

1 Blood-parasite infection intensity covaries with risk-taking personality in male

2 Carpetan rock lizards (*Iberolacerta cyreni*)

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32

33 **Abstract**

34

35 Identifying evolutionary and developmental mechanisms underlying consistent between-  
36 individual differences in behaviour is the main goal in ‘animal personality studies’. Here, we  
37 explored if activity and risk-taking varied consistently between individuals, and correlated to  
38 various – potentially fitness-linked – male traits in Carpetan rock lizards (*Iberolacerta*  
39 *cyreni*). Lizards showed significant consistency within both behaviours, implying the  
40 presence of activity and risk-taking personalities. However, there were no correlation between  
41 activity and risk-taking, neither on the between-, nor on the within-individual levels, implying  
42 the absence of a behavioural syndrome. We found a strong link between the intensity of  
43 blood-parasite (*Haemogregarinidae*) infection and risk-taking: lizards with higher infection  
44 intensity took more risk. While we cannot distinguish cause from causative in the parasite  
45 intensity – risk-taking correlation, our results are in line with the asset protection hypothesis  
46 predicting that individuals with lower future reproductive value should focus on the current  
47 reproductive event and take higher risk.

48

49 Keywords: animal personality, behavioural syndrome, behavioural type, individual quality,  
50 lizard, temperament

51

52 **Introduction**

53

54 Behavioural consistency within (animal personality) and across (behavioural syndrome)  
55 different behaviours have become well-studied during the last decade and they proved rather  
56 common among a wide range of animal taxa (Smith & Blumstein 2008; Garamszegi et al.  
57 2012). In general, behavioural consistency limits individual behavioural variation including  
58 adaptive plasticity, which seems intuitively maladaptive (Sih et al. 2004a, b, 2012; Bell 2005,  
59 2007; Sih & Bell 2008; Sih & Del Giudice 2012). Since behaviour is one of the most plastic  
60 quantitative traits of animals (West-Eberhard 2003), the most important question emerging is:  
61 why behavioural consistency exist in the first place? The importance of genetic and  
62 physiological constraints (proximal theory) alongside adaptive mechanisms (ultimate theory)  
63 are well cited in personality research (Koolhaas et al. 2007, Sih & Bell 2008). Recently,  
64 several studies aimed to establishing new conceptual frameworks based on life-history  
65 differences or combining proximate and ultimate mechanisms viewing behavioural  
66 personality from an adaptive perspective (see Pace of Life Syndromes, Réale et al. 2010 and  
67 behaviour-state feedbacks, Sih & Bell 2008; Dingemanse & Wolf, 2010; Sih et al. 2015).  
68 Besides of adaptive explanations for the existence of behavioural consistency, many scholars  
69 draw attention to the important role of ecological factors shaping behavioural variation within  
70 populations (Bell & Sih 2007; Cote et al. 2008; Sih et al. 2015).

71

72 One crucial step towards understanding the mechanisms behind behavioural variation in the  
73 wild is to link behaviour to individual quality, however, this is not straightforward in most  
74 cases, mainly because of the controversy around the definition and measurement of  
75 ‘individual quality’. Since individual quality can only be approached through fitness, a viable  
76 and relatively easy solution to this problem can be focussing on individual traits that are

77 linked to fitness (Wilson & Nussey 2010; Bergeron et al. 2011; Bajer et al. 2015). Importance  
78 of parasitism in changing behaviour of hosts has long been known and their role in the  
79 evolution of animal personalities and behavioural syndromes as potential selective agents  
80 gained much attention lately (Barber & Dingemanse 2010, Kortet et al. 2010; Hammond-  
81 Tooke et al. 2012; Poulin 2013; García-Longoria et al. 2014). For instance, parasites can act  
82 directly creating behavioural differences within and between populations (e.g. reducing  
83 exposure to parasites), affecting the emergence of behavioural consistency (Barber &  
84 Dingemanse 2010). Alternatively, since infection impacts hosts' condition, energy stores,  
85 reproductive value and vitality in a negative way, parasitism can trigger behavioural changes  
86 indirectly by altering the state of an individual (Barber & Dingemanse 2010; Kortet et al.  
87 2010; Sih et al. 2015). Hence, using parasite infection-rate as a fitness proxy gives us the  
88 possibility to establish relationships between fitness and individual behaviour, ultimately  
89 leading to hypotheses about the behaviour – individual quality link we were looking for.

90

91 Negative effects of blood parasite infection on fitness are known from many reptile species  
92 (Amo et al. 2004, 2005; García-Ramírez et al. 2005; Garrido et al. 2014, Molnár et al. 2013).  
93 In Carpetan rock lizards (*Iberolacerta cyreni*), it is known that parasite load is an indicator of  
94 individual quality since the rate of blood-parasite (*Haemogregarinidae*) infection was found  
95 to be positively correlated with the body condition in the males of this species (Amo et al.  
96 2004). Besides of this, *I. cyreni* has become one of the most studied reptiles in the past 15  
97 years and it is known that several individual traits of males play an important role in both  
98 intra- and intersexual selection of the species. For instance, number and asymmetry of  
99 femoral pores of male Carpetan rock lizards provide information about the individuals'  
100 genetic quality, fighting ability and condition ( Martín & López 2000, 2006; López et al.  
101 2002, 2003, 2006). In addition, head and body size are both known to affect dominance in

102 reptiles, moreover, the length of limbs is also a potential fitness proxy due to its link to sprint  
103 speed (Bauwens et al. 1995; Gvozdik & Van Damme 2003; Roff 1992). Therefore, *I. cyreni*  
104 provides an excellent model to link behaviour to individual quality. Further, behavioural  
105 consistency research on reptiles is negligible compared to mammals, birds, or fishes (Smith &  
106 Blumstein 2008; Garamszegi et al. 2012, 2013), thus using a lizard as model can be beneficial  
107 to broaden the taxonomical sample in this area.

108

109 In this paper, we studied whether (i) wild-caught male *I. cyreni* during the mating season  
110 showed behavioural consistency and, assuming that individual behavioural variation is  
111 present, (ii) individual behaviour covaried with blood parasite load and other potentially  
112 fitness-related traits. To this end, we performed behavioural experiments under semi-natural  
113 conditions to assess activity and risk-taking of reproductive, adult male lizards. We followed  
114 a repeated-measure design in which we assayed each individual 5-6 times over a 13 day  
115 period. Since haemogregarines has negative, but not directly lethal effects on their lizard hosts  
116 (Oppliger et al. 1996; Veiga et al. 1998; O'Dwyer et al. 2004; Bouma et al. 2007) parasite –  
117 behavioural links are expected (Barber & Dingemanse 2010, Kortet et al. 2010). However,  
118 considering the correlative nature of our study, separating cause and effect in our findings is  
119 not straightforward. For instance, individuals with higher behavioural activity may encounter  
120 parasites more frequently (García-Longoria et al. 2014) or individuals with higher parasite  
121 load and thus lower future reproductive value might take more risks following the asset  
122 protection principle (Clark 1994). Besides the intensity of blood-parasite infection, we also  
123 included a number of other potentially fitness-linked traits in our study to seek for other signs  
124 of behaviour – individual quality links.

125

126 **Methods**

127

128 *Study animals*

129

130 We noosed adult males (N = 24) with intact or well regenerated tails during the mating season  
131 (early June, 2013) at ‘Puerto de Navacerrada’ pass (Sierra de Guadarrama, Madrid Prov.,  
132 Spain, 1900 m asl approximately). During this season this habitat has relatively dense  
133 vegetation (e.g. shrubs and grass meadows) and there is also high cover of granite rock-  
134 boulders (Martín & Salvador 1997; Martín & López 2013). Before housing animals, we  
135 measured various morphological and colour traits and took blood samples to quantify the  
136 level of blood-parasite infection. The males were housed outdoors individually in grey,  
137 opaque boxes (56.5 cm × 36.5 cm × 31.4 cm; length, width, height, respectively) at ‘El  
138 Ventorrillo’ field station, 5 km from the capture site. In the boxes we used a layer of coconut  
139 fibres as substrate and hollow bricks were provided as shelters. Shelters were removed from  
140 the boxes every morning and replaced every evening to provide night-refuge but also to avoid  
141 the problems imposed by individuals being in shelter during movement activity assays. This  
142 procedure never caused any visible stress lasting longer than a few seconds. Between assays,  
143 the boxes were covered with a fine metal mesh to protect the lizards from bird predators.  
144 Before the onset of experiment, the animals were allowed to habituate to their new  
145 environment for 10 days. During this time, and later during the experiment, water and food  
146 (house crickets, *Acheta domestica*; Turkestan cockroaches, *Blatta lateralis*) were provided  
147 every afternoon (after 14.00 pm (UTC + 02.00), when the behavioural assays ended) *ad*  
148 *libitum*. We note that uneaten food was removed at the evening, so that food was only  
149 available for ca. 5 hours in excess every afternoon. Hence, lizards during the time of the  
150 behavioural assays (see below) were already foraging. At the end of the experiment, lizards  
151 were released at their original capture point.

152

153 *Individual traits*

154

155 Individual traits were measured at the ‘El Ventorrillo’ Field Station before transporting  
156 individuals to their home cages. Snout-vent length (SVL), head size (represented by head-  
157 length, head-width, jaw-width and head-height) and the length of the limbs were measured  
158 using a digital calliper to the nearest 0.01 mm. To characterise head size, we ran Principal  
159 Component Analysis on the head measures. We got a single principal component with strong  
160 positive loadings (proportion of variation explained = 66%; factor loadings > 0.67) and we  
161 used it as our head size variable. To characterise limb length, we measured the left and right  
162 femurs and tibias, and then summed the mean femur and tibia lengths for every individual.  
163 Due to the length of the experiment during which the animals received food *ad libitum*, we  
164 did not analyse body weight. Note that adding body weight measured at various stages during  
165 the experiment to our models never changed the results qualitatively (data not shown).

166

167 We used 25 G insulin syringes to take blood from the individuals. Blood was drawn from a  
168 large subcutaneous vessel on the ventral side of the animals to investigate the rate of blood-  
169 parasite (haemogregarine) infection. This method caused no permanent injuries and the  
170 animals showed no sign of abnormal behaviour after the procedure. Blood was collected using  
171 60 µl haematocrit capillary tubes (VWR International Ltd., Debrecen, Hungary) and blood  
172 smears were made by blowing a drop of blood onto the microscope slide. Smears were air-  
173 dried until coagulation. Fixation, staining of blood-smears and estimation of parasite intensity  
174 (corrected for red blood cell density) were done following the method of Molnár et al. (2013).

175

176 *Behavioural assays*



177

178 Activity and risk-taking of lizards were tested between 13 and 25 June, 2013 on sunny, low  
179 wind days. Observations took place in every second day to leave animals time to recover from  
180 the handling related to the risk-taking assay (we skipped an observation on 19 June because of  
181 thick cloud cover and light rain).

182

183 Activity of animals was measured five times (i.e. in five different days) in their home boxes.  
184 Video footages were made of the lizards' movements between 11.15 am and 12.15 pm (UTC  
185 + 02.00) using webcams (LifeCam HD-3000, Microsoft Co., Redmond, Washington, USA)  
186 and digital video cameras (Panasonic HC-V100, Panasonic Co., Kadoma, Osaka, Japan). We  
187 analysed the movements of the animals using the programme MATLAB (MathWorks, Natick,  
188 Massachusetts, USA). We used 30 minutes of every video footage (sum of three 10 minute  
189 intervals, distributed equally: 0-10 min., 25-35 min., 50-60 min.) to describe activity of the  
190 animals. Total distance moved was used to describe activity (see Réale et al. 2007). We  
191 applied a  $\log_{10}$  transformation to achieve normal distribution.

192

193 Risk-taking was tested six times (i.e. in six different days) during afternoons (between 12.30  
194 pm and 14.00 pm; UTC + 02.00) in unfamiliar, hence, potentially risky environments. These  
195 tests were run on the same days as the noninvasive activity assays (average time interval  
196 between activity and risk-taking assays was 15 minutes). However, due to camera  
197 malfunction, we had a day when only risk-taking could be measured. Eleven arenas (black  
198 plastic boxes, 36.5 cm  $\times$  22.4 cm  $\times$  25 cm, length, width, height, respectively) were used for  
199 the risk-taking tests. A smaller white opaque box (starter-box; 11.2 cm  $\times$  7.3 cm  $\times$  5.4 cm;  
200 length, width, height, respectively) with a manually removable cardboard door was placed in  
201 each arena. First, the test animals were caught and placed into the starter boxes, and we let

202 them acclimate for five minutes. Then, we removed the door and video recorded (Panasonic  
203 HC-V100, Panasonic Co., Kadoma, Osaka, Japan) the animals' behaviour for 10 min. Time  
204 till the lizards left their refuges (when the lizards' midbody [from head to the cloaca region]  
205 emerged from the shelter) was used as a proxy for risk-taking with individuals emerging  
206 quickly seen as risk-takers (Cote et al 2010, Beckmann & Biro 2013). Tests were performed  
207 in three turns on each day, to assay all lizards once in every test day. The order and placement  
208 of the animals were randomised within day. The risk-taking arenas and starter-boxes were  
209 washed thoroughly with detergent between tests to remove chemical stimuli that may have  
210 left by the last male.

211

212 Individuals that did not leave the refuge after 10 min were treated as expressing an extreme  
213 phenotype, being the 'shiest' (13 animals, 54 % of all assays), thus we did not exclude them  
214 from the analyses to avoid the loss of an important amount of information. On the other hand,  
215 giving them the maximal score (600 sec) would mislead us in calculating within-individual  
216 variance of risk-taking by arbitrarily decreasing it. Hence, we first rank-transformed the data  
217 and gave these individuals a random rank at the end of the distribution (Bajer et al. 2015).  
218 Data were then normalized using the Rankit method (Solomon & Sawilowsky 2009).

219

### 220 *Statistical analyses*

221

222 We used the repeated data on each individual as random observations because (i) they had 10  
223 days to acclimate to the settings before the first assay and one day recovery between assays,  
224 and thus habituation during the tests should be minimal and (ii) we used a semi-natural setup  
225 where the between-day environmental variation could not be controlled. However, to test for  
226 potential habituation effects directly, we performed random intercept-random slope linear

227 mixed models on both activity and risk-taking as response variables, including z-transformed  
228 order of trials as random slopes, individual as random effect and an intercept. We found no  
229 sign of habituation (data not shown).

230

231 Bivariate Mixed Models (BMMs) were used to partition variance components at different  
232 levels (Dingemanse & Dochtermann 2013) with the two behaviours as response variables in a  
233 model that contained only an intercept and individual as a random effect. We used the  
234 MCMCglmm R package (Hatfield 2010) that implements a Bayesian framework for model  
235 fitting, and in which we ran 1300000 iterations with 300000 burn-in period, and we sampled  
236 the Markov chain at each 1000th iteration. Within-behaviour consistency was estimated in the  
237 form of repeatability in activity and risk-taking separately. Because phenotypic behavioural  
238 correlations are unreliable in assessing behavioural syndromes, we decomposed phenotypic  
239 correlations between activity and risk-taking into within- and between-individual correlations  
240 (Dingemanse et al. 2012; Dingemanse & Dochtermann 2013; Garamszegi et al. 2013), where  
241 the latter is the true estimator of behavioural syndromes, which, by definition, describes  
242 between-individual variation across behaviours. The results are given as the estimates of  
243 repeatabilities and correlation coefficients and their 95% confidence interval. The model was  
244 run in MCMCglmm using R (R Development Core Team 2010). Since there was no sign of  
245 behavioural syndrome (see Results), we focussed on the individual behaviours in our later  
246 analyses.

247

248 Because both activity and risk-taking were repeatable within individuals across assays (see  
249 Results), we could use individual-specific estimates of these behaviours as traits reliably  
250 reflecting some aspects of an individual property. In further analyses, individual behaviour  
251 was represented by behavioural type (the mean of the subsequent measures). Since the two

252 behaviours were uncorrelated (see Results) we could test the link between behaviour and the  
253 other traits of interest by running separate General Linear Models (GLMs) for activity and  
254 risk-taking. In these GLMs, behavioural types were the response variables, and SVL, relative  
255 head size, relative limb length, number of femoral pores, and intensity of blood-parasite  
256 infection were the predictor variables. We used relative traits (i.e. residuals corrected for  
257 SVL) for the morphological variables in the GLMs instead of raw variables to avoid  
258 multicollinearity. We ran model-diagnostics based on variance inflation factor (VIF) that  
259 indicated no evidence for multicollinearity (all VIFs < 1.24). The GLMs were built without  
260 interactions. We tried backward stepwise model selection, but since the results never changed  
261 qualitatively, we report the original full models. Analyses were performed with R (R  
262 Development Core Team 2010).

263

## 264 **Results**

265

266 Both activity and risk-taking of *I. cyreni* males were significantly repeatable across 5 or 6  
267 assays, respectively (activity:  $r = 0.69$ , 95% CI range = 0.51 – 0.8; risk-taking:  $r = 0.22$ , 95%  
268 CI range = 0.11 – 0.41). We found no between-individual correlation between the studied  
269 behaviours ( $r = -0.15$ , 95% CI range = -0.61 – 0.24,  $N = 24$ ), which could have been  
270 suggestive of an activity – risk-taking behavioural syndrome. There was no sign of within-  
271 individual correlation either ( $r = 0.01$ , 95 % CI range = -0.2 – 0.19,  $N = 24$ ).

272

273 None of the predictor variables were related to activity (Table 1). However, there was a strong  
274 correlation between risk-taking and blood-parasite intensity, lizards with higher infection rate  
275 taking higher risk ( $t = -3.3$ ,  $P = 0.004$ ,  $r = -0.61$ , 95% CI = -0.79 – -0.23,  $N = 24$ ) (Fig. 1). The

276 effect size of this relationship can be interpreted to represent a large effect (Cohen, 1988).  
277 None of the other variables affected risk-taking (Table 1).

278

## 279 **Discussion**

280

281 The most prominent outcomes of the present work are two-fold. First, adult male *I. cyreni*  
282 showed significant activity and risk-taking personality over the observed period. Second, risk-  
283 taking was strongly and positively correlated to the intensity of haemogregarine infection  
284 across the studied individuals. We did not find any sign of a between-individual correlation  
285 regarding activity and risk-taking, hence, the presence of a behavioural syndrome was not  
286 supported.

287

288 We found that activity and risk-taking are both repeatable within-individuals. The  
289 repeatability of behaviour is generally around 0.3-0.4 (Bell et al. 2009). Hence, the  
290 behavioural consistency of *I. cyreni*'s activity ( $r = 0.68$ ) is high, while the consistency of risk-  
291 taking was rather low ( $r = 0.22$ ). This adds to the slowly accumulating literature of reptilian  
292 behavioural consistency, where the major personality axes (*sensu* Réale et al. 2007) are  
293 usually found to represent personality (Cote and Clobert 2007; Cote et al. 2008; Rodríguez-  
294 Prieto et al. 2011, Carter et al. 2012a, b; Le Galliard et al. 2013, 2015; McEvoy et al. 2013,  
295 2015; Highcock & Carter 2014; Teyssier et al. 2014, Bajer et al. 2015, Kuo et al. 2015).  
296 However, despite the support for behavioural consistency within behaviours, we found no  
297 evidence for behavioural consistency across behaviours as indicated by the low and  
298 nonsignificant between-individual correlation. This incongruence between the two levels of  
299 behavioural consistency strengthen the notion that behavioural consistencies within and  
300 between functionally different behaviours (animal personality and behavioural syndrome,

301 respectively) are different phenomena and should be treated as such (Garamszegi & Herczeg  
302 2012; Jandt et al. 2014).

303

304 Males with high blood-parasite (haemogregarine) infection took more risk than their healthier  
305 conspecifics. These parasites have been found in fishes, birds, amphibians and reptiles (Smith  
306 et al. 1994; Caudell et al. 2002; Lainson et al. 2003), including other lacertids (see e.g. Molnár  
307 et al. 2013; Garrido et al. 2014;). Haemogregarine infection has mild effects on the hosts,  
308 however, it does depress haematocrit levels which impacts (by the reduced haemoglobin  
309 concentration and insufficient oxygen supply of muscles) several physiological and  
310 behavioural traits (e.g. Veiga et al. 1998; O'Dwyer et al. 2004). In general, parasitism can be  
311 linked to risk-taking behaviour *via* numerous causal mechanisms (Kortet et al. 2010; Poulin  
312 2013). For example, as an outcome of high parasite-infection, individuals with low assets  
313 (low probability of survival till the next reproductive event) might apply higher risk-taking  
314 strategies in a current breeding situation than healthier conspecifics with high assets (asset  
315 protection hypothesis, Clark 1994). Further, an active and risk-taking behavioural strategy is  
316 expected to result in more contact with parasites and/or in immunosuppression that could lead  
317 to higher parasite levels in risk-taker individuals. However, parasites with strong negative  
318 effects on their hosts' health are expected to lower behavioural activity. Hence, higher risk-  
319 taking might be coupled with higher infection intensity with parasites with mild effects, a  
320 hypothesis that was supported by a recent comparative study using 44 birds species (García-  
321 Longoria et al. 2014) and is also in line with our results. It is known for both *I. cyreni* and  
322 *Lacerta viridis* that haemogregarine infection intensity correlates positively with male body  
323 condition during the reproductive season (Amo et al. 2004; Molnár et al. 2013), probably as a  
324 result of the higher testosterone levels of males in good body condition (Amo et al. 2004).

325 Since lizards are known to act as definitive hosts for haemogregarines, adaptive manipulation

326 of the host behaviour seems unlikely, however, parasites have the potential to alter the host's  
327 personality in a multidimensional way through pathological effects (Hammond-Tooke et al.  
328 2012; Poulin 2013). Activity was highly repeatable, representing a strong personality trait in  
329 our population. However, none of the predictors tested in this study were correlated with  
330 activity. Movement activity in a familiar environment might have strong physiological control  
331 unrelated to the measured individual characteristics, and be linked to life-history variation  
332 (Réale et al. 2010). Future studies should involve the relevant physiological and life-history  
333 traits as predictors.

334

335 Taken together, *I. cyreni* males have activity and risk-taking personalities during the mating  
336 season. We note that while the ca. two weeks period of our assays is insufficient for drawing  
337 conclusions about personalities lasting through the year or life, we are confident that the  
338 reported behavioural consistency is present during the relatively short and synchronised  
339 breeding season in our species. We did not find any trend indicating the presence of a  
340 behavioural syndrome, suggesting that animal personality and behavioural syndrome are not  
341 tightly linked phenomena. Finally, we found a strong positive correlation between blood-  
342 parasite infection intensity and risk-taking. This is in line with the predictions of the asset  
343 protection hypothesis. However, since our study is entirely correlative, it is also possible that  
344 risk-taker individuals simply have higher chance to be parasitized than risk-averse  
345 individuals. We note that our results seem to be somewhat incongruent with previous results  
346 reported by López et al. (2005), who found that healthier lizards with better body condition  
347 took higher risk. However, they assessed risk-taking in the lizards' own natural home ranges,  
348 while we assessed risk-taking in a novel area. The different situations might result in different  
349 costs and benefits for leaving a refuge after a simulated predatory attack. Future manipulative

350 experiments are necessary for a better understanding of risk-taking variation in this  
351 evolutionary ecology model species.

352

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354

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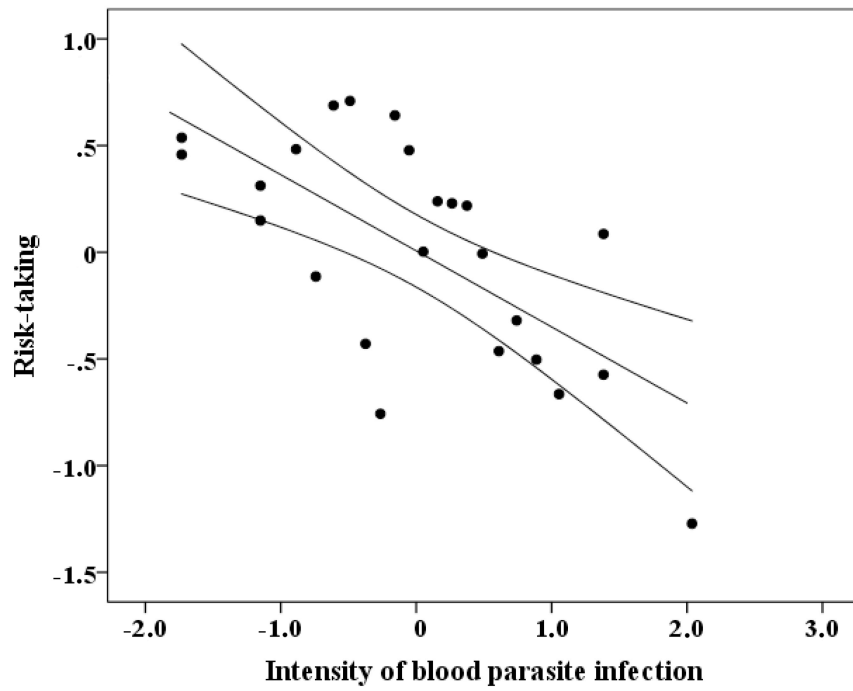
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562

563 Figure 1. Correlation between risk-taking and intensity of parasite infection in adult male

564 *Iberolacerta cyreni*. Intensity of parasite infection is represented by the number of

565 haemogregarinae parasites corrected for red cell count. Risk-taking is represented by latency

566 to leave refuge, hence, small values translate to high risk-taking. Both variables are

567 normalized.

568

569 Table 1. Results of the General Linear Models. t statistics (numerator df = 1; denominator df  
570 = 23) and their significances (in parentheses) are shown. Significant effects are in bold font.  
571

	Activity	Risk-taking
SVL	-0.62(0.55)	-0.45 (0.66)
Relative head size	-0.52 (0.61)	-0.32 (0.75)
Relative size of limbs	1.21 (0.24)	-0.42 (0.68)
Number of femoral pores	0.6 (0.56)	-1.42 (0.17)
Parasite intensity	0.77 (0.45)	<b>-3.3 (0.004)</b>

572