



Impact of blood parasites on the behaviour of two congeneric wall lizards (genus *Podarcis*)

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Abstract

Modern studies have shown how parasites add extra complexity to ecosystems through their potential effects on hosts. Blood parasites are common in lizards and various studies have suggested varying degrees of negative effects on these hosts. In this study, we investigate effects of infection by blood parasites on the boldness and aggressiveness of male lizards of two sympatric species living in North Portugal: *Podarcis bocagei* and *Podarcis lusitanicus*, known to host blood parasites of two protozoan orders: Adeleorina and Eimeriorina (Apicomplexa). We used a mirror to quantify behavioural interactions of the lizards with their specular images, which did not identify any influence of parasite infection on either species. Boldness was evaluated through exploratory tests, with an identified trend for parasitized *P. lusitanicus* towards higher exploratory activity and exposure time. This was independent of the intensity of infection. No such effect was found for *P. bocagei*. The behavioural changes for infected *P. lusitanicus* appear to be in the direction of increasing light exposure by spending more time directly under the light source, thus suggesting a link with thermoregulation, although further experiments to clarify this hypothesis are required. These results highlight the importance of understanding individual parasite-host relationships, as they show that the same parasites can have different effects across even closely related species.

Significance statement

Parasites can affect their host in a variety of ways. We used mirror-interaction and exploratory tests to assess the effects of blood parasites in the aggressiveness and boldness behavioural traits of two sympatric lizard species: *Podarcis bocagei* and *Podarcis lusitanicus*. No effect of blood parasite infection in these two behavioural traits was identified on *Podarcis bocagei*. *Podarcis lusitanicus* tended to demonstrate a response to infection by Adeleorina with an increase in boldness and willingness to increase exposure times, despite low intensity of infection. Our results show how the same parasites can differently affect closely related host taxa from the same system, and how their effects can be significant even when intensities of infection are low.

Keywords Lacertid · Adeleorina · *Schellackia* · Aggressiveness · Boldness

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Introduction

Parasitic relationships are defined as having a prejudicial effect on hosts. Different co-evolutionary stories and specific characteristics of both the parasite and host taxa will, however, result in different forms and levels of impact. These relationships are of considerable importance for ecological and conservation purposes, yet precise knowledge on them is scarce, especially when it comes to lizards. The order Adeleorina (Apicomplexa), includes the most common blood parasites of lizards in the western Mediterranean (Megía-Palma et al. 2023a); these are heteroxenous parasites, with asexual reproduction in a lizard host and both asexual and sexual reproduction cycles in an invertebrate host (Svahn 1975), with the latter acting as vector (Haklová-Kočíková et al. 2014). The genus *Schellackia* (Apicomplexa: Eimeriorina), part of the haemococcidians group, is also relatively common in some lizard hosts across the Iberian Peninsula (Megía-Palma et al. 2018), and has its full life cycle in a lizard definitive host, with hematophagous mites as the mechanical transmitters (Megía-Palma et al. 2013). Despite their commonness, the relationships of both these parasites with their lizard hosts remain uncertain across the many lizard taxa they infect.

Studies on adeleorine blood parasites impact on lacertid lizard hosts have identified negative effects on the thermoregulatory behaviour (Scholnick et al. 2010; Horváth et al. 2020), on blood oxygenation and haematocrit (Oppliger et al. 1996), and on regenerative capabilities (Oppliger and Clobert 1997), and increased reproductive effort and risk-taking behaviour (Sorci et al. 1996; Horváth et al. 2016; Megía-Palma et al. 2016). However, other assessments find no apparent effects regarding host survival (Sorci et al. 1996), physiology (Huyghe et al. 2010; Damas-Moreira et al. 2022), or behaviour (Ekner-Grzyb et al. 2013; Damas-Moreira et al. 2014). Adeleorine blood parasites have also been associated with effects on non-lacertid lizards, such as a reduction in home range (Bouma et al. 2007). Correlational studies suggest lizard hosts have limited recoverability from adeleorine blood parasites infections (Sorci 1995; Megía-Palma et al. 2023b), and some authors hypothesize lizards could adapt their behavior to mitigate negative impacts on survival caused by these parasites (Sorci 1995; Oppliger et al. 1996; Sorci et al. 1996). The abovementioned second group of blood parasites, the haemococcidians, have been associated with reduction of nuptial coloration and components of the agonistic behaviour of lacertid lizards (Megía-Palma et al. 2022, 2024b), but contrary to Adeleorina, no effect on thermoregulation was identified so far (Megía-Palma et al. 2024b).

When tackling questions of parasite-host relationship on reptilian hosts, other issues arise that can complicate the

identification and understanding of the infection effects. In this sense, parasite-host relationships differ across different taxa of both parasite and lizard host (Megía-Palma et al. 2023b). For example, Paranjpe et al. (2014) and Scholnick et al. (2010) identify contrasting effects of *Plasmodium mexicanum* on the thermoregulation of *Uta stansburiana* and *Sceloporus occidentalis*. The presence of multiple parasites in the same system also adds an extra layer of complexity, with co-infections producing different effects than single infections of either parasite taxa involved (e.g. Marzal et al. 2017), although this aspect often remains poorly investigated (Paranjpe et al. 2014; Horváth et al. 2020). Furthermore, the lack of a resolved phylogeny and related taxonomy of Adeleorina parasites of reptiles (Megía-Palma et al. 2023a; Parejo-Pulido et al. 2023) and widespread reliance on a single, slow-evolving molecular marker (18S rRNA) to screen for adeleorine blood parasites means the parasite diversity present in these systems cannot be fully assessed and is likely to be underestimated (e.g., Megía-Palma et al. 2024a).

The genus *Podarcis* includes several species of small wall lizards native to Europe and North Africa, known to host both Adeleorina (*Hepatozoon* and *Karyolysus*) and Eimeriorina (*Schellackia* and *Lankesterella*) (Maia et al. 2014), the first often with remarkably high prevalence in some populations, and with no apparent effect on host health and behaviour traits associated with locomotion and escape (Oppliger et al. 2004; Damas-Moreira et al. 2014, 2022). Building on Sorci's (1995) hypothesis, the limited impact of parasite infection on the host lizards' health could be due to parasitized individuals adapting behavioural traits associated with energy costs and survival that mitigate the impact of carrying the parasite infection. Aggressiveness, as active fighting behaviour or signalling of the intention for such, is a trait for which higher expression comes with associated costs (Nelson 2005). *Podarcis* lizards may have developed mechanisms to reduce aggressiveness to avoid the unnecessary expense (López and Martín 2001; Carazo et al. 2008; Abalos et al. 2016), suggesting such adaptations could possibly be extended to deal with the costs of parasite-infection. Moreover, lizards of the genus *Podarcis* can respond and interact with their specular image, which is interpreted as a response towards a congeneric contestant because reptiles lack the cognitive development to recognize themselves in a mirror (Basile et al. 2022), thereby allowing for a simple and harmless way to test for intraspecific aggressiveness (Scali et al. 2019). Boldness, as the propensity of a lizard to expose itself to potentially dangerous situations, such as exploration of open spaces (Sloan Wilson et al. 1994), is also a trait for which a higher expression will result in a higher probability of involvement in situations that increase energy costs, such as escaping from a predator (López et al. 2005; Horváth et al. 2020), and therefore could also be modulated

to compensate for ongoing infection. In the case of parasite infection increasing the lizard's preferred body temperature or affecting its thermoregulation performance (Horváth et al. 2020). However, an apparent increased boldness could be associated with parasitized lizards seeking longer exposition to sunlight that enabled attaining a precise body temperature (Megía-Palma et al. 2020a; but see Horváth et al. 2020).

With this study, we further attempt to identify and understand the putative impact of infections of blood parasites in behavioural traits of two lizard species of the family Lacertidae, *Podarcis bocagei* and *Podarcis lusitanicus*, by testing for changes in the intraspecific aggressiveness and exploratory boldness of the males. We expect aggressiveness would be lower for parasitized lizards, under the hypothesis that less aggressive behaviour would save energy that can otherwise be allocated to alleviate energy costs associated with the infection. Regarding boldness, the same reducing effect and causes can be hypothesized. However, if parasitized lizards prefer longer basking periods due to possible effects of infection on their thermoregulation, we could instead observe an increase of boldness as they spend more time outside refuge and seek better light exposition.

Material and methods

Study system

We captured 39 adult males (22 *P. bocagei* and 17 *P. lusitanicus*) from a sympatric lizard community of two *Podarcis* species in northern Portugal (Moledo, 41.84, -8.87) during April 2022. This season corresponds to the onset of the mating season for these populations and is therefore a period of high expected agonistic performance (Carretero et al. 2006).

Animal maintenance

Lizards were housed in individual transparent terraria (23.0 × 15.5 × 17.0 cm) that included a movable ceramic shelter with removable top. They were kept under a light cycle of 9 h between 9:00 am and 6:00 pm with both regular and ultraviolet lamps. They were provided with food (*Tenebrio molitor* larvae) and water ad libitum. One larva was offered to each lizard every morning, except for those undergoing the behavioural trials the following day to avoid disturbing them and potentially altering their behaviour. The latter lizards were fed just after the trials. The lizards were acclimatized to the terraria for a week prior to the first experiment and weighed weekly to monitor their health status. The movable ceramic shelters allowed for transporting the lizard between the terraria and the test arenas without directly touching the animal —by moving the whole shelter

with the lizard inside— to reduce any potential modification of their natural behaviour.

Experiments

The test arenas were comprised of rectangular (30.0 × 50.0 cm) opaque terraria made from acrylic plates, each with a removable central divider, an overhanging 46 W lightbulb at 65.0 cm height, and a closed-circuit television camera. Experiments in the test arenas were performed between 12:45 pm and 16:30 pm (within lizard activity time in the field), with the lights over them being turned on at least 30 min beforehand to guarantee they would reach a stable temperature. Test arenas were cleaned and disinfected with ethanol prior to and following every individual experiment. Air temperature on the area of the test arenas was monitored frequently and kept at around 20 °C for the duration of the experiments.

Two types of experiments were performed for every individual: an exploratory behaviour (EB) experiment, in which the movable shelter with lizard was placed on one of the sides of an unobstructed test arena and the behaviour of the lizard recorded for the 30 min immediately following placement, and a mirror interaction (MI) experiment. In this second experiment, the arena started with a central divider in place and a square mirror with 15.0 cm sides at a 95 degrees inclination to the ground for the reflective side on one of the halves, the movable shelter with lizard was placed on the unobstructed half of the arena, the topside of the shelter removed, and 15 min of acclimatization given before the central divider was removed and the behaviour of the lizard recorded for 15 min (Fig. 1A). The EB experiments were performed first, followed by two replicates for the MI experiments. EB and MI experiments were conducted with a 6 to 8 days interval for each lizard and the MI replicates with a 4 to 5 days interval, allowing for recovery from any test-induced stress and for the tested individual to be able to receive at least one meal while still respecting the decided feeding pattern.

Following all behaviour experiments, the snout to vent length (SVL) and body mass of every lizard was registered, and a blood smear prepared with the blood from a tail tip cut. SVL was measured with a digital calliper with two decimals of the millimetre, and body mass with Video recordings of the EB experiments were analysed by registering the position of the lizard within the arena every 5 s, within one of the following 6 zones (Fig. 1B): (1) inside refuge, (2) partially inside refuge (when a part of the lizard equal or larger to head size, excluding tail, was outside the refuge), (3) corners, (4) sidelines, (5) exposed centre but close to refuge, and (6) exposed centre. These locations are ordered from least to most exposed, considering the visual cover a similar situation would provide in the wild. Eight

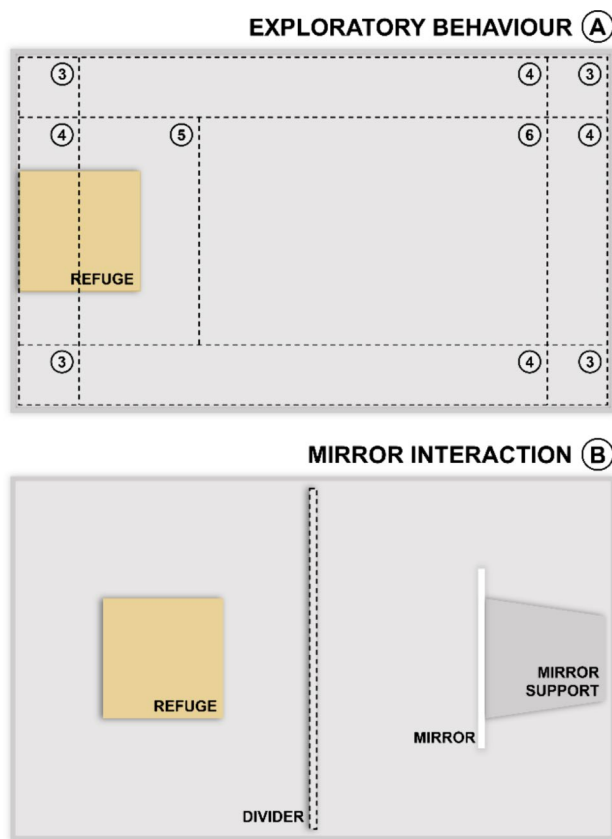


Fig. 1 Schematic of the test arenas as used for the EB (A) and MI (B) experiments. Dashed lines on A represent the limits of the outside zones considered for the experiment (zones 1 and 2 missing due to being inside the refuge). Dashed lines on B indicate the initial position of the central divider before being removed

behavioural variables (Table 1) were considered for analysing the behaviour of each lizard: (1) time to first peek, (2) time to first outing, (3) time outside, (4) time exposed, (5) percentage of time exposed, (6) number of exposures, (7) mean most favoured area, and (8) mode most favoured area.

Video recordings of the MI experiments were analysed by registering the interaction type of the lizard towards the mirror at every second, following five categories of interaction: (1) ignoring mirror, (2) staring at mirror (facing the mirror at a distance less than SVL but more than head-length), (3) approached mirror (faced mirror at a distance less than head-length), (4) non-aggressive interaction (gently touching the mirror with snout or licking the mirror), (5) aggressive interaction (clawing at the mirror or running and ramming onto it). Six behavioural variables (Table 1) were used for analysing the behaviour of each lizard: (1) interaction time (2) interaction instances, (3) active interaction time, (4) active interaction instances, (5) highest category of interaction, and (6) mode category of interaction.

Blood smears were analysed on a light microscope at an amplification of 400× and 2500 erythrocytes per sample were screened for the presence of blood parasites. Infection status was determined by the observation of at least 1 parasite in the sample and intensity of infection as the number of infected erythrocytes per 2500 erythrocytes.

To minimize observer bias, blinded methods were used during the experiments and for the recording of all behavioural and infection data.

Table 1 Explanation of behavioural variables considered for each of the experiments

Exploratory Behaviour (EB)	Description
Time to 1st peek	Time since beginning of experiment until part of the lizard is visible outside the shelter. Visible part excluding tail measures less than half SVL
Time to 1st outing	Time since beginning of experiment until most of the lizard is visible outside the shelter. Visible part excluding tail measures more than half SVL
Time outside	Time spent with most of the lizard (visible part excluding tail is more than half SVL) outside shelter
Time exposed	Time spent on zone 6 (centre of the arena)
Percentage of time exposed	Time spent on zone 6 (centre of the arena) as the percentage of time outside
Number of exposures	Number of separate instances the lizard entered zone 6 (centre of the arena)
Mean most favoured zone	Mean zone where the lizard spent the most time during the experiment
Mode most favoured zone	Mode zone where the lizard spent the most time during the experiment
Mirror Interaction (MI)	Description
Interaction time	Time spent interacting with mirror (average between replicates)
Interaction instances	Number of separate instances of interaction with the mirror (average between replicates)
Active interaction time	Time spent interacting with mirror (average between replicates), excluding time staring (category 2 interaction)
Active interaction instances	Number of separate instances of interaction with the mirror (average between replicates), excluding staring (category 2 interaction)
Highest category of interaction	Highest type of interaction exhibited amongst replicates
Mode category of interaction	Most common type of interaction exhibited during amongst replicates

Data analysis

The dataset included the infection status and intensity of infection. We evaluated body condition (BC) as the residuals from the linear regression of the decimal logarithm of body mass on the decimal logarithm of SVL (Warner et al. 2016). To exclude confounding dependencies and correlations between variables and groups, we tested for independence between species and infection status using a Chi-squared test and used Spearman's rank correlation to identify correlations for species with SVL and BC, infection status with SVL and BC, and intensity of infection with species, SVL, and BC.

Behavioural data from 33 lizards (22 *P. bocagei* and 11 *P. lusitanicus*) was used for the EB analyses, and from all the 39 lizards for MI analyses, although for 2 lizards only data from 1 replicate was used. The removed lizard data was due to external interference that invalidated those trials. We performed a principal component analysis (PCA, no factors, Varimax rotation; Budaev 2010) on the datasets for EB and MI separately (Horváth et al. 2016). For the MI analyses, the mean value of each behaviour variable from the two replicates was used on the PCA. The three resulting PCs (one for EB and two for MI, see Results) were used as response variables in further analyses. Using R software v4.4.0, we built linear models to test the effects of different sets and interactions of our variables (Table S3) on the behavioural PCs and used an information criterion corrected for small sample sizes to find the most informative models (i.e. AICc; Bedrick and Tsai 1994). Models with AICc scores differing less than 2.0 were considered equally likely, after which preference was given to models including variable interactions, as these are penalized by Akaike's criterion (Burnham and Anderson 2004). We tested the normality of the residual distribution of the most informative models with Shapiro–Wilk normality test and Q-Q plots, and their kurtosis and skewness with Anscombe–Glynn test and D'Agostino's K^2 test (package: *moments*; Komsta and Novomestky 2015). We also performed a likelihood-ratio test on them (package: *lmodel2*; Zeileis and Hothorn 2002). For models that passed all previous tests, we performed an ANOVA (package: *car*; Fox and Weisberg 2019) to identify significant relationships with the behavioural PCs (Table 2). We cross-validated the effects with a random k split of 3 (package: *DAAG*; Maindonald and Braun 2020).

Although we acknowledge small sample size of *Schellackia* was too small to obtain robust results, we attempted to assess for the possibility of effects of *Schellackia* infection or co-infections with *Adeleorina*. We tested an extra model for each of the PCs, including as explanatory variables the interactions between host species and the infection status of each parasite.

Table 2 ANOVA Tables for the most informative linear model after application of the Akaike's criterion for each behavioural PC (EB = Exploratory behaviour; MI = mirror interaction test). An asterisk (*) on the rightmost column represents a significant interaction ($\alpha < 0.05$), and a dot (.) a tendency ($0.1 < p < 0.05$)

PC-EB (exploratory behaviour variables)

	sum sq	df	F	p	
(Intercept)	1.5747	1	2.0671	0.161	
Species	9.3859	1	12.3211	0.001	*
Adeleorina infection status	0.0373	1	0.049	0.826	
Species: Adeleorina infection status	3.1018	1	4.0718	0.053	
Residuals	22.0916	29			

PC-MI-1 (mirror interaction variables concerning time and number of interactions)

	sum sq	df	F	p	
(Intercept)	0.4308	1	2.8524	0.100	
Species	0.4886	1	3.2354	0.080	
SVL	1.2729	1	8.4282	0.006	*
Residuals	5.4369	36			

PC-MI-2 (mirror interaction variables concerning category of interactions)

	sum sq	df	F	p	
(Intercept)	0.108	1	0.1055	0.747	
Species	0.247	1	0.242	0.626	
Residuals	37.753	37			

Results

Seven out of 22 *P. bocagei* (32%) and 7 out of 17 *P. lusitanicus* (41%) were infected with blood parasites. Intensity of infection with *Adeleorina* was generally low (average of 0.15% infected erythrocytes), but higher for *P. lusitanicus* (0.28%, with individual values under 0.23% except for one individual with 0.94%) than *P. bocagei* (0.12%), although the difference was non-significant ($\rho = 0.266$, $p = 0.403$). Infections with genus *Schellackia* were detected for both host species, with 1 individual of each species carrying only *Schellackia* parasites and 1 *P. bocagei* and 2 *P. lusitanicus* having mixed infections with *Adeleorina*; all instances of infection with *Schellackia* were of very low intensity (under 0.07%, less than 2 parasites per 2500 erythrocytes). No interactions were found between species, SVL, or BC with either infection status or intensity for any of the parasites.

For the EB experiments, the PCA produced a single principal component (PC) that was significantly correlated with all behavioural exploratory traits except time to first peak, Which correlation of 0.67 is below the standard threshold of 0.70 (Table S1). The most informative model included as important explanatory factor the interaction between host

species and Adeleorina infection status. A significant difference between the species was identified ($F(1)=12.321$, $p=0.001$), with *P. lusitanicus* having higher PC EB scores, corresponding to more time until first outing, less time spent outside, lower percentage of time outside spent in the exposed centre, and preference for less exposed areas. Although a significant correlation was not achieved, a significant trend was observed, that remained in the model after cross-validation, for the interaction between host species and Adeleorina infection status ($F(1)=4.072$, $p=0.053$), indicating *P. lusitanicus* infected with adeleorine blood parasites took less time until first outing, spent more time outside and a higher percentage of time outside in the exposed centre, and had a preference for more exposed areas than uninfected individuals of the same species (Fig. 2).

For the MI experiments, PCA produced two principal components (Table S2): PC-MI-1, including the behaviour variables related with interaction time and instances (MI variables 1–4, Table 1), and PC-MI-2 with the category of interaction variables (MI variables 5–6, Table 1). The most informative model for the PC-MI-1 included as explanatory variables host species and SVL, while for PC-MI-2 it included only host species. Models for PC-MI-1 also required a decimal logarithmic transformation to best fit a normal residual distribution. For this, a random value of 2 units was added to every PC-MI-1 score to avoid errors during the log-transformation of this component. A significant effect was found between SVL and PC-MI-1 ($F(1)=8.428$, $p=0.006$), with larger lizards having higher PC-MI-1 scores, and an almost significant trend was found for species ($F(1)=3.235$, $p=0.080$), with *P. lusitanicus* exhibiting lower PC-MI-1 scores. For PC-MI-2, the Omnibus test was not significant, meaning a random null model could not be rejected and indicating none of the explanatory variables could actually explain the observed variation of the behavioural traits summarized in this PC. These results indicate

that, although *P. bocagei* appears to be inherently more interactive, SVL was the main driver of this effect, with larger lizards interacting more frequently and spending more time during them, although these interactions were not necessarily more (or less) intense than those of smaller lizards. The observed significant interaction and trend were maintained after cross-validation.

Models including the infection status of *Schellackia* did not identify any effect of the presence of this parasite on the behavioural PCs. For the EB experiments, however, when plotting the effects of the interactions between host species and infection status of each parasite, the single *P. lusitanicus* individual with a mixed infection appears at the maximum of the distribution for Adeleorina-infected lizards, falling within the middle 50% distribution of Adeleorina-uninfected individuals (Fig. 3).

Discussion

Mirror interaction experiments showed no significant relationship between parasite infection and intraspecific interaction behaviour, suggesting Adeleorina infection plays no role in agonistic interactions between males of the same species for the studied taxa, contrary to what has been observed with intestinal coccidian parasites in small lizards other than Lacertidae (Megía-Palma et al. 2024b). Behavioural differences here seem to be dictated mostly by SVL, with larger lizards interacting more often and for more time (López and Martín 2001; Sacchi et al. 2009). Interestingly the intensity of the interactions was not related with either factor, indicating that although more interactive, larger individuals are not necessarily more aggressive than smaller individuals. *Podarcis* lizards are known to modulate their aggressiveness through chemical recognition and assessment of size difference of rivals (López and Martín 2001 and 2002), both of which

Fig. 2 Effect plot of the interaction between species and Adeleorina infection status on PC-EB (obtained through PCA of the behaviour variables considered for the Exploratory Behaviour experiments). Boxes indicate the interquartile range (IQR), middle line depicts the median value, and whiskers extend to the minimum and maximum values within $1.5 \times \text{IQR}$. Higher values of PC-EB correspond to a less exploratory and bold behaviour. A significant effect was identified for the lizard species, and a trend was identified for the interaction between species and infection status

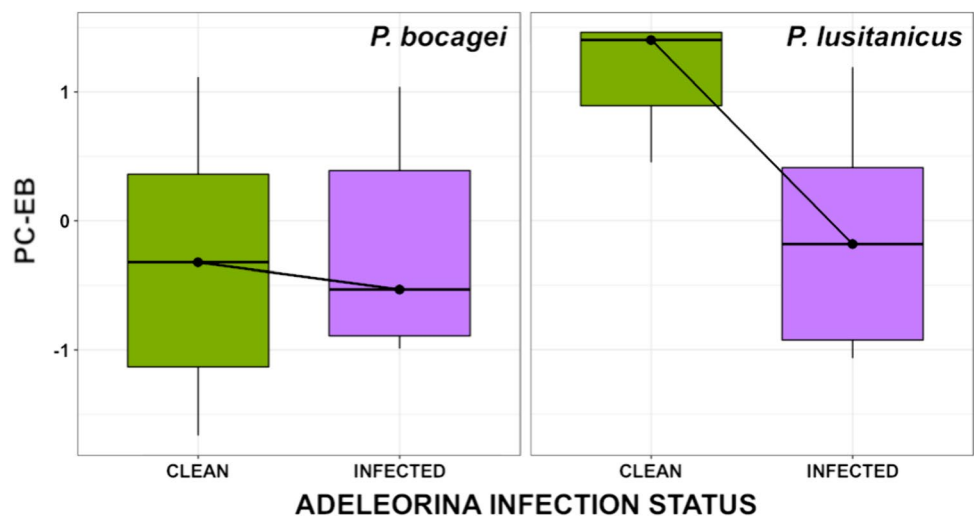
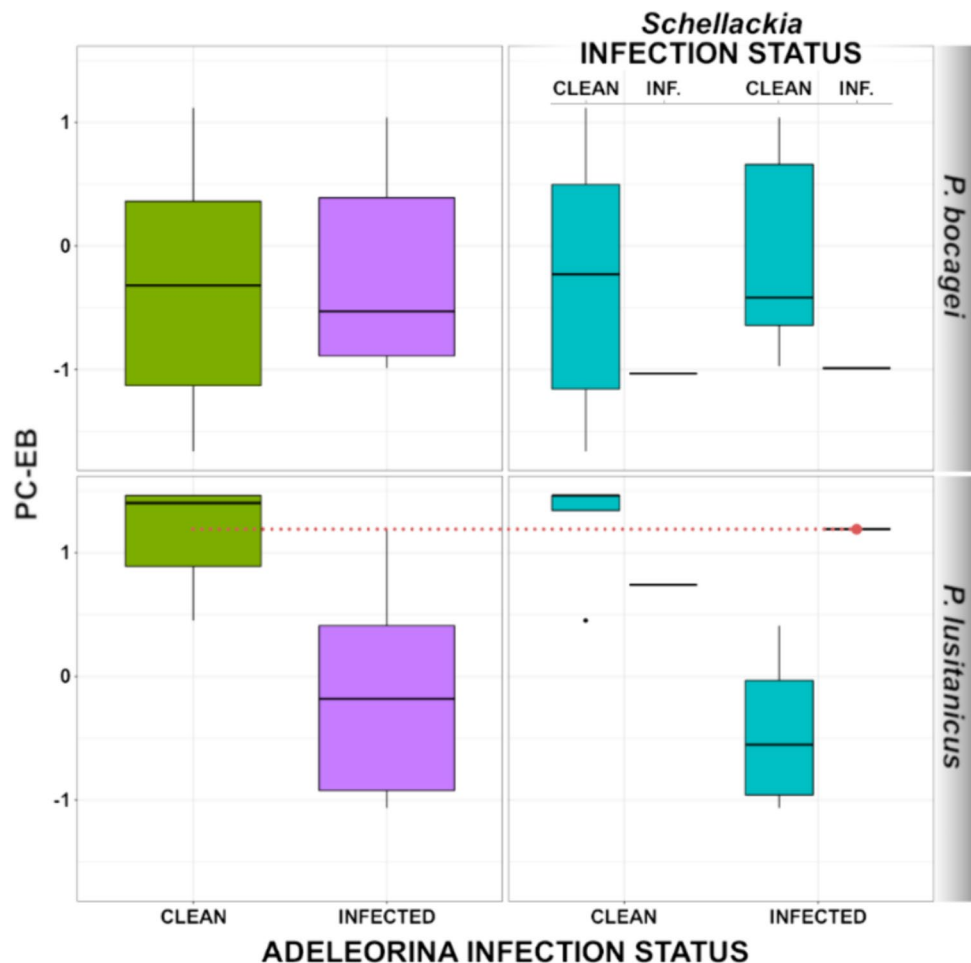


Fig. 3 Effect plots of the interaction between species and Adeleorina infection status (left) and between species with both Adeleorina and *Schellackia* infection status (right) on PC-EB (obtained through PCA of the behaviour variables considered for the Exploratory Behaviour experiments). Boxes indicate the interquartile range (IQR), middle line depicts the median value, whiskers extend to the minimum and maximum values within $1.5 \times \text{IQR}$, and the isolated dot marks an outlier. The single individual of *P. lusitanicus* infected with both parasites had the highest PC-EB score of the individuals infected with Adeleorina, falling within central 50% distribution of the clean individuals for this parasite taxa (red dotted line)



were null in our experiments and might explain the random distribution of results for intensity of interaction.

Exploratory behaviour experiments suggest an intrinsic difference between the two species, with *P. bocagei* appearing bolder when exploring new territories. Intrinsic differences in exploratory behaviour, neophobia, and boldness have already been observed for two other *Podarcis* species (*P. siculus* and *P. virescens*), with boldness being especially consistent within each species (Damas-Moreira et al. 2019). Together with our results, this might suggest the existence of a spectrum of boldness across the various species of the genus, likely specific to the evolutionary history of each species (Sih et al. 2012).

While not significant, the interaction between species and Adeleorina infection status appeared as an almost significant factor, indicating a trend for parasitised *P. lusitanicus* to display bolder and more exploratory behaviours: taking less time to leave the refuge, spending more time in the centre of the arena, and favouring more exposed zones of the arena. The fact that this trend was consistent across smaller random datasets during the cross-validation analysis strongly suggests that there may be an effect of Adeleorina infection

on *P. lusitanicus* behaviour, and that significance was not achieved in our study likely due to lack of enough statistical power due to the reduced sample size. We interpret that the observed bolder behaviour can be connected to a more eager search for a basking spot, as seen by the longer period in the exposed centre (right under the light bulb). This could suggest Adeleorina infection may not directly affect the behavioural trait of boldness, but rather the host's thermoregulation requirements (e.g., Megía-Palma et al. 2020a, b). Current evidence from lacertids infected with Adeleorina suggests this could be caused by a reduction in thermoregulatory precision (Horváth et al. 2020; but see also Megía-Palma et al. 2020a), although an increase in preferred body temperature has also been observed for malarial infection in other lizards (Scholnick et al. 2010). Given the taxonomical proximity with the system studied by Horváth et al. (2020) (same genus of parasite in a different lacertid species), there is a strong case for a reduction in thermoregulatory precision, although, we do not have the data to rule out the possibility of an increase in the preferred body temperature. Furthermore, Paranjpe et al. (2014) have studied a system in taxonomic proximity with that of

Scholnick et al. (2010) (*Plasmodium* sp. infecting lizards from the family *Phrynosomatidae*) with opposite results: a decrease in preferred body temperature. These studies demonstrate how parasitaemia effects can differ fundamentally between parasite-host pairs even between similar taxa, as also observed between the two *Podarcis* species, and further stresses the need for additional experiments to elucidate the relationship between parasitaemia and preferred body temperature within these systems. When studying the effects of Adeleorina in lacertids, Horváth et al. (2016, 2020) identified a positive correlation between boldness and intensity of infection, with boldness increasing gradually with the intensity of infection. While our results also identify an increase in boldness caused by infection, in our study infection status is the key factor for this behavioural change, with the presence of the parasite producing an abrupt change in boldness, rather than a gradual increase, despite the overall very low intensity of infection. Again, this demonstrates the difficulties of extrapolating results from one system to another, even when examining similar host-parasite models.

The physical traits SVL and BC, statistically independent of each other, did not seem to have any correlation with parasite infection status (SVL $\rho=0.276$, $p=0.088$; BC $\rho=0.074$, $p=0.654$) or intensity (SVL $\rho=0.287$, $p=0.365$; BC $\rho=0.466$, $p=0.127$). Extensive samplings of these populations by Maia (2015), between 2011 and 2013, identified a significant positive correlation between SVL and infection status for both species, however, this was not observed in our sampling. While a correlation between host lacertids' SVL and parasite infection status has been observed in several cases, leading to the hypothesis that larger and therefore older individuals have had more chances of infection during their lifetime (Amo et al. 2004, 2005a), others have not recovered this same correlation (Garrido and Pérez-Mellado 2013; Damas-Moreira et al. 2014), highlighting the complexity of such relationships. Other studies have identified positive relationships between BC and infection intensity (Amo et al. 2005b, 2006; Damas-Moreira et al. 2014), suggesting adult lizards with good body condition are better able to survive high intensity infection, but again, we did not recover such relationships. The relationships of SVL and BC with infection status and intensity could also differ between males and females, influencing the pattern observed in our all-male sampling, although this conclusion would require further assessment.

We did not identify effects of the second blood parasite observed, genus *Schellackia*, again the lack of statistical power due this time to the low representation of this parasite in the sample (3 *P. lusitanicus* and 2 *P. bocagei*), leaving open to question possible effects of this blood parasites on their host and interactions with Adeleorina for mixed infections (Megía-Palma et al. 2022). This lower prevalence is not surprising, however, as parasites of the *Schellackia* genus

may have co-evolved with their hosts (Megía-Palma et al. 2018, although see also Er-Rguibi et al. 2023), which would imply a more adapted immune-system control of the host towards infections by this parasite, leading to lower prevalence and intensity of infection (Megía-Palma et al. 2023b).

While statistical results of this study provide some support for a putative relationship of Adeleorina infection with the exploratory behaviour of adult males of *P. lusitanicus*, various questions remain regarding this parasite-host relationship. Temperature measurements of basking lizards would be important to confirm and clarify the effect of infection on host thermoregulation, and whatever the mechanism affecting thermoregulation, it would be unexpected if this increased boldness came without a survival trade-off, as spending more time basking would also increase exposure to risk factors (Horváth et al. 2020; Smolinský et al. 2022). Parasite infection effects on females or juveniles and subadults of both sexes could also vary from those on adult males (Damas-Moreira et al. 2014), directly affecting population dynamics of both host and parasite. Boldness has also been associated with flight-initiation and escape distances in lizards, and blood parasite infection on these has been shown to have different effects across species of the studied genus, with *P. lilfordi* having longer flight-initiation and shorter escape distances (Garrido et al. 2015) while *P. vaucheri* remained unaffected (Damas-Moreira et al. 2014). This further reinforces the evidence from our data that even closely related host species can react differently to the same parasite, making it also of interest to test these behaviours in *P. lusitanicus*.

It would generally be expected that closely related sympatric hosts, like those from this model system, would share their parasite communities and be similarly affected by them (Poulin et al. 2011 but see Dajčman et al. 2022; Žagar et al. 2022); however, this does not seem to be the case. The observed differences therefore raise questions regarding Adeleorina diversity and host-specificity. While Maia (2015) has identified the Adeleorina infecting the two populations from this study as two haplotypes from the same lineage and shared between both host species, other studies have shown remarkable diversity between morphologically very similar adeleorine blood parasites (Tomé et al. 2019), and suggested the existence of host-specific lineages (Maia et al. 2012; Megía-Palma et al. 2023a). Nonetheless, the widely used 18S rRNA gene fails to differentiate many cryptic Adeleorina lineages (Maia et al. 2012; Er-Rguibi et al. 2023), so although current evidence is that the same species of blood parasite infects both hosts, this has not been fully confirmed. The existence of unidentified host-specific lineages in the Moledo system could be an explanation for the difference in effect of parasite infection and even parasitaemia status between the two host species but can only be assessed through the development and deployment of additional,

more variable molecular markers. One other option for the different effect of *Adeleorina* on the studied *Podarcis* species could be the currently shared lineage was originally host specific to one of the species, producing different degrees of co-adaptation (Megía-Palma et al. 2018; cf. Megía-Palma et al. 2023a) with the parasite for each host species and thus resulting in different responses to the infection (Megía-Palma et al. 2023b).

Concerning conservation, such a change in *P. lusitanicus* behaviour stemming from a low intensity of parasite infection (average of 0.28% infected erythrocytes) suggests that, if infected lizards' survival is negatively affected by these changes, the host species can be very vulnerable to fluctuations in parasite prevalence, highlighting the need for further knowledge on this parasite-host relationship and parasite-host relationships in general.

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Data availability All metric data measured, generated, or analysed during this study are included in this published article and its supplementary information files. Imaging data of the videos recorded during experimentation can be made available on request to the corresponding author.

Declarations

Ethics approval All the organisms involved in this study were captured, handled, retained, and released with the authorization of Instituto da Conservação da Natureza e das Florestas (ICNF), Portugal, under the licenses 552–553/2022/CAPT e 09/2022/DET. All applicable international, national, and institutional guidelines for the use of animals were followed.

Conflict of interests The authors have no competing interests to declare that are relevant to the content of this article.

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