance conspicuous nuptial coloration on their throat patch peaking in ultraviolet and blue. It has previously been shown that components of the throat patch colour affect both female mate choice (Bajer et al. 2010) and male–male competition (Bajer et al. 2011) and that throat patch may act as a multiple signalling system (Molnar et al. 2012). One possible cost of development of the nuptial throat colour is the need for accurate thermoregulation (Bajer et al. 2012). Recent results also showed that belly coloration has peaks in the UV and green–yellow range and that components of belly colour are affected by both environmental temperature and food availability (Bajer et al., unpublished data). Hence, *L. viridis* provides an excellent model to study how parasite infections affect sexual signals in a reptile.

The aim of the present study was to test the intraspecific predictions of the Hamilton–Zuk hypothesis by investigating blood parasites in adult male *L. viridis* during the reproductive season. Our main questions were (1) Do adult male *L. viridis* carry blood parasites, and if so, what species are represented in the blood samples? (2) How high is parasite prevalence in the lizard population? (3) Is rate of infection (intensity) related to colour signals or other fitness-related traits of males?

Material and methods

Morphological and colour traits

During the mating season of 2010, a total of 24 adult males were captured and their morphological and colour variables were measured. Snout-to-vent length (SVL), head height,

head width and head length were measured to the nearest 0.01 cm using digital callipers (Mitutoyo, Kawasaki, Japan). Body weight was measured to the nearest 0.01 g with an analytical balance (PM 4800, Mettler Toledo, Greifensee, Switzerland). The number of femoral pores was counted on both sides for each male. Finally, the number of ectoparasites (*Ixodes* sp., Ixodidae) was counted for each individual.

Coloration was measured using an Ocean Optics USB4000 spectrometer, complete with a DT-Mini-2-GS light source and a QR400-7-SR/BX reflection probe, single end fixed in an RHP1 holder (Ocean Optics Inc., Dunedin, FL, USA), as explained earlier in detail by Bajer et al. (2010, 2011). We recorded three independent measurements on three randomly chosen spots of the throat patch and belly for every male, using separate probe contact per measurement and a constant 45° angle from the surface. We measured the total brightness ($R_{320–700}$) and UV chroma ($R_{320–400}/R_{320–700}$) for both the throat and belly of each individual. Additionally, we measured blue chroma ($R_{400–490}/R_{320–700}$) and yellow–green chroma ($R_{480–600}/R_{320–700}$) for throats and bellies, respectively.

Collecting blood samples

We collected blood samples from all individuals, using a 25-G insulin injection needle to draw blood from a large subcutaneous vessel on the ventral side. None of the animals showed signs of injuries or abnormal behaviour during the 24-h observational period after the sampling. We collected the blood with 60-μl haematocrit capillary tubes (Spektrum-3D Ltd., Budapest, Hungary) and created blood smears by blowing a drop of blood onto the microscope slide. Smears were air-dried until coagulation and then dipped into 96 % methanol for 60 s for fixation. After 60 s, we moved them to a plastic slide box, drained the alcohol and let them dry totally, before staining them. Staining was done in Coplin jars by adding sodium phosphate buffer (pH 7.2) to 3 ml of Giemsa (G4507, Sigma-Aldrich, Budapest, Hungary). Smears were kept in the staining solution for 50 min. Leftover paint was removed by rinsing, and all slides were then dried and placed in slide boxes.

Analysing smears

Smears were analysed using a microscope at ×1,000 magnification; rate of infection was characterized by number of endoparasites counted during three scanning sessions on each smear. Although there are numerous methods to estimate rate of infection per individual, most of these do not correct for red blood cell density (RBCD) in the smears (e.g. Bouma et al. 2007; Garcia-Ramirez et al. 2005). Since in our case RBCD showed high variability between fields (258.6±43.56 (mean ± SD)), we developed a method to correct the number of endoparasites for RBCD, thus making individuals comparable. For this, we first counted the total number of blood cells in four randomly chosen fields on each slide and took the average number of cells as an estimate of RBCD. We then calculated scanning time (aiming to cover the same number of red cells) for each sample by placing the RBCD values on a calibration curve. We scanned smears for the time given by the calibration curve, moving the slide continuously at a slow pace from a randomly chosen field, repeating the scanning sessions three times. Separate scans showed high repeatability ($R=0.93$, SE=0.013), and we used the average of three scans to characterize intensity of infection.

Statistical analyses

We ran a principal components analysis on the three head variables. Because the first component (PC1) explained 94.35 % of total variance in head size (eigenvalue=2.83, all factor loadings >0.97), we used PC1 as a surrogate for this variable in further analyses. We corrected head size and body weight for SVL by calculating residuals from linear regressions and used them as estimates of body condition and relative head size. Since rate of infection was not normally distributed, we log-transformed it to achieve normality (Kolmogorov–Smirnov test: $S=0.15$, $df=27$, $P=0.124$) and used the transformed variable in further analyses. Since femoral pore asymmetry has been shown to be a result of directional asymmetry (see Molnar et al. 2012), we used the signed difference between sides to describe asymmetry.

General linear models (GLMs) were used to search for possible correlations between endoparasite load and individual fitness-related traits. Predictor variables were body condition, throat and belly coloration, SVL, relative head size, number of femoral pores and level of asymmetry. We also tested the connection between endo- and ectoparasite loads, the latter being characterized by number of ticks after logarithmic transformation. Non-significant explanatory variables were deleted one by one in decreasing order of *P*, and final models included only the significant main effects. Model selection based on the *P* value is considered conservative in comparison with, for example, selection methods based on Akaike's or Bayesian information criteria and differs very little from the others in its predictive ability (Murtaugh 2009). Because significance values alone are restricted in their information content regarding importance of effects, we also present effect sizes as partial η^2 (Moller and Jennions 2002). All analyses were performed using the SPSS 17 (SPSS Inc., Chicago, IL, USA) software.

Results

We distinguished four different morphotypes in the samples (Fig. 1.). All were members of the family Haemogreagrinidae (*Apicomplexa*, *Coccidisina* and *Adeleorina*) (Barnard and Upton 1994), but for the present study we did not distinguish among parasite species or genera. Only one individual was uninfected, and thus, parasite prevalence was 0.958.

Our final model of the correlation between endoparasite load and other individual traits included six significant effects (Table 1). The effects were strong (effect sizes ranging between 0.23 and 0.69). Duller throat and belly coloration were associated with higher rates of infection (Table 1, Fig. 2, a and b). Males with larger body size and better body condition had higher endoparasite infection (Table 1, Fig. 2, c and d). Additionally, directional asymmetry correlated positively, whereas ectoparasite load correlated negatively to the intensity of Haemogreagrinidae infection (Table 1, Fig. 2, e and f).

Discussion

We found that (1) adult male *L. viridis* carry blood parasites, (2) parasite prevalence is very high and (3) infection intensity is negatively correlated with the colour intensity of at least one trait that is important in sexual selection. This latter finding supports the intraspecific prediction of the Hamilton–Zuk hypothesis (1982). In addition, we found several other strong correlations between endoparasite load and fitness-related traits.
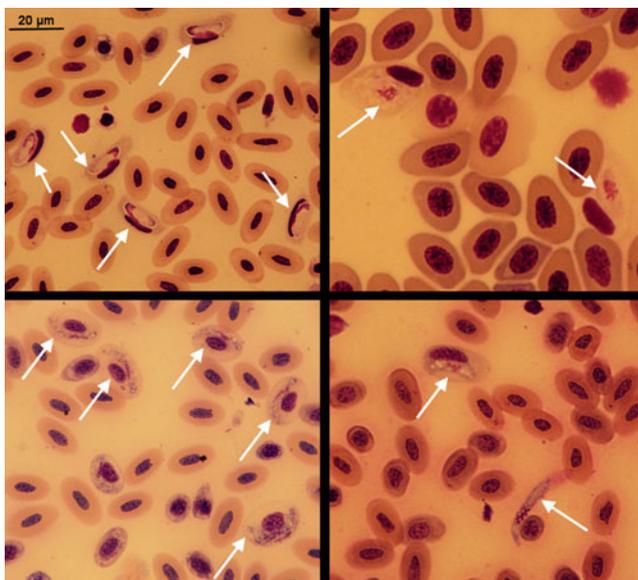
Fig. 1 The four blood parasite morphotypes found in blood smears of male European green lizards. All types belong to the family Haemogregarinidae

We demonstrated that European green lizards were infected by four haemogregarine morphotypes, which is the first report regarding *L. viridis*. Haemogregarines have also been previously found in fish (Davies et al. 2003), amphibians (Petit et al. 1990), snakes (Paperna and Lainson 2004; Brown et al. 2006) and several lizard species (Hussein 2006; Bouma et al. 2007; Lainson et al. 2007) including lacertids (Amo et al. 2005; Garcia-Ramirez et al. 2005; Martin et al. 2007). Although in some groups no associated cost of infection was reported (Brown et al. 2006), infected lizards had smaller home ranges (Bouma et al. 2007) and lower locomotor capacity (Oppliger et al. 1996). The haemogregarines have a negative (but not lethal) effect on their lizard hosts, and they are thus optimal for testing the Hamilton–Zuk hypothesis.

Haemogregarine blood parasites affected 95.83 % of the studied male *L. viridis*, showing that the population experiences high parasite prevalence. According to the predictions of the Hamilton–Zuk hypothesis, in species showing high parasite prevalence, individuals with more intense signals should also be less infected (Hamilton and Zuk 1982).

The UV component of male *L. viridis*'s structural throat patch colour has been shown to be a sexually selected trait (Bajer et al. 2010, 2011), and throat patch colour possibly acts as a multiple signalling system (Bajer et al. 2012; Molnar et al. 2012). Carotenoid-based coloration is related to sexual selection in house sparrows (*Passer domesticus*) (McGraw et al. 2002) and bluebirds (*Sialia mexicana*) (Budden and Dickinson 2009) and is related to immune capacity and parasite load in *Lacerta schreiberi* (Martin and Lopez 2009; Martin et al. 2008). Furthermore, structural and pigment-based colours have been shown to simultaneously affect female mate choice in *Urosaurus ornatus* (Hamilton and Sullivan 2005). Previous experimental results showed that carotenoid belly colour can be influenced by both nutritional state and environmental temperature in *L. viridis* (Bajer et al., unpublished data). It is therefore possible that belly colour serves as an honest signal in this species. We found that both nuptial throat and belly colour were strongly negatively correlated with the rate of endoparasite infection in male *L. viridis* during the reproductive season, in other words, individuals with higher parasite loads were duller in coloration. This supports the intraspecific prediction of the Hamilton–Zuk hypothesis and is one of the first to do so using the structural coloration of reptiles (but see Martin et al. 2008 on a carotenoid-based colour).

Body size and condition were both positively correlated with blood parasite load. Considering that reptiles grow indeterminately, larger individuals are presumably older (Hagelin 2002). A possible explanation for the body size pattern might be that infections had more time to develop in older males (as parasitic cells had more reproductive cycles) than in younger individuals, which may have been only

Table 1 Results from the GLM on the blood parasite infection intensity of male European green lizards

Variable	Effect	B	SE	F	ndf, ddf	P	Partial η^2
Intensity	**SVL**	**0.014**	**0.006**	**4.845**	**1, 16**	**0.043**	**0.232**
	Res. head	−0.073	0.288	0.065	1, 10	0.804	0.006
	Condition	**0.128**	**0.024**	**28.923**	**1, 16**	**<0.001**	**0.644**
	AFP	**−0.125**	**0.037**	**11.669**	**1, 16**	**0.004**	**0.422**
	FP	−0.023	0.032	0.554	1, 13	0.47	0.041
	Throat brightness	**−0.020**	**0.008**	**6.058**	**1, 16**	**0.026**	**0.275**
	Throat UV chroma	0.210	0.961	0.048	1, 11	0.831	0.004
	Throat blue chroma	−0.235	0.693	0.115	1, 12	0.74	0.01
	Belly brightness	**−0.024**	**0.04**	**35.621**	**1, 16**	**<0.001**	**0.69**
	Belly UV chroma	−0.639	0.828	0.597	1, 14	0.453	0.041
	Belly yellow–green chroma	−1.835	1.288	2.029	1, 15	0.175	0.119
	$Log_{10}Par$	**−0.050**	**0.009**	**31.631**	**1, 16**	**<0.001**	**0.664**

Non-significant effects are shown as seen at the time of removal during the stepwise backwards model selection. Significant effects are represented in bold font. Effect size (partial η^2), parameter estimates and their standard errors are shown

SVL snout-to-vent length, *res. head* head size corrected for SVL, *condition* body weight corrected for SVL, *AFP* level of femoral pore asymmetry, *FP* total number of femoral pores, *$Log_{10}Par$* number of ticks log-transformed, *ndf* numerator degrees of freedom, *ddf* denominator degrees of freedom

recently infested (Amo et al. 2005). Alternatively, older males may have a reduced immune system due to immunosenescence and thus suffer from a higher parasite load (Palacios et al. 2011). The positive correlation found between condition and endoparasite load could be due to a positive correlation between body condition and foraging time. Thus, intense infection rate may be a cost of higher activity (Leu et

al. 2010). For example, heightened rates of movement associated with higher foraging rates may depress immune function. Nevertheless, our data show that haemogregarines do not directly decrease their *L. viridis* hosts' body condition during the breeding season. Furthermore, individuals of better condition may have higher energy stores permitting them to tolerate a higher level of infection.
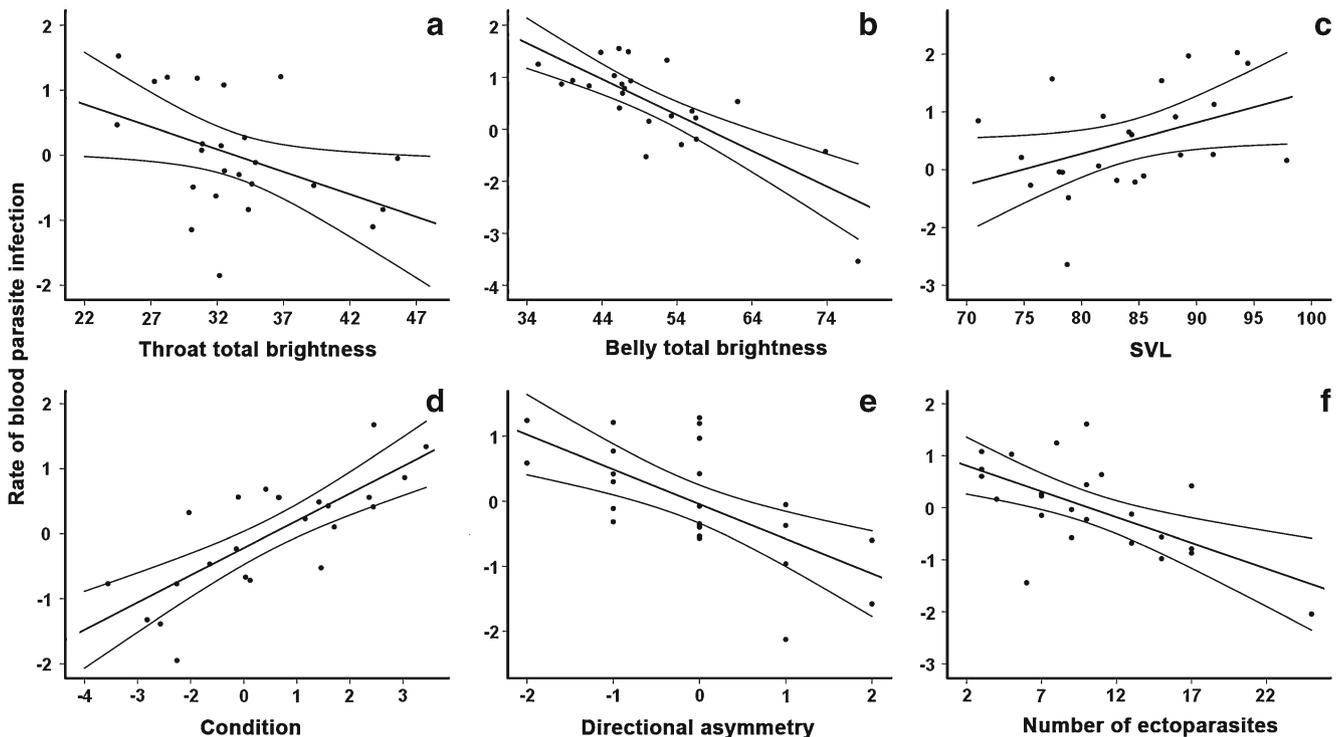
Fig. 2 Correlations between blood parasite load and *a* throat brightness, *b* belly brightness, *c* SVL, *d* condition, *e* level of femoral pores' directional asymmetry and *f* number of ticks in male European green lizards. Rate of infection is represented by model residuals

The three types of bilateral asymmetry distinguished are directional asymmetry (a consistent bias towards one side), antisymmetry (consistent bias towards a random side) and fluctuating asymmetry (small non-directional departures from perfect symmetry) (van Valen 1962; Palmer and Strobeck 1986). While directional asymmetry and antisymmetry are both usually seen as results of adaptive evolution, fluctuating asymmetry is caused by disturbed development and indicates ontogenetic developmental instability (van Valen 1962; Palmer and Strobeck 1986). Directional asymmetry in the femoral pores of male *L. viridis* was negatively correlated with endoparasite load, as individuals with more femoral pores on the left side (the dominant side) were found to carry higher number of parasites. A high level of directional asymmetry is favourable (e.g. Moller 1994); therefore, this result could be a function of an unobserved cost linked to the ontogenetic development of an advantageous trait. Finally, males with higher numbers of ectoparasites had lower endoparasite load. Although both ticks and haemogregarines infest lizards, ticks do not meet the requirements of the Hamilton–Zuk hypothesis, namely that they be latent or persist in chronic form (Hamilton and Zuk 1982). Ticks can be vectors of haemogregarines (Smallridge and Bull 1999), but a single bite can infest the host with parasitic cells capable of reproducing in the host organism (Roca and Galdon 2010; Al-Ghamdy 2011); therefore, there is no functional link expected between number of ticks and intensity of blood parasite infection. One possible explanation for the negative correlation between number of ticks and rate of blood parasite infection is that endoparasites somehow prohibit further vectors from attaching and transferring more parasitic cells into the host's system to decrease the risk of density-dependent intraspecific competition (Tripet and Richner 1999). Alternatively, tick bites can also induce an immune reaction, which in turn may reduce the number of blood parasites (Wikel et al. 1997). Nonetheless, the negative correlation between endo- and ectoparasite numbers cannot be sufficiently explained at this stage.

To our best knowledge, this is the first study conducted on the structural coloration of reptiles that supports the intraspecific prediction of the Hamilton–Zuk hypothesis for species with high parasite prevalence, namely that individuals with fewer blood parasites develop more intense coloration, thus signalling their higher resistance to infection. Our study revealed a possible mechanism for ensuring the honesty of colour signals and discovered numerous links between blood parasite infection and other fitness-related traits. These patterns show that haemogregarine infection can influence several fitness-related traits and is also advertised by sexual signals, together with having a possible role in the evolution of conspicuous coloration in *L. viridis*.

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