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

2   Carpetan rock lizards (*Iberolacerta cyreni*)

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31

32

Abstract

33

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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

3

Introduction

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

One crucial step towards understanding the mechanisms behind behavioural variation in the wild is to link behaviour to individual quality, however, this is not straightforward in most cases, mainly because of the controversy around the definition and measurement of 'individual quality'. Since individual quality can only be approached through fitness, a viable 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

5

reptiles, moreover, the length of limbs is also a potential fitness proxy due to its link to sprint

speed (Bauwens et al. 1995; Gvozdik & Van Damme 2003; Roff 1992). Therefore, *I. cyreni*

provides an excellent model to link behaviour to individual quality. Further, behavioural

consistency research on reptiles is negligible compared to mammals, birds, or fishes (Smith &

Blumstein 2008; Garamszegi et al. 2012, 2013), thus using a lizard as model can be beneficial

to broaden the taxonomical sample in this area.

In this paper, we studied whether (i) wild-caught male *I. cyreni* during the mating season

showed behavioural consistency and, assuming that individual behavioural variation is

present, (ii) individual behaviour covaried with blood parasite load and other potentially

fitness-related traits. To this end, we performed behavioural experiments under semi-natural

conditions to assess activity and risk-taking of reproductive, adult male lizards. We followed

a repeated-measure design in which we assayed each individual 5-6 times over a 13 day

period. Since haemogregarines has negative, but not directly lethal effects on their lizard hosts

(Oppliger et al. 1996; Veiga et al. 1998; O'Dwyer et al. 2004; Bouma et al. 2007) parasite –

behavioural links are expected (Barber & Dingemanse 2010, Kortet et al. 2010). However,

considering the correlative nature of our study, separating cause and effect in our findings is

not straightforward. For instance, individuals with higher behavioural activity may encounter

parasites more frequently (García-Longoria et al. 2014) or individuals with higher parasite

load and thus lower future reproductive value might take more risks following the asset

protection principle (Clark 1994). Besides the intensity of blood-parasite infection, we also

included a number of other potentially fitness-linked traits in our study to seek for other signs

of behaviour – individual quality links.

Methods

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 cased 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.

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

Activity and risk-taking of lizards were tested between 13 and 25 June, 2013 on sunny, low

wind days. Observations took place in every second day to leave animals time to recover from

the handling related to the risk-taking assay (we skipped an observation on 19 June because of

thick cloud cover and light rain).

182

Activity of animals was measured five times (i.e. in five different days) in their home boxes.

Video footages were made of the lizards' movements between 11.15 am and 12.15 pm (UTC

+ 02.00) using webcams (LifeCam HD-3000, Microsoft Co., Redmond, Washington, USA)

and digital video cameras (Panasonic HC-V100, Panasonic Co., Kadoma, Osaka, Japan). We

analysed the movements of the animals using the programme MATLAB (MathWorks, Natick,

Massachusetts, USA). We used 30 minutes of every video footage (sum of three 10 minute

intervals, distributed equally: 0-10 min., 25-35 min., 50-60 min.) to describe activity of the

animals. Total distance moved was used to describe activity (see Réale et al. 2007). We

applied a $\log_{10}$ transformation to achieve normal distribution.

192

Risk-taking was tested six times (i.e. in six different days) during afternoons (between 12.30

pm and 14.00 pm; UTC + 02.00) in unfamiliar, hence, potentially risky environments. These

tests were run on the same days as the noninvasive activity assays (average time interval

between activity and risk-taking assays was 15 minutes). However, due to camera

malfunction, we had a day when only risk-taking could be measured. Eleven arenas (black

plastic boxes, 36.5 cm × 22.4 cm × 25 cm, length, width, height, respectively) were used for

the risk-taking tests. A smaller white opaque box (starter-box; 11.2 cm × 7.3 cm × 5.4 cm;

length, width, height, respectively) with a manually removable cardboard door was placed in

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

12

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,

13

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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366

367 **Literature Cited**

368

369 Amo, L., López, P., Martín, J. 2004: Prevalence and intensity of haemogregarinid blood

370 parasites in a population of the Iberian rock lizard, *Lacerta monticola*. Parasitol Res **94**, 290–

371 293. doi:10.1007/s00436-004-1212-7.

372 Amo, L. López, P., Martín, J. 2005: Prevalence and intensity of haemogregarine blood

373 parasites and their mite vectors in the common wall lizard, *Podarcis muralis*. Parasitol Res

374 **96**, 378-381. doi: 10.1007/s00436-005-1354-2.

375   Bajer, K., Horváth, G., Molnár, O., Török, J., Garamszegi, L.Z., Herczeg, G. 2015: European

376   green lizard (*Lacerta viridis*) personalities: Linking behavioural types to ecologically relevant

377   traits at different ontogenetic stages. Behav Proc **111**, 67-74. doi:

378   10.1016/j.beproc.2014.11.020.

379   Barber, I. & Dingemanse, N.J. 2010: Parasitism and the evolutionary ecology of animal

380   personality. Phil Trans R Soc B **365**, 4077-4088. doi: 10.1098/rstb.2010.0182.

381   Beckmann, C. & Biro, P. 2013: On the validity of a single (boldness) assay in personality

382   research. Ethology **119**, 937-947. doi: 10.1111/eth.12137.

383   Bauwens, D., Garland, T.Jr., Castilla, A.M., Van Damme, R. 1995: Evolution of sprint speed

384   in lacertid lizards: morphological, physiological and behavioral covariation. Evolution. **49**,

385   848-863.

386   Bell, A.M. 2005: Behavioural differences between individuals and two populations of

387   sticklebacks Gasterosteus aculeatus. J Evol Biol **182**, 464-473. doi: 10.1111/j.1420-

388   9101.2004.00817.x.

389   Bell, A.M. 2007: Future directions in behavioural syndromes research. Proc R Soc B **274**,

390   755-761. doi:10.1098/rspb.2006.0199.

391   Bell, A.M. & Sih, A. 2007: Exposure to predation generates personality in threespined

392   sticklebacks (*Gasterosteus aculeatus*). Ecol Lett **10**, 828-834. doi: 10.1111/j.1461-

393   0248.2007.01081.x.

394   Bell, A.M., Hankinson, S.J., Laskowski, K. 2009: The repeatability of behaviour: a meta-

395   analysis. Anim Behav **77**, 771-783. doi: 10.1016/j.anbehav.2008.12.022.

396   Bergeron, P., Baeta, R., Pelletier, F., Réale, D.; Garant, D. 2011: Individual quality: tautology

397   or biological reality? J Anim Ecol **80**, 361-364. doi: 10.1111/j.1365-2656.2010.01770.x.

398   Bouma M.J., Smallridge C.J., Bull C.M., Komdeur J. 2007: Susceptibility to infection by a

399   haemogregarine parasite and the impact of infection in the Australian sleepy lizard Tiliqua

400   rugosa. Parasitol Res. **100(5)**, 949–954.

401   Carter, A.J., Heinsohn, R., Goldizen, A.W., Biro, P.A. 2012a: Boldness, trappability and

402   sampling bias in wild lizards. Anim Behav **83**, 1051-1058. doi:

403   10.1016/j.anbehav.2012.01.033.

404   Carter, A.J., Goldizen, A., Heinsohn, R. 2012b: Personality and plasticity: temporal

405   behavioural reaction norms in a lizard, the Namibian rock agama. Anim Behav **84**, 471-477.

406   doi: 10.1016/j.anbehav.2012.06.001.

407   Caudell, J.N., Whittier, J., Conover, M.R. 2002: The effects of haemogregarine- like parasites

408   on brown tree snakes (*Boiga irregularis*) and slatey-grey snakes (*Stegonotus cucullatus*) in

409   Queensland, Australia. Int Biodet Biodegrad **49**,113–119.

410   Clark, C.W. 1994: Antipredator behaviour and the asset protection principle. Behav Ecol **5**,

411   159-170.

412   Cohen, J. 1988: Statistical power analysis for the behavioral sciences, 2nd edn. Lawrence

413   Erlbaum Associates. Hillsdale, NJ.

414   Cote, J. & Clobert, J. 2007: Social personalities influence natal dispersal in a lizard. Proc R

415   Soc B **274**, 383-390. doi:10.1098/rspb.2006.3734.

416   Cote, J., Dreiss, A., Clobert, J. 2008: Social personality trait and fitness. Proc R Soc B **275**,

417   2851-2858. doi:10.1098/rspb.2008.0783.

418   Cote, J., Clobert, J., Montes Poloni, L., Haussy, C., Meylan, S. 2010: Food deprivation

419   modifies corticosterone-dependent behavioural shifts in the common lizard. Gen Comp

420   Endocrinol **166**, 142-151. doi: 10.1016/j.ygcen.2009.11.008.

421   Dingemanse, N.J. & Wolf, M. 2010: Recent models for adaptive personality differences: a

422   review. Phil Trans R Soc B **365,** 3947-3958. doi: 10.1098/rstb2010.0221.

423   Dingemanse, N.J., Dochtermann, N.A. 2013: Quantifying individual variation in behaviour:

424   mixed-effect modelling approaches. J Anim Ecol **82**, 39-54. doi: 10.1111/1365-2656.12013.

425   Dingemanse, N.J., Dochtermann, N.A., Nakagawa, S. 2012: Defining behavioural syndromes

426   and the role of 'syndrome deviation' in understanding their evolution. Behav Ecol Sociobiol

427   **66**, 1543–1548. doi: 10.1007/s00265-012-1416-2

428   Garamszegi, L.Z. 2006: Comparing effect sizes across variables: generalization without the

429   need for Bonferroni correction. Behav Ecol **17**, 682-687. doi: 10.1093/beheco/ark005.

430   Garamszegi, L. Z., & Herczeg, G. 2012: Behavioural syndromes, syndrome deviation and the

431   within-and between-individual components of phenotypic correlations: when reality does not

432   meet statistics. Behav. Ecol. Sociobiol **66**, 1651-1658.

433   Garamszegi, L.Z., Markó, G., Herczeg, G. 2012: A meta-analysis of correlated behaviours

434   with implications for behavioural syndromes: mean effect size, publication bias, phylogenetic

435   effects and the role of mediator variables. Evol Ecol **26**, 1212-1235. doi: 10.1007/s10682-

436   012-9589-8. doi: 10.1111/j.1461-0248.2010.01536.x.

437   Garamszegi, L.Z., Markó, G., Herczeg, G., 2013: A meta-analysis of correlated behaviours

438   with implications for behavioural syndromes: relationships between particular behavioral

439   traits. Behav Ecol **24**, 1068–1080, doi:10.1093/beheco/art033.

440   García-Longoria, L., Garamszegi, L.Z., Møller, P. 2014: Host escape behavior and blood

441   parasite infections in birds. Behav Ecol **25**, 890-900. doi:10.1093/beheco/aru066.

442   García-Ramírez, A., Delgado-García, J.D., Foronda-Rodríguez, P., Abreu-Costa, N. 2005:

443   Haematozoans, mites and body condition in the oceanic island lizard *Gallotia atlantica*

444   (Peters and Doria, 1882) (Reptilia: Lacertidae). J Nat Hist **39(17)**, 1299-1301. doi:

445   10.1080/00222930400015590.

446   Garrido, M., Pérez-Mellado, V., Cooper Jr., W.E. 2014: Complex relationships amongst

447   parasite load and escape behaviour in an insular lizard. Ethology **120**, 1-9. doi:

448   10.1111/eth.12322

449   Gvozdik, L., Van Damme, R. 2003: Evolutionary maintenance of sexual dimorphism in head

450   size in the lizard Zootoca vivipara: a test of two hypotheses. J Zool. **259**, 7-13.

451   doi:10.1017/S0952836902003308.

452   Hammond-Tooke, C.A., Nakagawa, S., Poulin, R. 2012: Parasitism and behavioural

453   syndromes in the fish *Gobiomorphus cotidianus*. Behaviour **149**, 601-622. doi:

454   10.1163/156853912X648903.

455   Hatfield, J.D. 2010: MCMC Methods for Multi Response Generalized Linear Mixed Models:

456   The MCMCglmm R Package. J Stat Soft **33(2)**, 1-22. http://www.jstatsoft.org/v33/io2/

457   Highcock, L. & Carter, A.J. 2014: Intraindividual variability of boldness is repeatable across

458   contexts in a wild lizard. PLoS ONE. **9(4)**, e95179. doi: 10.1371/ journal.pone.0095179.

459   Kortet, R., Hedrick, A.V., Vainikka, A. 2010: Parasitism, predation and the evolution of

460   animal personalities. Ecol Lett **13**, 1449-1458. doi: 10.1111/j.1461-0248.2010.01536.x.

461   Koolhaas, J.M., De Boer, S.F., Buwalda, B., Van Reenen, C.G. 2007: Individual variation in

462   coping with stress: a multidimensional approach of ultimate and proximate mechanisms.

463   Brain Behav Evol **70**, 218–226. doi:10. 1159/000105485.

464   Kuo, C.Y., Irschick, D.J., Lailvaux, S.P. 2015: Trait compensation between boldness and the

465   propensity for tail autotomy under different food availabilities in similarly aged brown anole

466   lizards. Funct Ecol **29(3)**, 385-392. doi: 10.1111/1365-2435.12324.

467   Lainson, R., de Souza, M.C., Franco, C.M. 2003: Haematozoan parasites of the lizard *Ameiva*

468   *ameiva* (Teiidae) from Amazonian Brazil: a preliminary note. Mem Inst Oswaldo Cruz

469   **98,**1067–1070.

470 Le Galliard, J.F., Paquet, M., Cisel, M., Montes-Poloni, L. 2013: Personality and the pace-of-

471 life syndrome: variation and selection on exploration, metabolism and locomotor

472 performances. Funct Ecol **27**, 136-144. doi: 10.1111/1365-2435.12017.

473 Le Galliard, J.F., Paquet, M., Mugabo, M. 2015: An experimental test of density-dependent

474 selection on temperament traits of activity, boldness and sociability. J Evol Biol **28(5)**, 1144-

475 1155. doi: 10.1111/jeb.12641.

476 López, P., Munoz, A., Martín, J. 2002: Symmetry, male dominance and female mate

477 preferences in the Iberian rock lizard, Lacerta monticola. Behav Ecol Sociobiol **52**, 342-347.

478 doi: 10.1007/s00265-002-0514-y.

479 López, P., Hawlena, D., Polo, V., Amo, L., Martín, J. 2005: Sources of individual shy-bold

480 variations in antipredator behaviour of male Iberian rock lizards. Anim Behav **69**, 1-9. doi:

481 10.1016/j.anbehav.2004.05.010.

482 López, P., Amo, L., Martín, J. 2006: Reliable signaling by chemical cues of male traits and

483 health state in male lizards, *Lacerta Monticola*. J Chem Ecol **32**, 473-488. doi:0.1007/s10886-

484 005-9012-9.

485 Martín, J. & Salvador, A. 1997: Microhabitat selection by the Iberian rock lizard *Lacerta*

486 *monticola*: Effects on density and spatial distribution of individuals. Biol Cons **79**, 303-307.

487 Martín, J. & López, P. 2000: Chemoreception, symmetry and mate choice in lizards. Proc R

488 Soc B **267**, 1265-1269. doi: 10.1098/rspb.2000.1137.

489 Martín, J. & López, P. 2006: Vitamin D supplementation increases the attractiveness of

490 males' scent for female Iberian rock lizards. Proc R Soc B **273**, 2619–2624.

491 doi:10.1098/rspb.2006.3619.

492 Martín, J. & López, P. 2013: Responses of female rock lizards to multiple scent marks of

493 males: Effects of male age, male density and scent over-marking. Behav Proc **94**, 109-114.

494 doi:10.1016/j.beproc.2013.01.002.

495   McEvoy, J., While, G.M., Sinn, D.L., Wapstra, E. 2013: The role of size and aggression in

496   intrasexual male competition in a social lizard species, *Egernia withii*. Behav Ecol Sociobiol

497   **67**, 79-90. doi: 10.1007/s00265-012-1427-z.

498   McEvoy, J., While, G.M., Sinn, D.L., Carver, S., Wapstra, E. 2015: Behavioural syndromes

499   and structural and temporal consistency of behavioural traits in a social lizard. J Zool **296**, 58-

500   66. doi: 10.1111/jzo.12217.

501   Møller, A.P. & Jennions, M.D. 2002: How much variance can be explained by ecologists and

502   evolutionary biologists? Oecologia **132**, 492–500. doi: 10.1007/s00442-002-0952-2.

503   Molnár, O., Bajer, K., Mészáros, B., Török, J., Herczeg, G. 2013: Negative correlation

504   between nuptial throat colour and blood parasite load in male European green lizards supports

505   the Hamilton–Zuk hypothesis. Naturwissenschaften **100**, 551-558. doi: 10.1007/s00114-013-

506   1051-4.

507   O'Dwyer, L.H., Moc¸o, T.C., da Silva, R.J. 2004: Description of the gamonts of a small

508   species of *Hepatozoon* sp. (Apicomplexa, Hepatozoidae) found in *Crotalus durissus terrificus*

509   (Serpentes, Viperidae). Parasitol Res **92,**110–112.

510   Oppliger A., Celerier M.L., Clobert J. 1996: Physiological and behaviour changes in common

511   lizards parasitized by haemogregarines. Parasitology **113**,433–438.

512   Poulin, R. 2013: Parasite manipulation of host personality and behavioural syndromes. J Exp

513   Biol **216**, 18-26. doi:10.1242/jeb.073353.

514   R Development Core Team 2010: R: A language and environment for statistical computing. R

515   Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL

516   http://www.R-project.org.

517   Réale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V., Montiglio, P.O. 2010:

518   Personality and the emergence of the pace-of-life syndrome concept at the population level.

519   Phil Trans R Soc B: Biol Sci **365**, 4051–4063.

Roff, D.A. 1992: The Evolution of Life Histories: Theory and Analysis. Chapman and Hall, New York.

Réale, D., Reader, S.M., Sol, D., McDougall, P.T., Dingemanse, N.J. 2007: Integrating animal temperament within ecology and evolution. Biol Rev **82**, 291-318. doi: 10.1111/j.1469-185X.2007.00010.x.

Rodríguez-Prieto, I., Martín, J., Fernández-Juricic, E. 2011: Individual variation in behavioural plasticity: direct and indirect effects of boldness, exploration and sociability on habituation to predators in lizards. Proc R Soc B **278**, 266-273. doi: 10.1098/rspb.2010.1194.

Sih, A. & Bell, A.M. 2008: Insights for behavioural from behavioural syndromes. In: Advances in the Study of Behaviour Vol. 38 (Brockmann, H.J., Roper, T., Naguib, M., Wynne-Edwards, K., Barnard, C., Mitani, J., eds.). Academic Press, Waltham, Massachusetts. pp. 227-281.

Sih, A. & Del Guidence, M. 2012: Linking behavioural syndromes and cognition: a behavioural ecology perspective. Phil Trans R Soc B **367**, 2762-2772. doi:10.1098/rstb.2012.0216.

Sih, A., Bell, A., Johnson, J.C. 2004a: Behavioural syndromes: an ecological and evolutionary overview. Trends Ecol Evol **19**, 372-378. doi: 10.1016/j.tree.2004.04.009.

Sih, A., Bell, A.M., Chadwick J.J., Ziemba, R.E. 2004b: Behavioural syndromes. an integrate overview. Q Rev Biol **79**, 241-277.

Sih, A. Cote, J., Evans, M., Fogarty, S., Pruitt, J. 2012: Ecological implications of behavioural syndromes. Ecol Lett **15**, 278–289. doi: 10.1111/j.1461-0248.2011.01731.x.

Smith T.G., Desser S.S., Martin D.S. 1994: The development of *Hepatozoon sipedon* n. sp. (Apicomplexa: Adeleina: Hepatozoidae) in its natural host, the Northern water snake (*Nerodia sipedon sipedon*), the culicine vectors, *Culex pipiens* and *Culex territans*, and an intermediate host, Northern leopard frog (*Rana pipiens*). Parasitol Res **80**,559–568

545   Sih, A., Mathot, K.J., Moirón, M., Montiglio, P.O., Wolf, M., Dingemanse, N.J. 2015:

546   Animal personality and state–behaviour feedbacks: a review and guide for empiricists. Trends

547   Ecol Evol **30(1)**, 50-60. doi: 10.1016/j.tree.2014.11.004.

548   Smith, B.R. & Blumstein, D.T. 2008: Fitness consequences of personality: A meta-analysis.

549   Behav Ecol **19(2)**, 448-455. doi:10.1093/beheco/arm144.

550   Solomon, S.R. & Sawilowsky, S. S. 2009: Impact of rank-based normalizing transformations

551   on the accuracy of test scores. J Mod App Stat Meth **8(2)**, 448-462.

552   Teyssier, A., Bestion, E., Richard, M., Cote, J. 2014: Partners' personality types and mate

553   preferences: predation risk matters. Behav Ecol **25(4)**, 723-733. doi: 10.1093/beheco/aru049.

554   Veiga, J.P., Salvador, A., Merino, S., Puerta, M. 1998: Reproductive effort affects immune

555   response and parasite infection in a lizard: a phenotypic manipulation using testosterone.

556   Oikos **82**, 313– 318.

557   West-Eberhard, M.J. 2003: Developmental Plasticity and Evolution. Oxford Univ. Press.,

558   Oxford, United Kingdom.

559   Wilson, A.J. & Nussey, D.H. 2010: What is individual quality? An evolutionary perspective.

560   Trends Ecol Evol **25**, 207–214. doi: 10.1016/j.tree.2009.10.002.

561
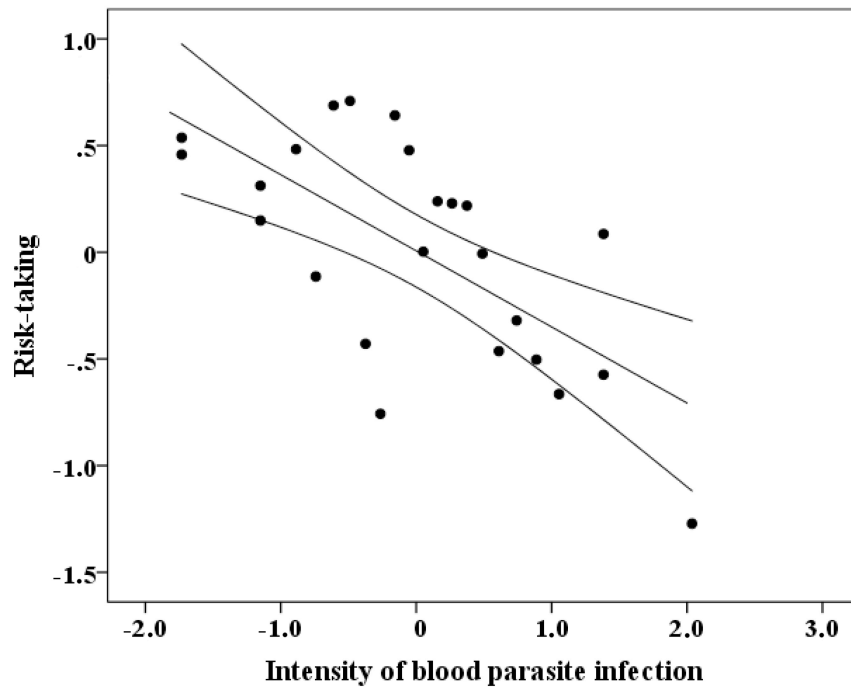
562

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)	**-3.3 (0.004)**

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