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31 **ABSTRACT**

32 Research focusing on among-individual differences in behaviour (“animal personality”) has
33 been blooming for over a decade. One of the central theories explaining the maintenance of
34 behavioural variation posits a trade-off between behaviour and survival with individuals
35 expressing greater “risky” behaviours suffering higher mortality. Here, for the first time, we
36 synthesize the existing empirical evidence for this key prediction. Our results did not support
37 this prediction as there was no directional relationship between riskier behaviour and greater
38 mortality; however there was a significant absolute relationship between behaviour and
39 survival. In total, behaviour explained a significant, but small, portion (4.4%) of the variance
40 in survival. We also found that risky (versus “shy”) behavioural types live longer in the wild,
41 but not in the laboratory. This suggests that individuals expressing risky behaviours might be
42 of overall higher quality but the lack of predation pressure and resource restrictions mask this
43 effect in laboratory environments. Our work implies that individual differences in behaviour
44 explain important differences in survival but not in the direction predicted by theory.
45 Importantly, this suggests that the models predicting survival trade-offs may need revision
46 and/or empiricists may need to reconsider their proxies of risky behaviours when testing such
47 theory.

48 **INTRODUCTION**

49 Across the animal kingdom, individuals within populations differ in their average behavioural
50 expression (Bell *et al.* 2009; Holtmann *et al.* 2017). Studying the causes and consequences of
51 among-individual variation in behavioural expression (also termed “animal personality”) has
52 been a major focus in the fields of animal ecology and evolutionary biology for more than a
53 decade. Indeed, individual differences in behavioural expression have been found to play a key
54 role in biological invasions (Fogarty *et al.* 2011; Chapple *et al.* 2012; Carere & Gherardi 2013),
55 population dynamics (Dall *et al.* 2012), dispersal (Cote *et al.* 2010), predator-prey interactions
56 (Pruitt *et al.* 2012; DiRienzo *et al.* 2013; McGhee *et al.* 2013; Pettorelli *et al.* 2015), and also
57 suggested to affect fitness components such as survival and longevity (reviewed in Dingemanse
58 & Reale 2005; Réale *et al.* 2007; Smith & Blumstein 2008).

59 Several evolutionary hypotheses have been proposed as mechanisms explaining how
60 individual differences in behavioural expression can be maintained within the same population
61 (Wilson *et al.* 1994; Réale *et al.* 2007; Stamps 2007; Biro & Stamps 2008a; Wolf & Weissing
62 2010; Sih *et al.* 2015). These hypotheses generally assume that individual differences in
63 behaviour are linked to individual differences in fitness components such as longevity and
64 survival (Stamps 2007; Biro & Stamps 2008a; Réale *et al.* 2010; Dammhahn *et al.* 2018). For
65 instance, life-history theory predicts that individuals resolve the trade-off between current
66 reproduction and future survival differently (Stearns 1992) and that behaviours mediate such
67 trade-offs at the individual level (Réale *et al.* 2010; Dammhahn *et al.* 2018). Thus, adaptive
68 individual differences in behaviour result from divergent life-history strategies with more
69 active, bold or risk-taking individuals reproducing rapidly (i.e. invest more heavily in resource
70 acquisition and reproduction) but dying early in life (i.e. increased risk of mortality) (“pace-of-
71 life syndrome hypothesis”, Réale *et al.* 2010; Dammhahn *et al.* 2018; Royauté *et al.* 2018).
72 Assuming that (risky) behaviours act as mediators of the trade-off between current and future
73 reproduction, the specific prediction is that expression of risky behaviours is negatively

74 associated with survival and longevity (hereafter, survival) (Réale *et al.* 2010; Dammhahn *et*
75 *al.* 2018).

76 Labile traits, such as behaviours, vary both among- and within-individuals: individuals
77 differ relative to one another in their mean behavioural expression, while, at the same time,
78 change their behavioural expression from one instance to the next, respectively (Dingemanse
79 & Dochtermann 2013). Both individual differences and reversible plasticity in the expression
80 of labile traits are predicted to be independently associated with survival (Sih *et al.* 2004b;
81 Ratikainen & Kokko 2019). Moreover, the direction of the associations between traits often
82 differs at the among- versus within-individual levels (Adolph & Hardin 2007; Brommer 2013;
83 Niemelä & Dingemanse 2018b). The models predicting a negative association between survival
84 and risky behavioural types explicitly state that those traits covary at the among-individual level
85 of variation (Stamps 2007; Biro & Stamps 2008a; Réale *et al.* 2010). Thus, unbiased testing of
86 the theoretical prediction at the among-individual level of variation requires study designs and
87 statistical analyses that allow researchers to partition behavioural (co)variance to its among-
88 and within-individual levels (Brommer 2013; Dingemanse & Dochtermann 2013; Niemelä &
89 Dingemanse 2018a). Nevertheless, such partitioning is currently still rare in the empirical
90 behavioural ecology literature (Niemelä & Dingemanse 2018a, b; Royauté *et al.* 2018). This is
91 probably the main reason why a previous meta-analysis focusing on animal personality and
92 survival was conducted at the (unpartitioned) phenotypic level instead of among-individual
93 level of variation (Smith & Blumstein 2008). A systematic review testing whether empirical
94 work supports this theoretical prediction at the among-individual level is therefore still lacking.

95 In this study we conducted the first-ever meta-analysis to estimate the overall empirical
96 support for the hypothesis predicting among-individual differences in (risky) behaviour to
97 negatively correlate with survival (Stamps 2007; Biro & Stamps 2008a; Réale *et al.* 2010;
98 Dammhahn *et al.* 2018). Because published among-individual level estimates were largely
99 absent (only 3% of studies reported actual among-individual level estimates; see below), we

100 proceeded to identify which studies in our systematic literature review contained adequate data
101 (repeated measures of behaviour) even if the published statistical analyses were performed at
102 the phenotypic level. We then contacted the authors for the raw datasets. Using the collected
103 datasets, we re-analysed the data at the among-individual level. We tested three key predictions.
104 First, we investigated whether higher levels of bold, active, aggressive and/or explorative
105 behaviour were associated with decreased survival at the among-individual level (Stamps 2007;
106 Biro & Stamps 2008a; Réale *et al.* 2010; Dammhahn *et al.* 2018). Previous research has
107 suggested that females incur a stronger survival cost than males at the phenotypic level, even
108 though sexes do not differ in their mean behavioural expression or in the variance in behaviour
109 (Tarka *et al.* 2018). Therefore, as a second step, we tested whether females differ in the strength
110 of the correlation between behaviour and survival compared to males at the individual level.
111 Finally, we explored whether the relationship between behaviour and survival was different
112 when it was measured in the wild versus in the laboratory as predation pressure and resource
113 constraints, two key ecological features predicted to affect the costs and benefits of behavioural
114 expression, are present in the wild but not in the laboratory environments.

115

116 **METHODS**

117 **(a) Collection of meta-analytical data**

118 We conducted a literature search in Web of Science and Scopus on 26 September 2018 to
119 retrieve papers presenting data on behaviour (with repeated measures, or with single
120 measurements and reporting repeatability estimates for the focal dataset) and survival variables
121 following the preferred reporting items for systematic reviews and meta-analyses (PRISMA)
122 approach (Liberati *et al.* 2009; Moher *et al.* 2009) (electronic supplementary material, Fig. S1).
123 We used search terms that would identify papers focusing on among-individual associations
124 (e.g., “animal personality” and “behavioural syndrome”) between behaviour and survival
125 (search terms are presented in electronic supplementary material, Text S1). In our Web of

126 Science search, we used “Zoology”, “Behavioral sciences”, “Ecology”, “Biology”,
127 “Evolutionary biology”, and “Multidisciplinary sciences” as topic fields. In our Scopus search,
128 we used “Agricultural and Biological Sciences” as the topic field. Altogether the searches
129 retrieved 674 papers from 2007-2018. We also screened papers cited in Table 1 of Smith &
130 Blumstein (2008) to retrieve those studies (published prior 2007) reporting individual-level
131 correlations between behaviour and survival. Because the vast majority of studies (see below)
132 presented repeated measures of behaviour but did not make use of them statistically (i.e.,
133 reported unpartitioned phenotypic correlations instead of among-individual correlations), we
134 contacted the authors of those studies and requested the primary dataset. We also posted a
135 message on Twitter and directly asked colleagues who work on the topic of individual
136 differences in behaviour and survival, to contribute primary datasets (details about datasets can
137 be found in electronic supplementary material, Table S1). With all the collected datasets, we
138 estimated (unpublished) among-individual correlations between behaviour and survival.

139 Our search retrieved a total of 125 estimates from 34 studies with primary datasets
140 collected (plus estimates from one published study) from which we had to drop seven studies
141 due to convergence problems (see below). From the remaining 27 studies with primary datasets
142 collected (Table 1): five were fully unpublished, 20 were published but did not estimate among-
143 individual correlations (rather they used the unpartitioned phenotypic correlations), and two
144 published studies did estimate among-individual correlations but used a different statistical
145 approach than a bivariate model. In total from these 27 studies, we collected 41 datasets which
146 we re-analysed to get comparable estimates across all studies. From these 41 datasets, 18 had
147 information on males, 16 had information on females and in seven datasets, the sex was
148 unknown. These datasets comprised a wide range of taxa, from mammals, fish, insects,
149 molluscs, reptiles and birds (Table 1, Fig. S2).

150 From each dataset we extracted the following information: type of behaviour (e.g.
151 exploration, activity, boldness, aggression), type of fitness component (longevity, survival), sex

152 (male, female, unknown), whether measurements were taken in the laboratory or in the wild,
153 species name and sample sizes (number of individuals and number of observations). Each
154 dataset often comprised several behaviours and/or survival estimates. Following Niemelä &
155 Dingemanse (2018), we changed the values of the behavioural trait within the data sets (by
156 multiplying it by -1) to ensure that higher values indicated more risky behaviour (*sensu* Réale
157 *et al.* 2007): higher levels of boldness, activity, exploration or aggressiveness, and lower levels
158 of docility (see the electronic supplementary material, Table S1 for which estimates were
159 multiplied by -1).

160

161 **(b) Statistical methods for extraction of the estimates for meta-analytic models**

162 In order to collect correlation coefficients at the among-individual level (r_i) from the data sets
163 described above, we constructed four types of bivariate models depending on the error
164 distribution of behavioural and survival data: 1) binary behaviour and binary survival, 2) binary
165 behaviour and Gaussian survival, 3) Gaussian behaviour and Gaussian survival and 4) Gaussian
166 behaviour and binary survival. For one dataset (Quinn *et al.* 2009), the residuals of longevity
167 data were Poisson distributed, and we changed the link function to Poisson.

168 Since survival is by definition a fixed trait (i.e. it is only expressed once for each
169 individual) and thus does not harbour within-individual variation, we fixed the residual variance
170 of survival to one. We also fixed the residual variance to be one for behaviours with binary
171 error distribution. Residual covariance between behaviour and survival was restricted to be not
172 estimated. One could argue that non-biological residual variation may still exist in any fixed
173 trait due to the measurement error (Brommer 2013). However, measurement error should not
174 be generally correlated with the trait value (i.e., the residual covariation due to measurement
175 error should be zero) (Brommer 2013), and thus, is likely not pooled to the among-individual
176 level correlations. In all models, we set the behaviour and survival as the two response variables

177 and individual identity as random effect and estimated the among-individual level correlation
178 coefficients with 95% Credible Intervals.

179 We also had eight data sets where the behaviour was measured only once, but
180 repeatability estimates (R_y) for the all the behaviours were available for the focal dataset.
181 Normally, it is not possible to estimate among-individual correlations in the absence of repeated
182 measurements. However, since survival is a fixed trait ($R_z = 1$ in Eqn. 1), the residual part in
183 the equation describing the association between different levels of correlations (Eqn.1) is
184 dropped and, thus, simplified to Eqn.2. In this way, we can estimate the among-individual
185 correlation by estimating the phenotypic correlation between behaviour and survival (i.e. r_{p_y,p_z})
186 and then, dividing the posterior distribution of r_{p_y,p_z} by $\sqrt{R_y}$ (Eqn.3).

187

$$188 \quad r_{p_y,p_z} = r_{i_y,i_z} \sqrt{R_y R_z} + r_{e_y,e_z} \sqrt{(1 - R_y)(1 - R_z)} \quad \text{Eqn.1}$$

$$189 \quad r_{p_y,p_z} = r_{i_y,i_z} \sqrt{R_y} \quad \text{Eqn.2}$$

$$190 \quad r_{i_y,i_z} = r_{p_y,p_z} / \sqrt{R_y} \quad \text{Eqn.3}$$

191 where r_{p_y,p_z} , r_{i_y,i_z} and r_{e_y,e_z} are the phenotypic, among-individual and within-individual
192 correlations between the behavioural trait y and survival z , respectively. R_y and R_z are the
193 repeatabilities of behaviour and survival, respectively.

194 We ran the bivariate models using the R-package *MCMCglmm* (Hadfield 2010) in the
195 statistical environment R 3.5.1. (R Core Team 2017). The chain length varied between
196 2,300,000 to 10,300,000 depending on the model to ensure sufficient sampling of the chain. We
197 always used a burn-in of 300,000 and sampled the chain every 2,000 iterations. We used four
198 different parameter expanded priors tailored specifically for each of the four types of bivariate
199 models used (electronic supplementary material, see Text S2). We had to drop seven data sets

200 due to convergence problems (mostly caused by very low sample sizes in number of
201 individuals). This led to a final sample size of 125 correlation coefficients from 27 studies with
202 primary data collected and one published study (Table 1).

203

204 **(c) Statistical methods for meta-analytic models**

205 We estimated the i) average among-individual level correlation between behaviour and survival
206 (i.e. r_{i_y, i_z}), ii) average absolute magnitude (i.e. $|r_{i_y, i_z}|$) and iii) squared average absolute
207 magnitude of that correlation (i.e. $|r_{i_y, i_z}|^2$) of that correlation. The first estimate describes the
208 linear statistical relationship between two traits, the second estimate describes the absolute
209 magnitude of the correlation between two traits while the latter represents the proportion of
210 among-individual variance in behaviour (i.e., animal personality) that is attributable (in a
211 statistical sense) to among-individual variation in survival. We applied the “analyse-then-
212 transform” approach (Morrissey 2016), consisting of estimating the posterior distribution of the
213 average z-transformed correlation coefficient ($r_{i_y, i_z} Z$; Eqn. 4), back-transforming this posterior
214 to standard correlation coefficients (r_{i_y, i_z} ; Eqn. 5), folding the latter posterior to return the
215 absolute average magnitude of the correlations ($|r_{i_y, i_z}|$) (Eqn. 7 in Morrissey 2016), and squaring
216 the folded posterior distribution to estimate $|r_{i_y, i_z}|^2$ (Niemelä & Dingemanse 2018a). This
217 approach is more accurate than the alternative “transform-then-analyse” approach (Morrissey,
218 2016; Nakagawa & Lagisz, 2016), where correlations are transformed into absolute values prior
219 to analysis. Since we used posterior distributions for each estimate, we were able to take the
220 uncertainty forward in each step of the modelling process. For each focal posterior distribution
221 (i.e. r_{i_y, i_z} , $|r_{i_y, i_z}|$, or $|r_{i_y, i_z}|^2$), we estimated the mode and 95% Credible Intervals (95% CI). We
222 also estimated total heterogeneity (I^2 total), residual heterogeneity (I^2 residual), phylogenetic
223 heterogeneity (I^2 phylogeny) and study heterogeneity (I^2 study) while statistically controlling
224 for sampling error variance (Higgins & Thompson 2002) (Table 3). I^2 is an estimation of the

225 proportion of variance among effect sizes explained by a focal variance component, after
226 controlling the effect sizes for sampling variance.

$$227 \quad Z_r = \frac{1}{2} \ln \frac{1+r}{1-r} \quad \text{Eqn. 4}$$

$$228 \quad r = \frac{\exp(2Z_r)-1}{\exp(2Z_r)+1} \quad \text{Eqn. 5}$$

229 We applied multilevel meta-analytic models (i.e. intercept models) for all estimates of
230 among-individual correlations between behaviour and survival (i.e. global model), for studies
231 conducted in the wild and in the laboratory, and for females and males separately. We controlled
232 for sampling variance in all models as a way to control the correlation coefficients for statistical
233 noise (e.g. differences in sample size across correlation coefficients). By controlling for
234 sampling variance the precision of estimated effect size is greatly increased (Morrissey 2016;
235 Nakagawa & Lagisz 2016). Sampling variance was calculated from the standard error (using
236 Eqn. 6). Thus, the 95% Credible Intervals from each 125 correlation coefficient were
237 transformed into standard errors prior to calculating sampling variance by using Eqn. 7. We
238 included data set identity and phylogeny as random effects in all meta-analytic models. Our
239 models are thus controlled for pseudo-replication caused by the inclusion of repeated
240 correlation coefficients from the same data set and, for evolutionary divergence of the species.
241 Our pooled data contained 28 data sets (27 data sets with published and unpublished primary
242 data, plus one published study with published correlation coefficient estimates) and the
243 phylogeny was constructed of 24 different species (Table 1, Fig. S2). The meta-analytical
244 models were run using the R-package *MCMCglmm* (Hadfield 2010) in the statistical
245 environment R 3.5.1. (R Core Team 2017) . Estimates with 95% Credible Intervals not
246 overlapping with zero were viewed as indicating statistically important effects. All meta-
247 analytic models were run with chain length of 2,300,000 with burn-in 300,000 and sampling
248 rate of 2000, and with inverse-gamma priors.

249 $Var Z_r = SE^2 \left(\frac{1}{(1+r)(1-r)} \right)^2$ Eqn. 6

250 $SE = \frac{(upper\ 95\% CI - lower\ 95\% CI)}{2t_{n-3}}$ Eqn. 7

251 In Eqn. 4 – Eqn. 7, r represents the focal correlation coefficient, Z_r represents the Z-transformed
252 r , n the number of individuals, SE the standard error, and 95% CI the 95% Credible Intervals.

253

254 **(d) Directional bias in the estimates**

255 The majority of the datasets we used in our analyses were associated with published studies
256 (five datasets were unpublished, Table 1); however our (re-) analysis of these data resulted in
257 new correlation coefficients that are previously unpublished. Indeed, only three out of 125
258 among-individual correlation coefficients were included in the published (all three estimates
259 came from a single study) studies we used, and so we cannot estimate the publication bias in
260 our correlation coefficients. Instead, our test of “publication bias” represents the general
261 directional bias in our (unpublished) data. To visualize such potential directional bias in our
262 correlation coefficients, we constructed a funnel plot for the main meta-analytic model by fitting
263 precision (i.e., the inverse of sampling variance) as a function of meta-analytic residuals
264 (Nakagawa & Santos 2012). We further used Egger’s regression analysis to statically test
265 whether the distribution of correlation coefficients was more asymmetrical than expected by
266 chance (Stuck *et al.* 1998). Following Nakagawa and Santos (2012), meta-analytic residuals
267 were calculated using the R-package *MCMCglmm* (Hadfield 2010), and Egger’s regression
268 conducted using the R-package *metaphor* (Viechtbauer 2010).

269

270 **RESULTS**

271 *Among-individual correlations between behaviour and survival*

272 Contrary to our first prediction, we did not find evidence that the average among-individual
273 correlation between survival and behaviour was different from zero ($r = [\text{mean, 95\% CI}] 0.072$
274 $(-0.105, 0.201)$); that is, individuals that exhibited riskier behaviour did not suffer greater
275 mortality. In regards to our second prediction, we did not find evidence that females differed in
276 their strength of correlation compared to males (Table 2). However, we did find that the average
277 correlation estimated from data collected in the wild was positive ($r = 0.156 (0.019, 0.314)$),
278 while the correlation did not differ from zero when the data was collected in the laboratory
279 environment ($r = -0.043 (-0.284, 0.261)$). This result indicates that in the wild more risky (i.e.
280 more active, explorative, aggressive and bold) individuals live longer compared to less risky
281 individuals.

282 The absolute average correlation was important in all meta-analytic models (range
283 $0.157\text{--}0.267$) (Table 2), indicating that the correlation between behaviours and survival is on
284 average different from zero (irrespective of the direction of the correlation). Finally, behaviours
285 globally explained 4.4% of the variation in survival at the among-individual level ($|r|^2$ in global
286 model = 0.044, Table 2). The proportion of variance in survival explained by the individual level
287 behavioural expression did not differ between wild and laboratory conditions, or between males
288 and females (Table 2).

289 *Sampling variance*

290 We found no directional bias in our (mostly unpublished) correlation coefficients given that the
291 funnel plot was symmetrical (Fig. 1) and the Egger's regression indicated lack of bias
292 ($p=0.218$). The total heterogeneity was high (79%; Table 3) following Higgins & Thompson
293 (2002) classification (i.e. 25%: small, 50%: medium, 75%: high). This means that statistical
294 noise or sampling error, (i.e. sampling variance) explained only a small amount of the total
295 variance in our data of correlation coefficients (i.e. 21%). Study-level heterogeneity was
296 moderate (36%), meaning that the magnitude and/or sign of correlations differed between

297 studies (Table 3). Residual heterogeneity was moderate to small (27%; Table 3), indicating that
298 within a study, the correlations were relatively similar. Phylogeny explained only a small
299 amount of variation and had large standard deviation (16%; Table 3). This indicates that 1) the
300 evolutionary signal in correlation coefficients between behaviour and survival is weak and 2)
301 that there might be low genetic variation among species in the correlation between behaviour
302 and survival.

303

304 **DISCUSSION**

305 Contrary to our prediction, we did not find evidence for a negative relationship between
306 behaviour and survival. That is, risky behavioural types (i.e., more active, bold and/or more
307 explorative individuals) did not generally pay a survival cost. While the previous meta-analysis
308 performed by Smith & Blumstein (2008) identified significant associations between behaviour
309 and survival (i.e., negative association of survival with boldness, and positive with exploration),
310 our results are, however, not comparable with them. This is because the meta-analysis by Smith
311 & Blumstein (2008) synthesized studies that investigated the association between behaviour
312 and survival at the (unpartitioned) phenotypic level while our work explicitly focuses at among-
313 individual level of (co)variation. Overall, our results show that empirical evidence does not
314 support one of the central theories explaining maintenance of behavioural variation at the
315 among-individual level of variation (e.g. Sih *et al.* 2004a; Stamps 2007; Biro & Stamps 2008;
316 Réale *et al.* 2010; Dammhahn *et al.* 2018) and thus, suggests that theory might need to be
317 revised. Alternatively, theory might still be valid but empiricists are not testing it correctly
318 either by failing to measure the correct behaviours (e.g. truly risky behaviours) (Carter *et al.*
319 2013) and/or survival without bias (Biro & Dingemanse 2009; Biro 2012; Stuber *et al.* 2013;
320 Niemelä *et al.* 2015). Nevertheless, the absolute magnitude of the correlation was different from
321 zero ($|r| \sim 0.21$), meaning that the direction of the correlation simply differs across studies (i.e.

322 large among-study heterogeneity, Table 3). Since behaviour explained around 4% of the
323 variation in survival, our results indicate that behaviour is an important (although weak)
324 predictor of survival, but not in the way predicted by predominant theory.

325 Interestingly, our meta-analysis revealed that individuals that displayed risky
326 behavioural types live longer in the wild but this association was absent under laboratory
327 conditions. This difference might occur because of (at least) three (non-exclusive) reasons.
328 Firstly, the species composition in studies conducted in the wild versus in the laboratory may
329 differ systematically. If species differ in the strength of among-individual correlation between
330 behaviours and survival, this could cause the correlation coefficients to differ substantially
331 across environments. Indeed, studies carried out in the wild focused almost solely on birds and
332 small mammals while studies conducted in the laboratory used almost entirely invertebrates
333 (Table 1, Fig. S2). However, our results do not provide strong support for this interpretation;
334 variance explained by the phylogeny in our global model was small (and with large error term,
335 Table 3). Secondly, the positive association between risky behaviours and survival in the wild
336 could have been partly caused by higher encounter rates of risky (compared to shy) behavioural
337 types. Indeed, there is increasing evidence for sampling bias towards risky behavioural types in
338 the wild (Stuber *et al.* 2013; Niemelä *et al.* 2015). We, however, excluded data sets where the
339 survival estimates could have been biased by higher encounter rates of risky behavioural types.
340 All the wild studies included in our meta-analysis were either i) conducted in closed
341 populations, ii) reported extremely high encounter rates or iii) were studies where direct
342 mortality was observed. Thus, our meta-analytic estimate is most likely representing true
343 variation in survival rates rather than variation in encounter rates. The third, and we argue most
344 likely, explanation is that the selection pressures differ across the two environments (Frankham
345 2008; Niemelä & Dingemanse 2014). Risky behaviours are predicted to facilitate higher
346 resource acquisition in the wild, potentially leading to a subsequent increase in body condition,
347 but at the cost of higher predation risk (Stamps 2007; Biro & Stamps 2008b; Réale *et al.* 2010).

348 However, in laboratory environments, those environmental factors determining the causes and
349 consequences of the expression of risky behaviours are largely removed; i.e., risky behaviours
350 do not facilitate higher resource acquisition nor lead to higher mortality due to predation,
351 breaking the functional association between behaviour and survival. This means that empiricists
352 are most likely measuring biologically different phenomena in the wild versus laboratory (i.e.,
353 intrinsic mortality in the laboratory and extrinsic mortality in the wild), making the correlations
354 differ across environments. Nevertheless, given that we found a positive correlation between
355 expressions of risky behaviours and survival in the wild, our results may actually indicate that
356 risky behavioural types in the wild can avoid or reduce the costs associated with predation
357 (compared to shy types), potentially because they are able to acquire better or more resources,
358 and therefore, present greater body condition and competitive abilities.

359 Another major finding is that very few studies that set out to study the association of
360 among-individual variation in behaviour and survival were partitioning the behavioural
361 variance into its among- and within-individual components. Thus, empiricists are mainly testing
362 the theory at a different level of variation (i.e. unpartitioned phenotypic level) compared to where
363 the theory has been laid out (i.e. among-individual level). Generally, there is an increasing
364 concern that empiricists are using inappropriate data collection methods and/or statistical tools
365 when testing theories related to animal personality, i.e., individual differences in behavioural
366 expression (Niemelä & Dingemanse 2018a, b; Royauté *et al.* 2018). For example, a previous
367 meta-analysis showed that ~80% of studies claiming to test individual-level theory used
368 methods that did not allow for answering individual-level questions (Niemelä & Dingemanse
369 2018a). Our study shows that only 3% (3/100) of the papers that were present in the last stage
370 of the PRISMA-protocol, delivered actual among-individual level parameter estimates
371 (Bergeron *et al.* 2013; Niemelä *et al.* 2015; Boulton *et al.* 2018). In the rest (97% of the studies),
372 authors provided unpartitioned phenotypic level estimates and applied the “individual gambit”,
373 i.e. assumed that the among- and within-individual patterns of co-variation are similar in

374 strength and direction (Brommer 2013; Dingemanse & Dochtermann 2013; Niemelä &
375 Dingemanse 2018b). Partitioning behavioural variance into its among- and within-individual
376 components not only provides important insights about the detailed biological mechanisms
377 underlying behavioral expression (Dingemanse *et al.* 2010), but more importantly, if the models
378 and predictions are developed at a specific level of variation (e.g., the focal theory tested in this
379 work explicitly lays out among-individual level predictions), the unpartitioned phenotypic data
380 can therefore not test theory in an unbiased manner. A remarkable example of individual-level
381 study in the context of our meta-analysis is Boulton *et al.* (2018), where authors used bivariate
382 mixed-effects models to estimate (unbiased) among-individual level correlations between
383 behaviour and longevity. Generally, information about appropriate data collection designs and
384 statistical tools to test (among-) individual level theory is widely available (e.g., van de Pol &
385 Wright 2009; Dingemanse & Dochtermann 2013). In the future, we hope that empiricists
386 increasingly apply these tools to expand the proportion of studies that firmly test the focal
387 theory at the appropriate level of variation.

388

389 CONCLUSION

390 Individual variation in behaviour is predicted to be related to differences in individual fitness
391 components such as survival and longevity. Using meta-analytic techniques, we were able to
392 show that there is indeed a significant relationship between behaviour and survival, with
393 behavioural variation explaining about 4% of the variance in survival. However, this
394 relationship was not in the direction predicted by the key models, implying that current
395 theoretical predictions are not capturing the whole complexity of the phenomenon. Current
396 theory suggesting negative associations between individual level expression of risky behaviours
397 and survival is almost solely based on verbal models (Mathot & Frankenhuis 2018). We
398 therefore need more formal mathematical models that assess under which conditions risky

399 behavioural types would or would not incur a survival cost, encouraging further theoretical
400 work on developing environmental-specific hypothesis and empirical work on testing the
401 validity of those predictions.

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602 **TABLES**

603 **Table 1.** Summary of data from each study used in the meta-analyses. For each study, we print
 604 an abbreviated reference to the study (“Study”), the Latin name of the study species (“Species”),
 605 the study environment (“Environment”), and the number of estimates *per* study (“Estimates”).

Study	Species	Environment	Estimates
(Schuett <i>et al.</i> 2015)	<i>Acyrtosiphon pisum</i>	lab	2
(Lapiedra <i>et al.</i> 2018)	<i>Anolis sagrei</i>	wild	4
(Piquet <i>et al.</i> 2018)	<i>Atlantoxerus getulus</i>	wild	4
(Foster <i>et al.</i> 2017)	<i>Chlorostoma funebris</i>	lab	2
(Keiser <i>et al.</i> 2018)	<i>Chlorostoma funebris</i>	lab	6
(Jablonszky <i>et al.</i> 2018)	<i>Ficedula albicollis</i>	wild	1
(Niemelä <i>et al.</i> 2019)	<i>Gryllus bimaculatus</i>	lab	4
(Santostefano <i>et al.</i> 2017)	<i>Gryllus bimaculatus</i>	lab	8
(Fisher <i>et al.</i> 2015)	<i>Gryllus campestris</i>	wild	10
(Niemelä <i>et al.</i> 2015)	<i>Gryllus campestris</i>	wild	2
(Akçay <i>et al.</i> 2015)	<i>Melospiza melodia amaka</i>	wild	6
(Marshall <i>et al.</i> 2016)	<i>Mungos mungo</i>	wild	6
(Réale & Festa-Bianchet 2003)	<i>Ovis canadensis canadensis</i>	wild	2
(van Overveld <i>et al.</i> 2015)	<i>Parus major major</i>	wild	2
(Quinn <i>et al.</i> 2009)	<i>Parus major major</i>	wild	2
(Kain & McCoy 2016)	<i>Physella acuta</i>	lab	3
(Hulthén <i>et al.</i> 2017)	<i>Rutilus rutilus caspicus</i>	wild	1
(Santicchia <i>et al.</i> 2018)	<i>Sciurus vulgaris orientis</i>	wild	4
(Morales <i>et al.</i> 2013)	<i>Sitophilus zeamais</i>	lab	20
(Shackleton <i>et al.</i> 2005)	<i>Teleogryllus commodus</i>	lab	1
(Monceau <i>et al.</i> 2017)	<i>Tenebrio molitor</i>	lab	8
(Boulton <i>et al.</i> 2018)	<i>Xiphophorus birchmanni</i>	lab	3
(Kralj-Fišer <i>et al.</i> 2017)	<i>Zygiella x-notata</i>	lab	6
Polverino (unpublished)	<i>Gambusia holbrooki</i>	lab	2
Niemela (unpublished)	<i>Gryllus campestris</i>	wild	4
Pruitt (unpublished)	<i>Strongylocentrotus purpuratus</i>	lab	4
Salandova (unpublished)	<i>Pisaura mirabilis</i>	lab	4
Lundy sparrow project (unpublished)	<i>Passer domesticus domesticus</i>	wild	4

606 ***footnote:** We obtained four datasets from colleagues: 1) Salandova (unpublished data), 2)
 607 Fisher *et al.* 2015, 3) Pruitt (unpublished), and 4) Santostefano *et al.* 2017. We obtained the
 608 datasets of Lundy sparrow project (Unpublished data) and Polverino (Unpublished data) via
 609 Twitter; and included two of our own datasets: Niemelä (Unpublished data) and Niemelä *et al.*

610 2019. The datasets from van Overveld et al. 2015 and Kralj-Fišer et al. 2017 present the original
611 published data from the paper plus additional unpublished data. The dataset of Lundy sparrow
612 project (unpublished data) present data partially published in Sánchez-Tójar *et al.* 2017.

613 **Table 2.** Estimates of r (correlation coefficient), $|r|$ (absolute magnitude of correlation
614 coefficient) and $|r|^2$ (squared absolute magnitude of correlation coefficient) between behaviour
615 and survival from our meta-analytic models. We show the point mode estimates with 95%
616 Credible Intervals (in brackets). Sample sizes (n= number of estimates) are indicated after the
617 description of the focal model.

Model	r	r	$r ^2$
Global (n=125)	0.072 (-0.105;0.201)	0.209 (0.155;0.324)	0.044 (0.024;0.105)
Wild (n=46)	0.156 (0.019;0.314)	0.267 (0.174;0.382)	0.072 (0.030;0.146)
Laboratory (n=79)	-0.043 (-0.284;0.261)	0.250 (0.126;0.495)	0.036 (0.014;0.238)
Females (n=43)	0.088 (-0.021;0.240)	0.157 (0.077;0.288)	0.025 (0.003;0.073)
Males (n=60)	0.058 (-0.132;0.238)	0.231 (0.157;0.376)	0.053 (0.016;0.128)

618 **Table 3.** Heterogeneity estimates (I^2) with the associated standard deviation (in brackets) for
619 the global meta-analytic model. I^2 refers to the proportion of variance among effect sizes
620 explained by a focal variance component after excluding the total sampling error variance. We
621 present heterogeneity estimates for study identity and phylogeny and, the residual and total
622 heterogeneity.

	I^2 Study	I^2 Phylogeny	I^2 Residual	Total heterogeneity
Global model	0.36 (0.16)	0.16 (0.17)	0.27 (0.10)	0.79 (0.06)

623 **FIGURES**

624 **Figure 1.** Funnel plot of precision for z-transformed among-individual correlation coefficients
625 (r_Z) between survival and behavioural traits. Inner and outer dashed lines indicate pseudo- 95%
626 and 99% confidence intervals, respectively. The solid red vertical line indicates the deviation
627 of the distribution of r_Z from the zero effect.

