SALAMANDRA 53(1) | 10–17 | 15 February 2017 | ISSN 0036–3375

City life has fitness costs: reduced body condition and increased parasite load in urban common wall lizards, *Podarcis muralis*

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Manuscript received: 3 February 2015
Accepted: 23 June 2015 by Alexander Kupfer

Abstract. Animals living in urban areas experience additional stress compared to those inhabiting more natural habitats. This could influence their physical state and ability to cope with parasites. Here, effects of environmental disturbances on body condition and prevalence and load of blood parasites in the common wall lizard (*Podarcis muralis*) were investigated by comparing these indices between five urban and five rural populations. The physical condition index was lower in urban areas, and females were the most affected sex. This suggests significant fitness costs, as survival and reproductive output are often tightly linked to body condition. Prevalence of blood parasites was more variable in urban (2.5–100%) compared to rural (50.0–75.6%) populations, with no statistically significant differences between the two habitats. Prevalence of blood parasites increased with body size. Parasite load was significantly higher in urban lizards, suggesting strong effects of urbanisation on host–parasite interaction. An increased concentration of blood parasites should affect fitness since various aspects of physiology are compromised in parasitised animals. Larger animals were more frequently and more severely infected, most likely due to their being longer and more frequently exposed to parasites. No differences between sexes in both prevalence and intensity were found, suggesting equal susceptibility or exposure to parasites.

Key words. Haemogregarinae, physical condition, stress, Lacertidae.

Introduction

Urbanisation has been increasing in the past decades and it is predicted to increase even faster in the future as more and more people live in cities (Crane & Kinzig 2005). Natural habitats are continuously being transformed into urban areas at an accelerated rate, causing major changes in ecosystems. Although all free-ranging animals undergo a wide range of types of stress during their lives, those inhabiting urban areas should experience additional ones. Urban animals are often exposed to high concentrations of heavy metals (Conti et al. 2004) and a wider range and higher concentrations of toxins (Shochat et al. 2006). Also, temperatures tend to be higher in cities (Oke 1973), as well as noise and light pollution (Longcore & Rich 2004, Barber et al. 2010). Finally, for species perceiving humans as predators, human presence alone can be considered stressful (Blumstein 2006).

Under such environmental pressures, the body condition of animals can be seriously affected (Liker et al. 2008). Body condition is tightly linked to overall health and fitness and represents an individual's physical or nutritional status, meaning that animals with superior body condition have greater energy reserves and vice versa. It indicates the animal's past foraging success and is correlated to many aspects of the immune system (Møller et al. 1998), the animal's physical abilities, and its capability to deal with environmental pressures (Jakob et al. 1996). Moreover, reproductive output and survival are often linked to body condition at the beginning of the season (Radder & Shanbhag 2004, Hofman & Henle 2006), suggesting that body condition should be a reliable indicator of overall quality.

Furthermore, by affecting the immunological response, environmental disturbances can also induce changes in host–parasite relationships (Lafferty 1997, Lafferty & Kuris 1999, Daszak et al. 2001, Lafferty & Holt 2003) and possibly alter the trade-offs between parasitisation and other ecological pressures acting on hosts (Clobert et al. 2000). Simulation models suggest that interaction between stress factors and parasitism should be highly complex (Lafferty & Holt 2003). As a result, there are several hypotheses, with contrasting predictions on what to expect of parasite abundance when host populations experience additional stressful conditions. On the one hand, when animals experience unfavourable environmental conditions, the function of the immune system can be compromised, the animal's resistance to parasites may decrease and as a consequence lead to increased prevalence and concentration of parasites (Lafferty & Holt 2003). On the other hand, environmental stress can have a negative effect on the parasite itself or its vector (Evans 1982, Siddall & Des Clers, 1994). In this case, parasite abundance is likely to decrease (Lafferty 1997, Lafferty & Kuris 1999). When acting in synergy, environmental stress and parasites can lower the survival rate of infected animals, again, resulting in decreased parasite prevalence (Marcogliese & Pietrock 2011). Nevertheless, in some cases, urbanisation has been shown to have a beneficial effect for the host, with parasite prevalence being reduced in a city environment (Geue & Partecke 2008, Evans et al. 2009). Despite mixed results, several reviews and meta-analyses suggested the same: when animals are exposed to environmental stress, particularly to an anthropogenic one, increases in parasite prevalence and concentration are to be expected (Bradley & Altizer 2007, Vidal-Martínez et al. 2010, Marcogliese & Pietrock 2011).

Lizards are recognized as highly sensitive to heavy metals and other pollutants (Márquez-Ferrando et al. 2008, Marsili et al. 2009), temperature stress (Braña & Ji 2000), and human presence (Amo et al. 2006). Among European species, the common wall lizard (*Podarcis muralis*) is an excellent model for studying the effects of urbanisation, as it is widely distributed in both natural and urban habitats (Schulte 2008). Haemogregarines are among the most common parasites of reptiles (Telford 2008). They are haemoprotozoan parasites belonging to the phylum Apicomplexa with an indirect life cycle that infect lizards through intermediate vectors such as ticks and mites (Telford 2008). In lacertids, many costs associated with haemogregarinae infections have been described, including anaemia, decreased tail regeneration (Oppliger & Clobert 1997), decreased locomotor performance (Oppliger et al. 1996, Garrido & Pérez-Mellado 2013a), and reduced survival of reproductive individuals (Sorci et al. 1996), which suggest a significant fitness cost. However, numerous studies report no negative effect at all (Ekner-Grzyb et al. 2013, Damas-Moreira et al. 2014).

Attenuation of body condition and increased prevalence and/or concentration of blood parasites have been previously detected in lizards inhabiting suboptimal environments. Reduced body condition was observed in a *P. muralis* population inhabiting areas with high levels of tourism (Amo et al. 2006), in populations of *Iberolacerta cyreni* inhabiting ski slopes (Amo et al. 2007a), as well as in populations of *Anolis carolinensis* inhabiting agricultural fields (Battles et al. 2013). Lizards exposed to heavy metals (Salice et al. 2009) and pesticides (Amaral et al. 2012) also exhibited a reduced body condition. The abundance of blood parasites was found to be increased in populations of *Psammodromus algirus* living in deteriorated habitats (Amo et al. 2007b). Similarly, the prevalence and concentration of blood parasites was shown to increase in populations of *Zootoca vivipara* living in low-quality habitats (Oppliger et al. 1998) as well as in *Podarcis bocagei* populations inhabiting areas with a high usage of pesticides (Amaral et al. 2012). Nevertheless, in some cases, environmental disturbances apparently had no effect on blood parasite prevalence and concentration (French et al. 2008).

In this paper, the effects of environmental stress on body condition and parasitaemia are investigated by comparing these indices between five urban and five rural populations of the common wall lizard, *Podarcis muralis*. We specifically tested the hypothesis that due to exposure to multiple disturbing factors (higher concentration of heavy metals and other pollutants, higher temperature, human presence, etc.), urban lizards will display a reduced body condition, and prevalence and concentration of blood parasites will be increased compared to rural ones.

Materials and methods

Data collection

For this study, 370 adult individuals of *P. muralis* were sampled using a standard noose technique (García-Muñoz & Sillero 2010) from mid-April to mid-July of 2012 (Table 1) in ten populations: five rural and five urban ones, all within the area of Niš in southern Serbia (for a detailed description see Lazić et al. 2013). The urban population samples were collected from separate sites within the city of Niš, 2 to 7 km apart. These included railroad tracks, fortress walls, abandoned military warehouses, and other infrastructure. These lizards were exposed to high levels of heavy metals (Škrbić et al. 2002, Nikić et al. 2009, Jovanović et al. 2011), air pollutants (Djordjević 2008, Djordjević et al. 2011), and to benzene, polycyclic aromatic hydrocarbons, and persistent organic pollutants (Škrbić & Miljević, 2002). The five rural samples were collected in the surroundings of the city, 10 to 30 km from the city centre, to minimize the effects of genetic diversity and variation in climate. Lizards were collected from the countryside, on walls of abandoned forest huts, forest paths, and stonewalls. We consciously chose areas with no intensive agricultural activity in proximity to limit or prevent contamination by pesticides, fertilizers, and other contaminants stemming from agricultural pollution. Since body condition and the concentration of blood parasites may differ temporally (Sorci 1995, Garrido & Pérez-Mellado 2013b), sampling was conducted only during the reproductive season.

Captured lizards were transported to the laboratory at the Faculty of Sciences and Mathematics, University of Niš, where they were sexed and measured for body mass and snout–vent length (SVL). Animals larger than 49.78 mm with developed secondary sexual traits were considered

Table 1. Habitat types, sample sizes (N) for males (M) and females (F), prevalence and concentrations of blood parasites (mean±SD and range) for all populations studied.

Habitat type	Population	Sex	N	Prevalence	Concentration (mean SD and range)
Rural	S	M	17	52.94%	13.11±9, 0-28
		F	20	65.00%	6.23±3.83, 0-13
	X	M	15	66.67%	6±5.12, 0-18
		F	13	46.15%	3.33±3.38, 0-10
	B	M	24	50.00%	6.16±7.14, 0-27
		F	20	60.00%	5.91±6.43, 0-23
	DD	M	22	63.64%	19.35±13.78, 0-45
		F	19	89.47%	20.64±27.21, 0-101
	K	M	27	59.26%	9.56±5.97, 0-23
		F	23	39.13%	4.88±4.93, 0-17
Urban	Ni	M	19	84.21%	17.06±31.6, 0-133
		F	20	80.00%	14.25±15.16, 0-67
	E	M	7	28.57%	5.5±6.26, 0-10
		F	14	42.86%	24.83±25.76, 0-71
	P	M	23	4.35%	–
		F	17	0%	–
	A	M	21	71.43%	18.26±19.30, 0-76
		F	20	65.00%	6.92±7.71, 0-30
	M	M	17	100%	28.23±28.90, 3-103
		F	12	100%	17.5±19.63, 1-72

adults (Schulte 2008). A digital calliper with 0.01 mm precision and a compact digital scale with a precision of 0.1 g were used to measure SVL and body mass, respectively.

In order to analyse the prevalence and concentration of blood parasites, thin blood smears were made from blood obtained by cutting off the tip of the tail (Sevinc et al. 2000). Blood smears were air-dried and stained, using a standard May-Grünwald-Giemsa staining procedure. Slides were investigated for intraerythrocytic parasites at 400× magnification, using a Leica DFC-320R2 light microscope by a single observer (MML). Parasite prevalence was estimated as the percentage of infected lizards in a population, while parasite concentration was evaluated as the number of infected red blood cells per 2,000 analysed. All lizards were then returned to the sites of capture. at which they had been captured.

Statistical analysis

All statistical analyses were performed in RStudio Version 0.96.122 (2012). As a measure of body condition, we used a scaled mass index (SMI) as proposed by Peig & Green (2009, 2010) as the most reliable and unbiased measure. SMI standardises body mass for a predefined value of body size according to the equation SMI = Mi(Lo/Li)bSMA, where Mi is the body mass of ith individual; Li body size of ith individual; Lo is an arbitrary, predefined value of body size; bSMA is the scaling exponent calculated by a standardised regression axis (SMA) of body mass on body size; and SMI is the predicted value of body mass for the individual for Lo standardised body size. The arithmetic mean of log SVL of the entire sample was taken as Lo, (1.741 mm). The scaling exponent (bSMA) differed between the two habitat types, with ß = 4.179 for urban and ß = 3.610 for urban. Also, the strength of the fit ($r^2 \times 100$) differed and was 60.70% for the urban and 67.10% for rural type. Consequently, we used the bSMA value calculated for the rural type to calculate the SMI for the entire sample, as suggested by Peig & Green (2010). The scaling exponent was calculated using the lmodel2 package for R (Legendre 2011).

SMI values were checked for normality (Kolmogorov-Smirnov test, $p > 0.05$) and homogeneity of variances between habitats (Bartlett's test, $p > 0.05$) and sexes (Bartlett's test, $p > 0.05$). To test for possible differences in SMI, we specified an ANOVA model on individual SMI values, in which habitat type, population nested in type, sex, and interactions were used as explanatory variables. Tail condition (complete vs. broken/regenerated) was initially added to the model because autotomised tails may influence body condition. However, the effect was insignificant ($p > 0.1$) and tail condition was therefore removed from the analysis.

Parasite prevalence was analysed using generalized linear models (GLM). In the first step, we fitted a global model with specified binomial error distribution and a logit link function containing the following variables: sex, population, habitat type, SVL, and SMI. The goodness of fit of the model was then tested using a Chi-square test, which is based on the residual deviance and degrees of freedom. This test indicated that the binomial model fits the data ($p > 0.05$). In the next step, we used the glmulti function from the glmulti package (Calcagno & de Mazancourt 2010) for R to fit all possible models containing all conceivable combinations of main effects and possible first-order interaction effects. Models were then ranked according to the corrected Akaike information criterion (AICc) and we selected the top model with the highest level of empirical support. Chi-square test was then applied to test the significance of selected variables using the ANOVA function from the R package car (Fox & Weisberg 2011).

To analyse parasite concentration, we first fitted a global model with Poisson error distribution and a log link function with the same set of variables as for the prevalence analysis. However, this model did not fit the data (goodness-of-fit test, $p < 0.05$). To test for overdispersion, we used the qcc.overdispersion.test function from the qcc package (Scrucca 2004). This test showed significant overdispersion ($p < 0.01$) so that we fitted a new model with the same set of variables with a negative binomial error distribution specified and an estimated value of the dispersion parameter, theta = 1.375. Since this model now fitted the data (goodness-of-fit test, $p > 0.05$), we used the glmulti function to obtain the best possible model based on the AICc criteria. To test for variable significance, a Chi-square test was applied to the top model.

Table 2. Statistical results obtained from ANOVA on individual SMI values with sex, habitat type (urban vs. rural), and population nested within the population type as factors, and all interaction effects.

	df	SS	F	p
Sex	1	1.012	212.417	<0.001
Habitat type	1	0.225	47.3791	<0.001
Pop:Habitat type	8	0.383	10.056	<0.001
Sex:Habitat type	1	0.002	4.738	<0.005
Sex:Pop:Habitat type	8	0.08	2.115	<0.005
Residuals	350	1.667		

Results

Differences in the SMI were found between the sexes, with males being relatively heavier compared to females (Table 2). Differences were also found between animals inhabiting urban and rural areas, with the latter ones showing a higher body condition index. However, it appears that urbanisation did not affect both sexes equally as was suggested by the statistically significant type × sex interaction (Table 2). While body conditions were similar between males from urban and rural areas the same cannot be said for females. Namely, urban females exhibited a lower SMI compared to rural females. Also, significant interaction between sex and populations nested within the habitat types shows that females from some of the rural populations exhibit a higher SMI than males in some of the urban populations (Table 2, Fig. 1).

The only blood parasites found were haemogregarinae. However, due to the difficulty of identifying them to species level based only on the morphology of intraerythrocytic gametocytes precise identification was impossible.

The prevalence of haemogregarinae differed significantly between populations and ranged from 2.5 to 100% of infected animals in urban populations and from 50.0 to 75.6% in rural populations (Table 1). The glmulti function presented us with the most parsimonious model, the one that included SVL and population as the only variables. SVL had a significant effect on prevalence, with larger animals being more frequently infected ($\chi^2 = 14.090$, df = 1, $p < 0.001$; Fig. 2a). High differences in blood parasite prevalence between populations were also confirmed by the GLM analysis ($\chi^2 = 34.081$, df = 9, $p < 0.001$).

Haemogregarinae concentration differed significantly between animals and ranged from 1 to 133 infected erythrocytes per 2,000 analysed. The best GLM model according to the AICc criteria was the one containing the following variables: habitat type, populations nested within the population, and SVL. Blood parasite intensity differed between the two habitat types, with infections being more severe in the urban one ($\chi^2 = 13.599$, df = 1, $p < 0.001$). Significant variation in infection severity was detected between populations belonging to the two habitat types ($\chi^2 = 91.026$, df = 8, $p < 0.01$; Fig. 3), demonstrating that urbanisation has no uniform effect across all samples within the habitat types. As for the prevalence, the parasite load was higher in larger animals ($\chi^2 = 7.818$, df = 1, $p < 0.01$; Fig. 2b).

Discussion

As hypothesised, urban lizards exhibited a significantly lower mean body condition index compared to animals from rural areas. However, these differences were more pronounced in females than in males (Fig. 1). Interestingly, similar patterns were also observed in other lizard species: females, but not males, exhibited a reduced body condition index in populations of *Psammodromus algirus* (Amo et al. 2007b) and *Anolis carolinensis* (Battles et al. 2013) in anthropogenically modified habitats.

There are a few possible explanations for this pattern. First, food availability may be decreased in urban settings. This is a likely scenario since urbanisation has been identified as having a strong negative impact on species richness and abundance in various arthropod taxa (McIntyre 2000, Buczkowski & Richmond 2012, Penone et al. 2013). If food is less abundant, a reduced body condition index in females can be expected, as males are more active and travel longer distances and should therefore be more successful in foraging (Llorente 1988). Secondly, urban lizards of both sexes were shown to have smaller head sizes compared to rural ones (Lazić et al. 2015), which could impair their ability to handle larger prey. This reduction may constrain females even more, as their head size is

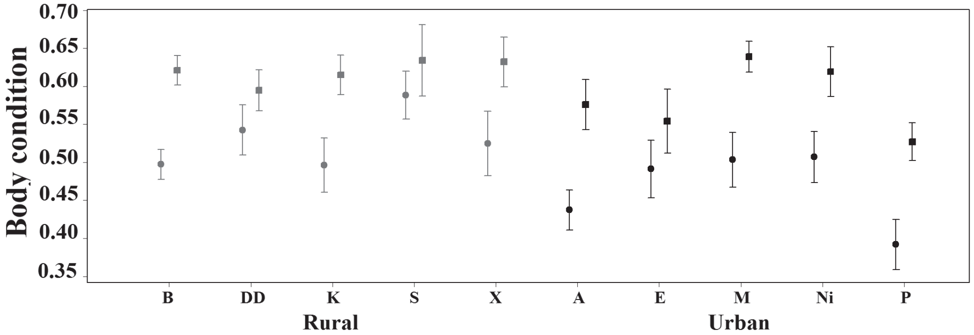

Figure 1. Body condition of males (squares) and females (circles) of *Podarcis muralis* in rural (grey symbols) and urban (black symbols) populations. Error bars represent 95% confidence intervals. See Table 1 for sampling sizes.

smaller anyway (Kaliontzopoulou et al. 2008). Thirdly, it was shown that females respond differently to high predation pressure (irrespective of whether it is real or perceived) than males in that they change their behaviour and start escaping at longer distances (Amo et al. 2007b). That means that females execute antipredator responses more frequently and this is associated with mass losses (Amo et al. 2007b, Amo et al. 2007c). Since lizards come into contact with humans more frequently in urban areas and often perceive them as predators, this is a likely explanation for the lower body condition index in urban females. However, it is hard to say at this moment which, if any, of the aforementioned hypotheses could better explain the observed patterns and this issue should be investigated in more detail in the future.

Irrespective of the real cause, reduced body condition is likely to have a negative effect on individual fitness since it is closely linked to the reproductive output of females (Radder & Shanbhag 2004, Hofman & Henle 2006). Females in better condition have higher energy reserves and can invest more energy into reproduction. This usually leads to having larger clutches and/or offspring of larger size (Olsson & Shine 1997, Radder & Shanbhag 2004, Hofman & Henle 2006). Consequently, offspring of larger size are more likely to survive (Sinervo et al. 1992, Díaz et al. 2005, Uller & Olsson 2010). Based on this, it is expected that urban females have offspring of poorer quality with lower chances of survival.

With regard to our analysis of blood parasites, our expectation of increased prevalence in urban areas was not supported. Significant differences in blood parasite prevalence were detected between populations but not between the two habitats. There are several possible explanations for the observed lack of differences in blood parasite prev-

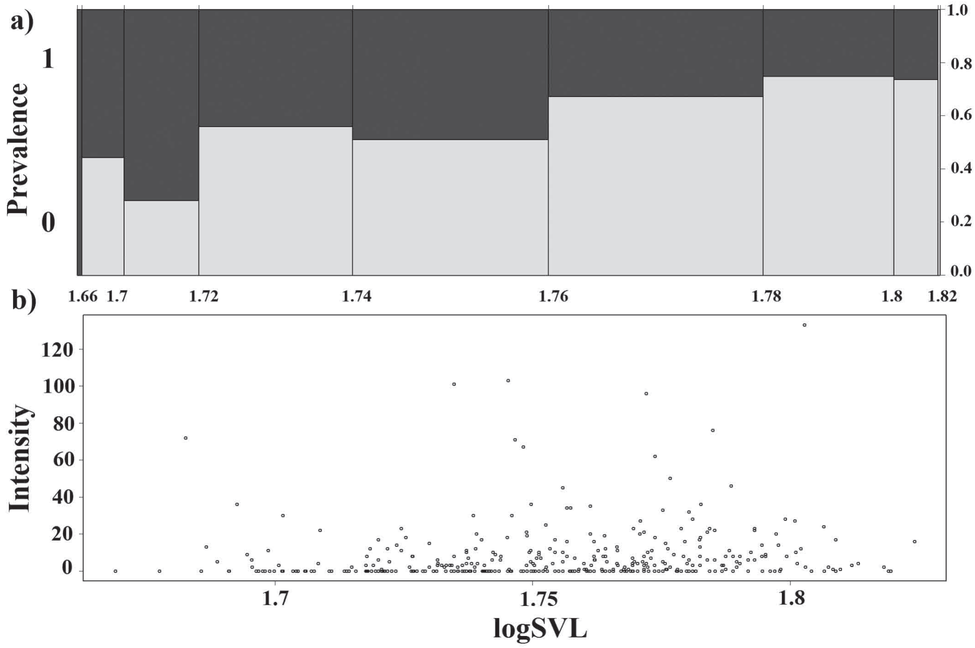

Figure 2. Relationships between logSVL and (a) blood parasite prevalence, and (b) blood parasite load. Raw data are plotted in both figures.

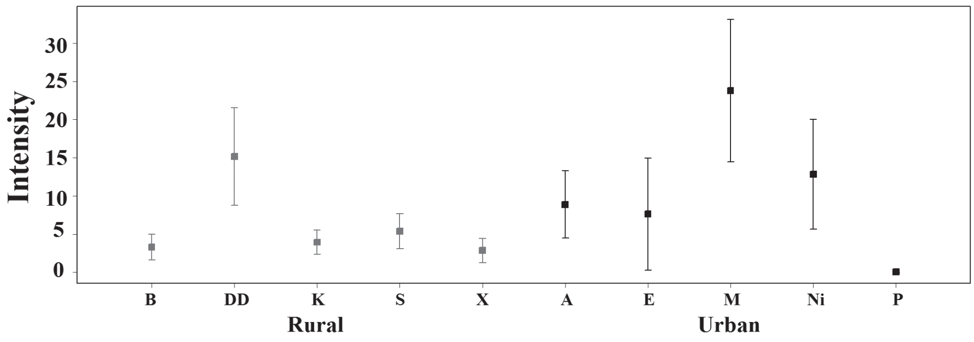

Figure 3. Mean parasite loads in rural (grey squares) and urban (black squares) populations of *P. muralis* from southern Serbia. Error bars represent 95% confidence intervals. See table 1 for sampling sizes.

alence between the two habitats. Firstly, it is possible that environmental disturbances that were previously shown to affect the developmental stability of meristic traits (Lazić et al. 2013), head shape allometry, head size, and degree of head shape asymmetry (Lazić et al. 2015) have no effect on blood parasite prevalence. This is likely since parasite prevalence can be strongly affected by stochastic processes and, hence, may be an unreliable indicator of environmental disturbance (Sures 2004). Secondly, urban and rural lizards may be equally exposed to mites and ticks. However, urban lizards were shown to host more ectoparasites in the previous year (Lazić et al. 2012), suggesting that a low prevalence of blood parasites is not due to a low presence of vectors. Thirdly, infected lizards are known to suffer from reduced concentrations of haemoglobin, reduced capacity for oxygen transportation (Oppliger et al. 1996, Veiga et al. 1998), as well as reduced burst speed (Oppliger et al. 1996, Garrido & Pérez-Mellado 2013a). When infection acts together with environmental stress, their combined effects are likely to compromise survival (Marcogliese & Pietrock 2011). As a result, the most highly infected animals within the population could have perished, resulting in a low prevalence at population level. This seems to be in the origin of the observed patterns, particularly when keeping in mind the lower body condition index in urban lizards.

Our analysis also showed that larger animals tend to be more frequently infected, a pattern that is frequently observed in lizards (Oppliger et al. 1999, Amo et al. 2004, Garrido & Pérez-Mellado 2013b, but see Amo et al. 2005, Damas-Moreira et al. 2014). Larger, and therefore most likely older, lizards have more chances to be in contact with parasites at some or other point during their lifetime, which in turn may lead to a higher prevalence in larger animals.

Parasite concentration was, as hypothesized, increased in urban populations compared to rural ones, in spite of the high variation between populations within the two habitat types (Fig. 3). These differences were not due to a positive relationship between SVL and concentration, as there were no significant differences in SVL between the two habitats (results not presented here).

There are many types of anthropogenic disturbances that are hypothesised to cause an increase in parasite concentration. Heavy metals, other pollutants, and stress factors commonly present in urban areas can negatively affect immunological response (Crain & Guillette 1998), compromising the ability of animals to combat infections. Experimental studies on lizards demonstrated that environmental disturbances can indeed cause an increase in blood parasite concentration (Oppliger et al. 1998). This was also observed in free-ranging lizards inhabiting areas polluted by the intensive application of chemicals used in crop production (Amaral et al. 2012). This is a likely explanation for the observed pattern, as increased concentrations of benzene, polycyclic aromatic hydrocarbons, heavy metals, and persistent organic pollutants were detected in the city of Niš (Škrbić et al. 2002, Nikić et al. 2009, Jovanović et al. 2011). Unfortunately, studies investigating the effects of human disturbance on lizard immunology are scarce and should be corroborated in *Podarcis muralis*.

Blood parasite concentrations were also higher in larger lizards. Recovery from blood parasite infections was shown to be low in lizards (Sorci 1995) and frequent contact of older and larger lizards with blood parasites is likely to cause multiple reinfections, thus resulting in higher concentration (Bouma et al. 2007).

Overall, the results of this study show that anthropogenic disturbance can have a negative consequence of the nutritional status of female lizards. Moreover, the evidence obtained here suggests that anthropogenic disturbance can cause an increase in parasite load. It is not clear at this point which stress factors cause these effects and future studies, evaluating the effects of individual stress types related to urbanisation on immunological response, parasitaemia and body condition should be performed.

Acknowledgements

We thank Antigoni Kaliontzopoulou, Neftalí Sillero, Catarina Rato, and Miodrag Misha Ignjatović for their assistance in field and lab work. We are grateful to an anonymous reviewer for critical comments on a previous version of the manuscript. MML, UŽ, and JCI were supported by Grant No. 173025, funded by the Ministry of Education, Science and Technological Development of the Republic of Serbia. MAC was supported by FCOMP-01-0124-FEDER-007062 project PTDC/BIA-BEC/101256/2008 by the FCT (Portugal), and partially by the project "Biodiversity, Ecology and Global Change" co-financed by the North Portugal Regional Operational Programme 2007/2013 (ON.2–O Novo Norte), in the National Strategic Reference Framework (NSRF), through the European Regional Development Fund (ERDF). The collaboration between the Portuguese and Serbian teams was also supported by an integrated action co-funded by the FCT (Portugal) and MESTD (Serbia). Lizards were collected and handled as per permit No. 353-01-505/2012-03 issued by the Ministry of Environment and Spatial Planning of Republic of Serbia.

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