


Haemosporidian infections in wild populations of *Podarcis muralis* from the Italian Peninsula

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Research Article

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Abstract

Parasites can significantly influence the ecology, behaviour and physiology of their hosts sometimes with remarkable effects on their survivorship. However, endemic parasites or those not associated with obvious clinical disease have been partly neglected in the past decades comparatively to the most pathogenic ones. Apicomplexa are an important example of blood parasites that have been broadly investigated, although it can be difficult to determine the effects of infections at the population level, especially in widespread species. Such is the case of the common wall lizard (*Podarcis muralis*). We investigated 61 populations across Italy between 2008 and 2017 and recorded snout–vent length, latitude, date of collection and took blood samples for parasite count. We modelled parasite prevalence and load in a Bayesian framework. Parasites were present in all populations but 1 and in 13 of them all individuals were parasitized. We recorded almost identical responses for probability of infection and parasite load in both sexes, directly proportional to body size and inversely proportional to latitude, with a peak in cooler months. Therefore, haemosporidians can be very common in *P. muralis*, although their presence can vary significantly. Moreover, such a high prevalence makes it necessary to investigate to what extent haemosporidians affect hosts' survivorship, taking into consideration abiotic and biotic factors such as temperature, hormone levels and immune response.

Introduction

To understand the role of parasites in their hosts' ecology and population dynamics it is crucial to investigate their effects on the hosts themselves and how they cope with parasitic infections (Smallridge and Bull, 2000). Although the effects of infectious organisms have been widely investigated in the past decades, most research has been focused on pathogenic ones affecting mainly humans and domesticated animals, while little attention has been paid to persistent and endemic parasites in wild populations of reptiles (Anderson, 1995), taking into consideration the potential impacts of such parasites on hosts' ecology, behaviour and physiology (Mendoza-Roldan *et al.*, 2021) as well. Therefore, the reciprocal interactions between parasites not associated with obvious clinical disease and their natural hosts are still an open field for research as it is still complex to determine the magnitude and impact of the parasite infection on the hosts' survivorship or, alternatively, whether they can coexist without major consequences for the host (Jacobson, 2007).

Under this perspective, blood parasites of wild vertebrates have been investigated widely in previous research, especially those taxa that undergo reproduction *via* gametocytes in the blood cells of their host such as *Plasmodium*, *Hepatozoon*, *Leucocytozoon* and *Haemoproteus* (Lei *et al.*, 2013; Netherlands *et al.*, 2015; Naqvi *et al.*, 2017). These taxa have been studied intensively because of their remarkable distribution within wild populations of vertebrates (Davies and Johnston, 2000) assessing their role in causing major detrimental effects on their hosts (e.g. anaemia, leucocytosis, liver/spleen enlargement). Moreover, endemic parasite presence has been used in terms of haematology and blood cytology, which are important tools to assess physiological adaptations of the hosts to special environmental conditions (Martínez-Silvestre and Arribas, 2014).

On a wider scale it is more complicated to assess the impact of endemic intracellular parasites on wild populations of widespread species due to the broad spectrum of environmental conditions that are experienced by different populations. This is the case of the common wall lizard (*Podarcis muralis*), which is commonly present in most countries from central-southern Europe ranging from Northern Spain (Ji and Braña, 2000), to Germany and Czech Republic (Jablonski *et al.*, 2019) and to Turkey across the Balkans (Yildirimhan and Sümer, 2019). Furthermore, the ecological requirements of this species cover a wide variety of environmental conditions that allow it to inhabit a great variety of habitats (While *et al.*, 2014). For these reasons, *P. muralis* has been investigated intensively in the last decades from several perspectives, such as behavioural ecology (Coladonato *et al.*, 2020), feeding ecology (Herrel *et al.*, 2001), morphology (Calsbeek *et al.*, 2010; Urošević *et al.*, 2015), physiology (Bonati *et al.*, 2008, 2009), phylogeny and phylogeography (Gassert *et al.*, 2013; Yang *et al.*, 2020). In contrast, little

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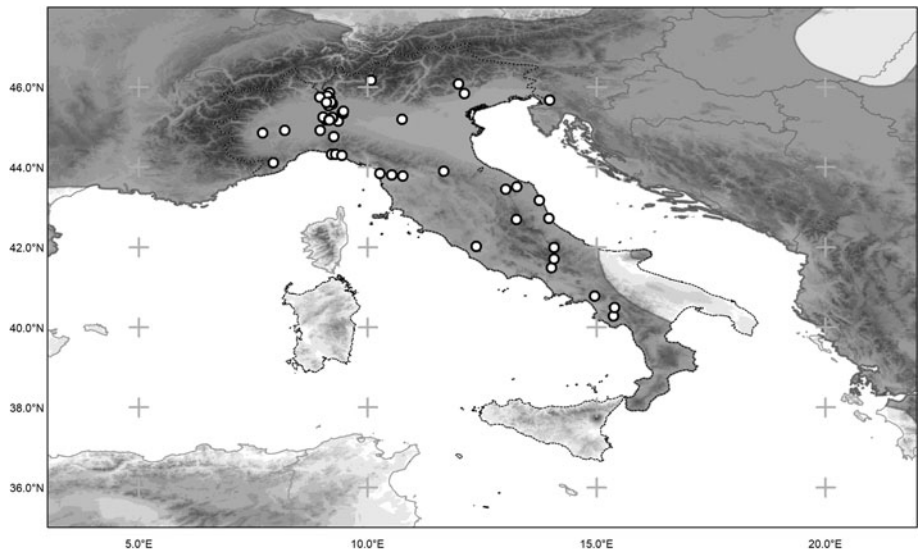


Fig. 1. Distribution map of the 61 populations of the common wall lizard sample all over Italy. The dark grey area corresponds to the distribution range of the species.

effort has been addressed at studying its interactions with parasites, especially with intracellular ones, as most research focused on a limited number of populations in relatively small areas and under specific environmental conditions (Amo *et al.*, 2004). Hence, the interactions between lizards and their parasites at wider geographic scales are still an open field for investigation to determine how wild populations interact with endemic parasites under different conditions. Furthermore, taking into consideration biological (e.g. age class, body condition index, sex) and ecological variables (local climate, altitude, diet composition) can provide robust support to such purpose.

Under this perspective, the common wall lizard appears to be an excellent model species, given its wide distribution in the central-southern Europe region and also due to the partial lack of knowledge in terms of interactions with parasites. Hence, we investigated a large number of populations of *P. muralis* from the Italian Peninsula, covering also a significant range of environmental conditions, with the aim to assess the entity of haemoparasites occurrence in wild populations according to environmental and biological factors in terms of the host–parasites interaction and its ecological drivers and constraints.

Materials and methods

Data sampling

We collected adult common wall lizards by noosing (Blomberg and Shine, 2006) during March–September between 2008 and 2017 in 61 sites within the whole species distribution in Italy (Fig. 1). Overall, we captured 892 individuals (549 males and 343 females), and on average (\pm S.D.) 9 ± 11 males (range: 0–77) and 6 ± 6 females (range: 0–38) for each population. After capture, the snout–vent length (SVL) of each lizard was measured with a digital calliper. Males and females measured on average 63.5 ± 5.2 mm (range: 47.1–84.0 mm) and 59.3 ± 5.5 mm (range: 43.5–76.2 mm), respectively.

Blood samples (15–20 μ l) were collected in heparinized capillary tubes from the postorbital plexus (MacLean *et al.*, 1973). Air-dried smears were stained with May–Grünwald/Giemsa stain and scanned using a light microscope at 60 \times following standard routines (Canfield, 1998; Latimer and Bienzle, 2000). For each prepared sample, red blood cells (RBCs) and haemoparasites were counted in 50 explored fields; parasites were morphologically determined at the order level (Frye, 1981). On average (\pm S.E.) 5811 ± 81 RBCs were counted, and parasite load was standardized to 10 000 erythrocytes (Godfrey *et al.*, 1987).

Table 1. Posterior probability distributions of the coefficients of the Bayesian GLMM model for the effect of body size (standardized SVL), latitude (standardized UTM_y coordinate) and season (amplitude and phase in cosinor structure) on the parasite prevalence (probability of infection) of male and female common wall lizards in Italy

Variable	Males	Females
SVL	0.330	0.432
	(−0.233 to 0.905)	(0.183–0.696)
	$P_{\beta>0} = 0.875$	$P_{\beta>0} = 0.999$
Latitude	−0.472	−0.298
	(−1.213 to 0.238)	(−0.811 to 0.202)
	$P_{\beta<0} = 0.883$	$P_{\beta<0} = 0.904$
Amplitude	0.717	0.369
	(0.137–1.88)	(0.065–0.989)
	$P_{\beta>0} = 0.999$	$P_{\beta>0} = 0.999$
Phase	0.049	−0.092
	(−2.646 to 0.837)	(−1.372 to 0.303)
	$P_{\beta>0} = 0.555$	$P_{\beta>0} = 0.421$

HSM, HDI50 (in brackets) and the probability of the distribution to deviate from zero.

Statistical analyses

Haemoparasites were analysed following 2 approaches: firstly, we modelled the probability of parasite infection through a random intercept generalized linear model (GLMM) with binomial error distribution, then we analysed the parasite load by using a random intercept zero inflated negative binomial (ZINB) model.

To account for seasonal variation of parasites, we used multiple-components cosinor models (Halberg *et al.*, 1967; Cornelissen, 2014; Sacchi *et al.*, 2021; Storniolo *et al.*, 2021 for details on the method), which use linear combinations of cosine functions to assess the amplitude (A) and phase (φ) of seasonal rhythms around the average value [i.e. the midline estimating statistic of rhythm (MESOR)] over the period (τ). We used a single-component cosinor model:

$$Y(t) = M + A \cos\left(\frac{2\pi t}{\tau} + \varphi\right) + e(t),$$

including time (t) expressed as Julian date (1 = 1 January) and $\tau = 365$ to account for effect of circannual rhythms around the

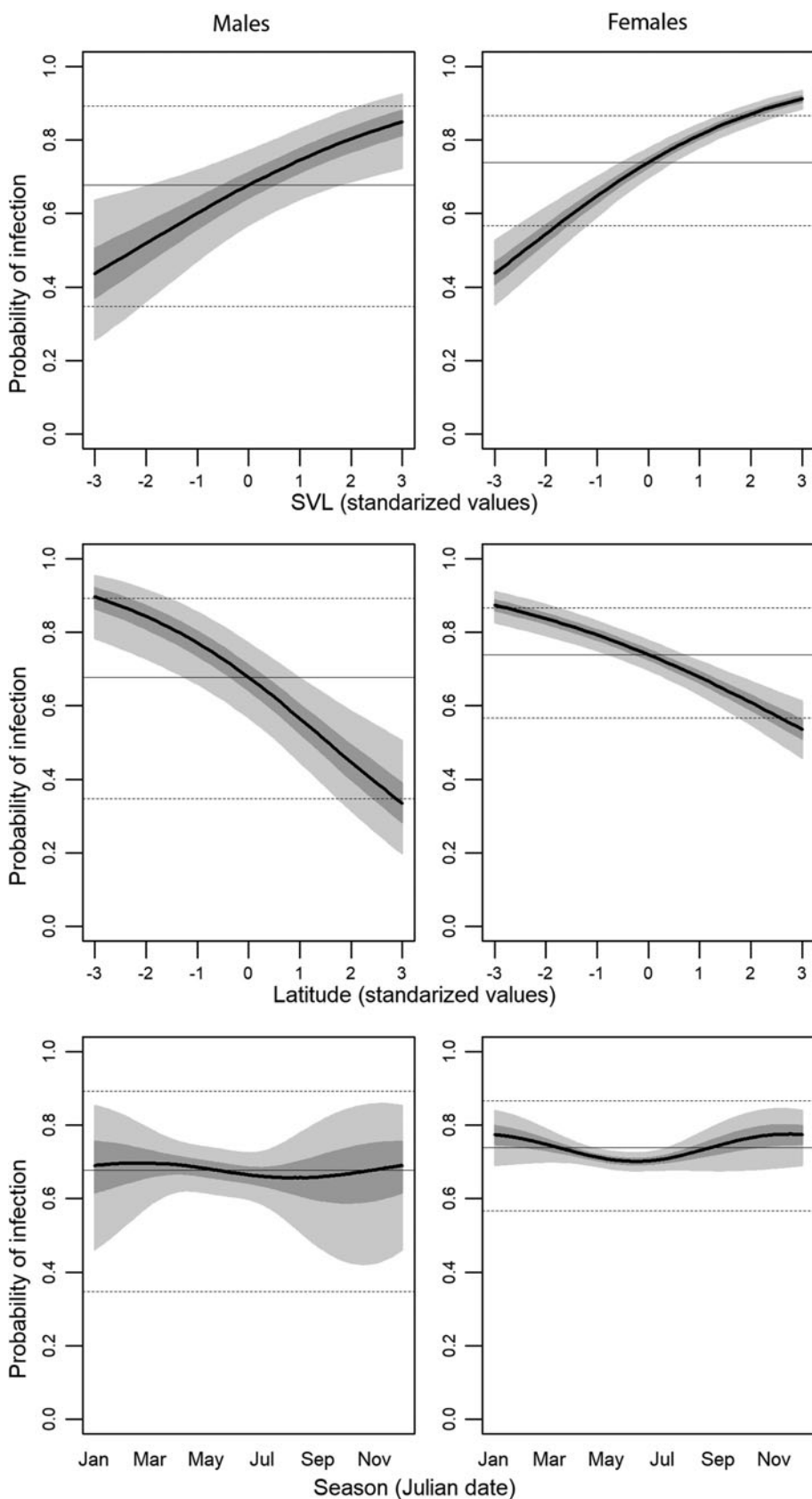


Fig. 2. Posterior probability distributions of the susceptibility to *Haemoproteus* infection (probability) in male and female common wall lizards in Italy in response to body size, latitude and season as estimated by a Bayesian GLMM. HSM (thick black solid line), HDI₅₀ (dark grey polygons) and HDI₉₅ (light grey polygons) estimates are shown. The horizontal lanes are for the HSM (solid line) and HDI₉₅ (dotted lines) for the baseline (MESOR).

baseline of parasite load. This model was incorporated into GLMM and ZINB models as fixed effect. Sex, body size (standardized SVL, by subtracting the mean and dividing by standard deviation) and latitude (standardized UTM coordinate) also entered the models as fixed effects. We also added the cosinor \times sex, cosinor \times body size and cosinor \times latitude interactions to

account for possible sex, size and geographical specific patterns in circannual rhythms on parasite occurrence and parasite load. The population entered the models as a random intercept to account for unexplained variation at the population level (σ^2_{pop}) when controlling for the explanatory variables (Sacchi *et al.*, 2021).

Table 2. Posterior probability distributions of the coefficients of the Bayesian ZINB model for the effect of body size (standardized SVL), latitude (standardized UTM_y coordinate) and season (amplitude and phase in cosinor structure) on the parasite load (*N* parasites per 10 000 erythrocytes) of male and female common wall lizards in Italy

Variable	Males	Females
SVL	0.268	0.392
	(−0.111 to 0.684)	(0.204–0.598)
	$P_{\beta>0} = 0.873$	$P_{\beta>0} = 0.999$
Latitude	−0.304	−0.202
	(−0.863 to 0.154)	(−0.603 to 0.156)
	$P_{\beta<0} = 0.855$	$P_{\beta<0} = 0.821$
Amplitude	0.403	0.303
	(0.097–0.956)	(0.080–0.709)
	$P_{\beta>0} = 0.999$	$P_{\beta>0} = 0.999$
Phase	−0.010	−0.096
	(−1.476 to 0.317)	(−0.985 to 0.192)
	$P_{\beta>0} = 0.491$	$P_{\beta>0} = 0.400$

HSM, HDI₅₀ (in brackets) and the probability of the distribution to deviate from zero.

Models were fit in a Bayesian analytical framework available in the package R2jags (Su *et al.*, 2015) in R 4.3.3 (R Core Team, 2018), which uses the samplers implemented in JAGS 4.3.0. Uninformative normal priors ($\mu = 0$ and $\sigma = 0.001$) were used for model's coefficients, and γ priors ($a = 0.001$ and $b = 0.001$ corresponding to $\mu = 1$ and $\sigma = 1000$) were used for both the error (σ) and the random intercept (σ_{pop}). Three chains were run using randomly selected initial values for each parameter within a reasonable interval, and conventional convergence criteria were checked. The number of iterations was selected for each run to obtain at least 10 000 valid values for each chain after convergence and thinning. The results from the posterior distribution indicate the probability of the described event to be true and are reported as the half-sample mode (HSM, Bickel and Frühwirth, 2006) with 95 and 50% highest density intervals (HDI₉₅, Kruschke, 2010).

Results

Haemoparasites were found in all but one of the 61 sampled populations, and in 13 populations (22%) all individuals were infected. The parasite prevalence within population was on average (\pm S.D.) 66.5 \pm 29.7% and 65.5 \pm 34.8% in males and 65.0 \pm 29.9% in females, respectively. The parasite load was on average (\pm S.D.) 49 \pm 109 parasites per 10 000 erythrocytes, ranging from 1 to 1285, 71 \pm 136 and 32 \pm 88 parasites per 10 000 erythrocytes in females and males, respectively.

The logistic Bayesian model confirmed the observation in rough data and showed that the HSMs (HDI₉₅) of the posterior probabilities of parasite prevalence were 0.68 (0.35–0.89) for males and 0.74 (0.57–0.86) for females, and changed according to body size, season and, to a lesser extent, also according to latitude (Table 1). Indeed, the probability of infection increased with body size in both sexes (Table 1, Fig. 2), with slight differences between males and females ($P_{\delta<\varphi} = 0.70$, Fig. 2). In both sexes, the probability of infection decreased northward (Fig. 2), without any evident difference between males and females ($P_{\delta>\varphi} = 0.49$, Fig. 2). The analysis of the cosinor components showed that amplitude was not null, in both males and females (Table 2), supporting the occurrence of a seasonal pattern of haemosporidians prevalence in blood cells. However, seasonal amplitude was slightly higher in females than in males ($P_{\delta<\varphi} = 0.67$, Fig. 2).

Phases did not deviate from zero (Table 1), with a slight difference between sexes ($P_{\delta<\varphi} = 0.621$), so seasonal trends were not synchronous between sexes, and parasite prevalence tends to be higher during cool months (Fig. 2).

The Bayesian ZINB model supplied for parasite load similar pattern of responses than Bayesian GLMM did for parasite prevalence. Indeed, the HSMs (HDI₉₅) of the posterior probabilities of MESORs estimated by the model were 2.38 (0.95–6.04) and 2.86 (1.45–5.98) parasites per 10 000 erythrocytes for males and females, respectively. There was not any support for a difference between sexes ($P_{\delta>\varphi} = 0.228$). However, these parasite load baseline values changed depending mainly on body size and season, and marginally on latitude (Table 2). Parasite load increased with increasing body size (Fig. 3), and differently between males and females ($P_{\delta<\varphi} = 0.771$). Parasite load decreased from south to north (Fig. 3), even without any difference between sexes ($P_{\delta<\varphi} = 0.405$). The cosinor component supported the occurrence of a seasonal pattern of variation given that amplitudes were not null in both males and females (Table 2). In this case, males seemed to have a slightly higher amplitude than females ($P_{\delta>\varphi} = 0.703$). Phases did not deviate from zero (Table 2) and differently between sexes ($P_{\delta<\varphi} = 0.746$), suggesting that seasonal patterns of variation were not synchronous, but reaching the peak during the cool months in both sexes (Fig. 3).

Discussion

Wild populations of vertebrates need to cope with numerous constraints to survive in their natural habitat, namely environmental conditions, food resources, inter and intraspecific competition for such resources and territory, avoidance of predators and strategies to capture prey, that are complex to isolate and define separately. Furthermore, the interaction with parasites happens to be another major stressor for the hosts and, as a result, their fitness can be affected significantly by the presence of such foreign organisms (Sindermann, 1987). Hence, the presence of persistent parasites in wild populations deserves a closer attention because their role and impact on such populations still need to be defined thoroughly in reptiles as it was shown for amphibians (Daversa *et al.*, 2017) and birds (van Rooyen *et al.*, 2013) that parasite infections can affect the ecology and behaviour of their hosts.

In this research, parasite prevalence and parasite load were found in the studied populations for both males and females with no intersexual difference. However, given that reptiles grow continuously throughout their life span, both models indicated that age (standardized SVL) plays a major role in parasite susceptibility as larger (i.e. older) individuals are parasitized more frequently and intensely than younger ones. Such observation is consistent with the behaviour and phenology of lizards as they are likely to share basking spots or shelters where the acquisition of parasites *via* haematophagous ectoparasites is more probable, whereas juveniles are often segregated in marginal spots to reduce competition with adults, where the contact with conspecifics and parasites is less frequent (Smallridge and Bull, 2000); moreover, adults could be more parasitized because they have made contact more frequently with parasites during their lifetime (Amo *et al.*, 2004).

Concerning the latitudinal pattern we observed, blood parasite prevalence and load are known to be significantly variable according to a broad variety of biotic and abiotic factors such as host phenology, activity and hormone levels, the ecology of vectors under different environmental conditions and in relation to the host's immune system, rainfall, temperature and anthropogenic factors as well (Schall and Marghoob, 1995; Schall and Pearson, 2000). In our study, we detected that parasite load in northern populations is lower, in accordance with some findings indicating

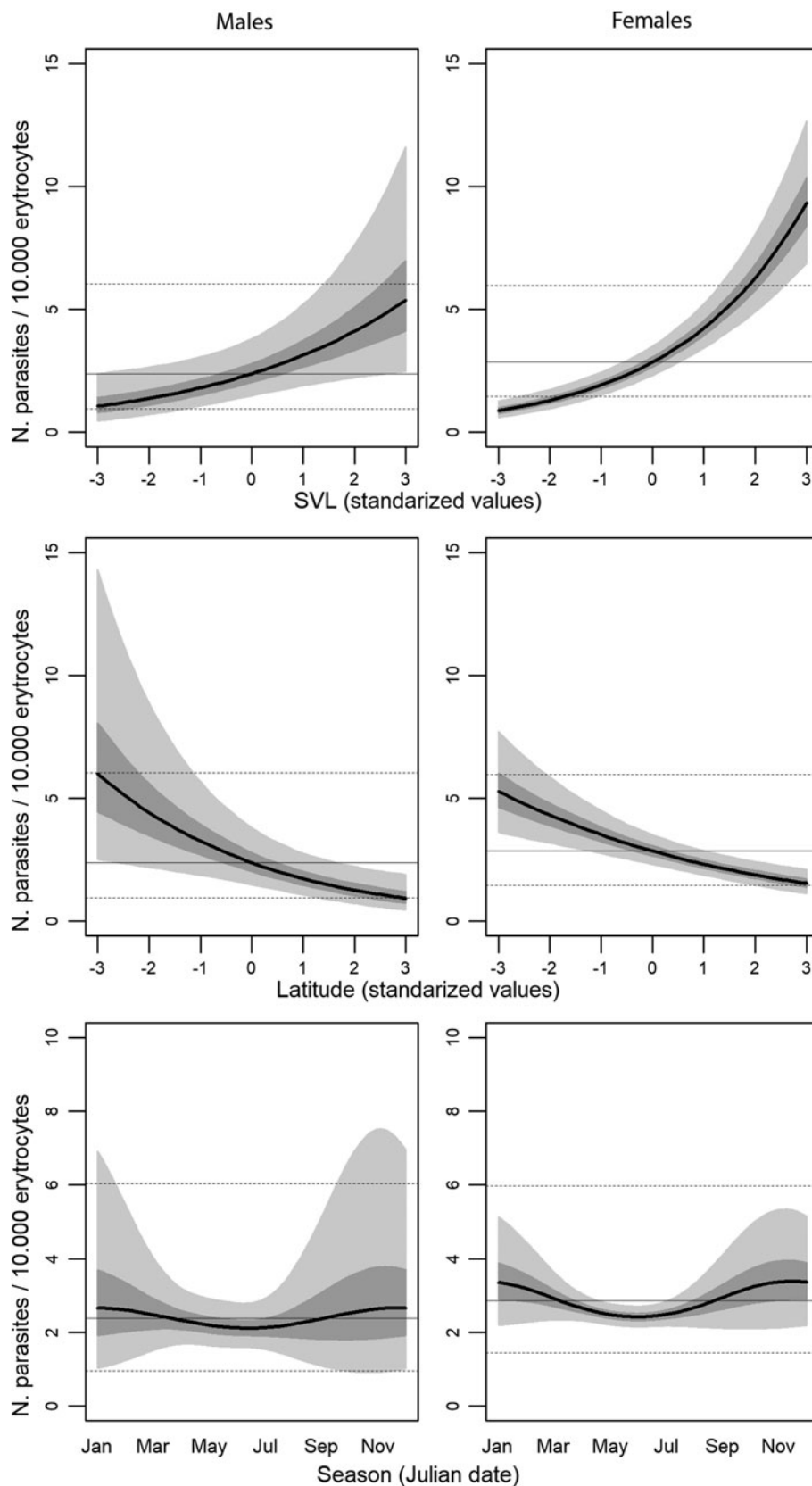


Fig. 3. Posterior probability distributions of the parasite loads (*N.* of parasites per 10 000 erythrocytes) in male and female common wall lizards in Italy in response to body size, latitude and seasons estimated by a Bayesian zero-inflated negative binomial (ZINB) model. Symbols and colours as in Fig. 2.

that parasites are more abundant in tropical regions (Møller, 1998). Such hypothesis is consistent with the common knowledge that reptiles, as ectotherms, tend to have longer seasonal activity periods in warmer environments thus extending the period during which they are potentially exposed to the acquisition of parasites through their vectors (Salkeld *et al.*, 2008). Mediterranean lizards in fact are generally inactive during cold months as their

activity period normally ranges from March to October, although northern populations are likely to be active for a shorter period, thus reducing exposure to the parasite.

In terms of seasonality, reptiles depend on environmental temperature for their physiological functions and parasitic infections can affect significantly behavioural thermoregulation (Schall and Sarni, 1987; Main and Bull, 2000). Therefore, in colder months,

reptiles are metabolically less efficient, and this can influence how they respond to parasitic infections. The studied lizards were parasitized more intensely in colder months rather than during the peak of the reproductive season, albeit parasite prevalence was less markedly variable than parasite load. Although our findings seem to be consistent with such hypothesis, it is necessary to point out that susceptibility to parasites (i) is influenced by how the immune system can respond to infections, (ii) can be influenced strongly by how frequently the host interacts with conspecifics and (iii) is often highly dependent on the biology and ecology of the vectors in relation to the hosts'. During the peak of the reproductive season (warmer months), the levels of sex hormones (testosterone and oestrogen), generally considered immunosuppressors (Salvador *et al.*, 1996; Olsson *et al.*, 2000), are higher than in the rest of the year (Tokarz *et al.*, 1998). Furthermore, testosterone promotes higher aggressivity and mobility in males, resulting in more frequent encounters with conspecifics for either male–male fights or copulation with females too (Amo *et al.*, 2005). Hence, under this perspective, it would be reasonable to assume that in warmer periods parasite susceptibility should reach its peak, which contrasts with what we observed.

In conclusion, this investigation (2008–2017) showed that haemosporidian infection patterns in *P. muralis* can vary throughout the year and according to both age and latitude as well. Nevertheless, given that knowledge about vectors and their biology is still lacking for the model species, the evidence we gathered is still preliminary and highlights the importance to investigate this host–parasite–vector system thoroughly to understand how lizards cope with infections. Additionally, it appears evidently necessary to assess to what extent different biotic and abiotic factors affect such host–parasite interaction, especially taking into consideration how the immune system responds to ongoing infections and how and to what extent parasite infections affect lizards in terms of survivorship and fitness.

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