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REVIEW AND SYNTHESIS

Individual differences in behaviour explain variation in survival: a meta-analysis

Maria Moiron,[1]* **Kate L. Laskowski**[2] **and Petri T. Niemelä**[3]

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Abstract

Research focusing on among-individual differences in behaviour ('animal personality') has been blooming for over a decade. Central theories explaining the maintenance of such behavioural variation posits that individuals expressing greater "risky" behaviours should suffer higher mortality. Here, for the first time, we synthesize the existing empirical evidence for this key prediction. Our results did not support this prediction as there was no directional relationship between riskier behaviour and greater mortality; however there was a significant absolute relationship between behaviour and survival. In total, behaviour explained a significant, but small, portion (5.8%) of the variance in survival. We also found that risky (vs. "shy") behavioural types live significantly longer in the wild, but not in the laboratory. This suggests that individuals expressing risky behaviours might be of overall higher quality but the lack of predation pressure and resource restrictions mask this effect in laboratory environments. Our work demonstrates that individual differences in behaviour explain important differences in survival but not in the direction predicted by theory. Importantly, this suggests that models predicting behaviour to be a mediator of reproduction-survival trade-offs may need revision and/or empiricists may need to reconsider their proxies of risky behaviours when testing such theory.

Keywords

Among-individual variation, animal personality, bivariate model, fitness, longevity, repeatability, selection, systematic review.

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INTRODUCTION

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

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

Labile traits, such as behaviours, vary both among- and within-individuals: individuals differ relative to one another in their average behavioural expression (i.e. 'animal

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[1] *Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175 Campus CNRS, Montpellier, France*

[2] *Department of Evolution and Ecology, University of California Davis, Davis, CA, USA*

[3] *Behavioural Ecology, Department of Biology, Ludwig-Maximilians University of Munich, Planegg-Martinsried, Germany*

**Correspondence: E-mail: mariamoironc@gmail.com*

personality'), while, at the same time, change their behavioural expression from one instance to the next (i.e. 'reversible plasticity'), respectively (Dingemanse & Dochtermann 2013). Both individual differences and reversible plasticity in the expression of labile traits can be independently associated with survival (Sih *et al.* 2004b; Ratikainen & Kokko 2019). Moreover, the strength and direction of the associations between traits often differs between the among- vs. within-individual levels (Adolph & Hardin 2007; Brommer 2013; Niemelä & Dingemanse 2018a), leading phenotypic correlations to misestimate among-individual correlations (Dingemanse *et al.* 2012; Brommer 2013; Niemelä & Dingemanse 2018a). The models predicting a negative association between survival and expression of risky behaviors explicitly state that those traits covary at the among-individual level (Stamps 2007; Biro & Stamps 2008; Réale *et al.* 2010). Thus, unbiased testing of this theoretical prediction requires study designs and statistical analyses that allow researchers to partition behavioural variation to its among- and within-individual levels (Dingemanse *et al.* 2012; Brommer 2013; Niemelä & Dingemanse 2018b). Such partitioning is currently still rare in the empirical behavioural ecology literature (Royauté *et al.* 2018; Niemelä & Dingemanse 2018b). This is probably the main reason why a previous meta-analysis focusing on animal personality and survival was conducted at the (unpartitioned) phenotypic level instead of among-individual level of variation (Smith & Blumstein 2008). A systematic review testing whether empirical work supports this key theoretical prediction at the among-individual level is therefore still lacking.

In this study we conducted the first-ever meta-analysis to estimate the overall empirical support for the hypothesis predicting among-individual differences in (risky) behaviour to negatively correlate with survival (Stamps 2007; Biro & Stamps 2008; Réale *et al.* 2010; Dammhahn *et al.* 2018). Because published among-individual level estimates were largely absent (only 3% of studies reported actual among-individual level estimates; see below), we proceeded to identify which studies in our systematic literature review contained adequate data (repeated measures of behaviour) even if the published statistical analyses were performed at the phenotypic level. We then contacted the authors for the raw datasets. Using the collected datasets, we re-analysed the data at the among-individual level. First, we investigated whether higher levels of bold, active, aggressive and/or explorative behaviour were associated with decreased survival at the among-individual level (Stamps 2007; Biro & Stamps 2008; Réale *et al.* 2010; Dammhahn *et al.* 2018). Previous research has suggested that females incur a stronger survival cost than males at the phenotypic level, even though sexes do not differ in their mean behavioural expression or in their variance in behaviour (Tarka *et al.* 2018). Second, we tested whether females differ in the strength of the correlation between behaviour and survival compared to males at the among-individual level. Finally, we explored whether the relationship between behaviour and survival was different when it was measured in the wild vs. in the laboratory as predation pressure and resource constraints, two key ecological features predicted to affect the costs and benefits of behavioural expression, are present in the wild but, generally, not in laboratory environments.

METHODS

Collection of meta-analytical data

We conducted a literature search in Web of Science and Scopus on 26 September 2018 to retrieve papers presenting data on behaviour (with repeated measures, or with single measurements and reporting repeatability estimates for the focal dataset or population) and survival variables following the preferred reporting items for systematic reviews and meta-analyses (PRISMA) approach (Liberati *et al.* 2009; Moher *et al.* 2009) (Fig. S1). We used search terms that would identify papers focusing on among-individual associations (e.g. 'animal personality' and 'behavioural syndrome') between behaviour and survival (search terms are presented in Text S1). In our Web of Science search, we used "Zoology", 'Behavioral sciences', 'Ecology', 'Biology', 'Evolutionary biology', and 'Multidisciplinary sciences' as topic fields. In our Scopus search, we used 'Agricultural and Biological Sciences' as the topic field. Altogether the searches retrieved 674 papers from 2007 to 2018. We also screened papers cited in Table 1 of Smith & Blumstein (2008) to retrieve those studies published prior 2007 reporting individual-level correlations between behaviour and survival. Because the vast majority of studies (see below) presented repeated measures of behaviour but did not make use of them statistically (i.e. reported unpartitioned phenotypic correlations instead of among-individual correlations), we contacted the authors of those studies and requested the primary dataset. We also posted a message on Twitter and directly asked colleagues who work on the topic of individual differences in behaviour and survival, to contribute primary datasets (details about datasets can be found in Table S1). With all the collected datasets, we estimated (unpublished) among-individual correlations between behaviour and survival.

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

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

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

*We obtained four datasets from colleagues: 1) Salandova (unpublished data), 2) Fisher *et al.* 2015, 3) Pruitt (unpublished), and 4) Santostefano *et al.* 2017. We obtained the datasets of Lundy sparrow project (Unpublished data) and Polverino (Unpublished data) via Twitter; and included two of our own datasets: Niemelä (Unpublished data) and Niemelä *et al.* 2019. The datasets from van Overveld *et al.* 2015 and Kralj-Fišer *et al.* 2017 present the original published data from the paper plus additional unpublished data. The dataset of Lundy sparrow project (unpublished data) present data partially published in Sánchez-Tójar *et al.* 2017.

From each dataset, we extracted the following information: type of behaviour (e.g. exploration, activity, boldness, aggression), type of measured mortality (longevity, survival), sex (male, female, unknown), whether measurements were taken in the laboratory or in the wild, species name and sample sizes (number of individuals and number of observations). Each dataset often comprised several behaviours and survival estimates. Following Niemelä & Dingemanse (2018a), we changed the values of the behavioural trait within the data sets (by multiplying it by -1) to ensure that higher values indicated more risky behaviour (*sensu* Réale *et al.* 2007): higher levels of boldness, activity, exploration or aggressiveness, and lower levels of docility (see the Table S1 for which estimates were multiplied by -1).

Statistical methods for extraction of the estimates for meta-analytic models

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

Since survival is by definition a fixed trait (i.e. it is only expressed once for each individual) and thus does not harbour within-individual variation, we fixed the residual variance of survival to one. We also fixed the residual variance to be one for behaviours with Binary error distribution. Residual covariance between behaviour and survival was restricted to be not estimated. One could argue that non-biological residual variation may still exist in any fixed trait due to the measurement error (Brommer 2013). However, measurement error should not be generally correlated with the trait value (i.e. the residual covariation due to measurement error should be zero) (Brommer 2013), and thus, is likely not pooled to the among-individual level correlations. In all models, we set the behaviour and survival as the two response variables and individual identity as random effect and estimated the among-individual level correlation coefficients with 95% Credible Intervals.

We also had eight data sets where the behaviour was measured only once. Normally, it is not possible to estimate among-individual correlations in the absence of repeated measurements. However, it is possible to estimate among-individual correlations by using single measurements when the repeatability (R_y in eqn 1–3) is available for the focal data set (i.e. when behaviour is measured repeatedly for a subset of individuals in the focal dataset) or for the same focal population from which the data is collected. This is because survival is a fixed trait (there is no within-individual variation) ($R_z = 1$in Eqn 1) and so the residual part in the equation describing the association between different levels of correlations (eqn 1) can be dropped and, thus, simplified to eqn 2. Then, we can estimate the among-individual correlation by estimating the phenotypic correlation between behaviour and survival (i.e.r_{p_y,p_z}) and dividing the posterior distribution of r_{p_y,p_z} by $\sqrt{R_y}$ (eqn 3). Generally, eqn 3 also implies that studies estimating phenotypic correlations between behaviour and survival are expected to systematically underestimate the among-individual correlation. It is important, however, to notice that when adopting this method one should strictly use the repeatability estimate derived from the same focal population as repeatability estimates generally vary across populations.

$$r_{p_y,p_z} = r_{i_y,i_z}\sqrt{R_y R_z} + r_{e_y,e_z}\sqrt{\left(1-R_y\right)\left(1-R_z\right)} \tag{1}$$

$$r_{p_y,p_z} = r_{i_y,i_z}\sqrt{R_y} \tag{2}$$

$$r_{i_y,i_z} = r_{p_y,p_z}/\sqrt{R_y}, \tag{3}$$

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 correlations between the behavioural trait y and survival z, respectively. R_y and R_z are the repeatabilities of behaviour and survival, respectively.

We ran the bivariate models using the R-package *MCMCglmm* (Hadfield 2010) in the statistical environment R 3.5.1. (R Core Team 2017). The chain length varied between 2 300 000 and 10 300 000 depending on the model to ensure sufficient sampling of the chain. We always used a burn-in of 300 000 and sampled the chain every 2000 iterations. We used four different parameter expanded priors tailored specifically for each of the four types of bivariate models used (see Text S2). We had to drop seven data sets due to convergence problems (mostly caused by very low sample sizes in number of individuals). This led to a final sample size of 125 correlation coefficients from 27 studies with primary data collected and one published study (Table 1). Among-individual correlation estimates were robust to reasonable alternative priors (see Text S3, Table S2, Fig. S3). Additionally, correlation estimates did not differ when we modelled test sequence as a fixed effect to control for the order that the repeated measures in behaviour were taken (see Table S3, Fig. S4).

Statistical methods for meta-analytic models

We estimated the (1) average among-individual level correlation between behaviour and survival (i.e. r_{i_y,i_z}), (2) average absolute magnitude (i.e. $|r_{i_y,i_z}|$) and (3) squared average absolute magnitude of that correlation (i.e. $|r_{i_y,i_z}|^2$). The first estimate describes the linear statistical relationship between two traits, the second estimate describes the absolute magnitude of the correlation between two traits while the latter represents the proportion of among-individual variance in survival that is attributable (in a statistical sense) to among-individual variation in behaviour (i.e. animal personality) (Niemelä & Dingemanse 2018a). We applied the ‘analyse-then-transform’ approach (Morrissey 2016), consisting of estimating the posterior distribution of the average z-transformed correlation coefficient (Zr_{i_y,i_z}; eqn 4), back-transforming this posterior to standard correlation coefficients (r_{i_y,i_z}; eqn 5), folding this posterior to return the absolute average magnitude of the correlations ($|r_{i_y,i_z}|$) (eqn 7 in Morrissey 2016), and squaring the folded posterior distribution to estimate $|r_{i_y,i_z}|^2$ (Niemelä & Dingemanse 2018a). This approach is more accurate than the alternative ‘transform-then-analyse’ approach (Morrissey, 2016; Nakagawa & Lagisz, 2016), where correlations are folded into absolute values prior to analysis. This is because if correlations are folded prior to analysis, the sampling variances do not anymore fully match with the focal correlation values used in the meta-analytic model. Since we used posterior distributions for each estimate, we were able to take the uncertainty forward in each step of the modelling process. For each focal posterior distribution (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 also estimated total heterogeneity (I^2 total), residual heterogeneity (I^2 residual), phylogenetic heterogeneity (I^2 phylogeny), study heterogeneity (I^2 study) and animal group heterogeneity (I^2 group; several behaviours and thus correlations might have been measured from the same group of animals) while statistically controlling for sampling error variance (Higgins & Thompson 2002). I^2 is an estimation of the proportion of variance among effect sizes explained by a focal variance component, after controlling the effect sizes for sampling variance. We estimated $\mathrm{I}^{2'}$s for all meta-analytic models.

$$Z_r = \frac{1}{2} ln \frac{1+r}{1-r} \tag{4}$$

$$r = \frac{\exp(2Z_r)-1}{\exp(2Z_r)+1} \tag{5}$$

We applied multilevel meta-analytic models (i.e. intercept models) for all estimates of among-individual correlations between behaviour and survival (i.e. global model), for studies conducted in the wild and in the laboratory, and for females and males separately. We controlled for sampling variance in all models as a way to control the correlation coefficients for statistical noise (e.g. differences in sample size across correlation coefficients). By controlling for sampling variance the precision of estimated effect size is greatly increased (Morrissey 2016; Nakagawa & Lagisz 2016). To calculate the sampling variance, we first transformed the 95% Credible Intervals from each 125 correlation coefficient into standard errors using eqn 6. We then calculated the sampling variance from those standard errors using eqn 7. We included study identity, animal group identity and phylogeny as random effects in all meta-analytic models. Our models are thus controlled for 1) pseudo-replication caused by the inclusion of repeated correlation coefficients from the same study, 2) pseudo-replication caused by inclusion of repeated correlations from the same groups of animals (e.g. the same study can contain several correlations from males and females or from different treatment groups, generating non-independence between correlation coefficients) and, for 3) evolutionary divergence of the species. Our pooled data contained 28 studies (27 studies with published and unpublished primary data, plus one published study with published correlation coefficient estimates) and 53 animal groups. The phylogeny was constructed of 24 different species (Table 1, Fig. S2). The meta-analytical models were run using the R-package *MCMCglmm* (Hadfield 2010) in the statistical environment R 3.5.1. (R Core Team 2017). Estimates with 95% Credible Intervals not overlapping with zero were viewed as indicating statistically important effects. All meta-analytic models were run with chain length of 2 300 000 with burn-in 300 000 and sampling rate of 2000, and with inverse-gamma priors.

$$SE = \frac{(\text{upper } 95\%CI - \text{lower } 95\%CI)}{2t_{n-3}} \tag{6}$$

$$VarZ_r = SE^2\left(\frac{1}{(1+r)(1-r)}\right)^2 \tag{7}$$

In eqn 4–7*,* r represents the focal correlation coefficient, Zr represents the Z-transformed r*,* n the number of individuals, SE the standard error, t the student's t-distribution, and 95% CI the 95% Credible Intervals.

Directional bias in the estimates

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

RESULTS

Among-individual correlations between behaviour and survival

Contrary to our first prediction, we did not find evidence that the average among-individual correlation between survival and behaviour was negative (r = [mean, 95% CI] 0.047 (−0.128, 0.194)); that is, individuals that, on average, exhibited riskier behaviours did not live less long. We also did not find evidence that females and males differed in the correlation between behaviours and survival (Table 2, Fig. 1). However, we did find that the average correlation estimated from data collected in the wild was significantly positive (r = 0.147 (0.006, 0.326)), while the correlation did not differ from zero when the data was collected in the laboratory environment (r = −0.038 (−0.310, 0.309)). This result indicates that in the wild more risky (i.e. more active, explorative, aggressive and bold) individuals live longer compared to less risky individuals.

The absolute average correlation was important in all meta-analytic models (range 0.184–0.274) (Table 2, Fig. 1), indicating that the correlation between behaviours and survival is, on average, different from zero (irrespective of the direction of the correlation). Finally, behaviour globally explained 5.8% of the variation in survival at the among-individual level ($|r|^2$ in global model = 0.058, Table 2, Fig. 1). The proportion of variance in survival explained by the individual level behavioural expression did not differ between wild and laboratory conditions, or between males and females (Table 2, Fig. 1).

Sampling variance

We found no directional bias in our (mostly unpublished) correlation coefficients given that the funnel plot was symmetrical (Fig. 2) and the Egger's regression indicated lack of bias (P = 0.193). The total heterogeneity was high (80%; Table 3) following Higgins & Thompson (2002) classification (i.e. 25%: small, 50%: medium, 75%: high). This means that statistical noise or sampling error (i.e. sampling variance) explained only a small amount of the total variance in our data of correlation coefficients (i.e. 20%). The patterns of heterogeneity found in our meta-analysis are in accordance with general expectations in ecological studies: the average heterogeneity in ecological studies is *c.* 85% and researchers should typically expect heterogeneity between 60 and 90% in meta-analytical studies (Senior *et al.* 2016). Study-level heterogeneity was moderate (28%), meaning that the magnitude and/or sign of correlations differed among studies (Table 3). Animal group heterogeneity was small (16%) indicating that correlation coefficients vary more among studies (see above) than among groups of animals. Residual heterogeneity was small (21%; Table 3), indicating that within a study and groups of animals, the correlations were relatively similar. Phylogeny explained only a small amount of variation and had a large standard deviation (15%; Table 3). This indicates that (1) the evolutionary signal in correlation coefficients between behaviour and survival is weak and (2) that there might be low genetic variation among species in the correlation between behaviour and survival. Generally, the total heterogeneities were of similar magnitude in all meta-analytic models (Table 3).

Table 2 Estimates of r (correlation coefficient), $|r|$ (absolute magnitude of correlation coefficient) and $|r|^2$ (squared absolute magnitude of correlation coefficient) between behaviour and survival from our meta-analytic models

Model	r	$\|r\|$	$\|r\|^2$
Global (n = 125)	0.047 (−0.128;0.194)	0.236 (0.157;0.326)	0.058 (0.024;0.105)
Wild (n = 52)	0.147 (0.006;0.326)	0.274 (0.178;0.387)	0.079 (0.029;0.145)
Laboratory (n = 73)	−0.038 (−0.310;0.309)	0.308 (0.139;0.530)	0.108 (0.019;0.280)
Females (n = 43)	0.105 (−0.049;0.259)	0.184 (0.089;0.304)	0.038 (0.005;0.086)
Males (n = 60)	0.040 (−0.150;0.243)	0.256 (0.159;0.381)	0.069 (0.021;0.136)

We show the point mode estimates with 95% Credible Intervals (in brackets). Sample sizes (n = number of estimates) are indicated after the description of the focal model

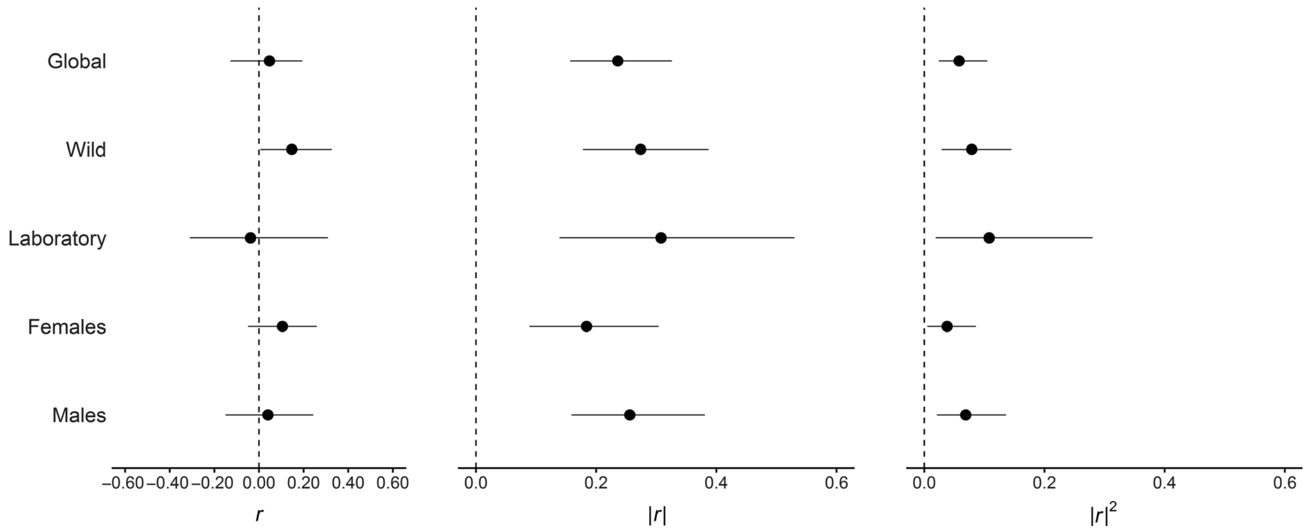

Figure 1 Forest plot showing the meta-analytic estimates of r (correlation coefficient), $|r|$ (absolute magnitude of correlation coefficient) and $|r|^2$ (squared absolute magnitude of correlation coefficient) between behaviour and survival. We show point estimates with 95% Credible Intervals.

DISCUSSION

Contrary to our prediction, we did not find evidence for a negative relationship between behaviour and survival. That is, risky behavioural types (i.e. more active, bold and/or more explorative individuals) did not generally pay a survival cost. While the previous meta-analysis performed by Smith & Blumstein (2008) identified significant associations between behaviour and survival, our results are, however, not comparable with them. This is because the meta-analysis by Smith & Blumstein (2008) synthesized studies that investigated the association between behaviour and survival at the (unpartitioned) phenotypic level while our work explicitly focuses at among-individual level of (co)variation. Overall, our results show that empirical evidence does not support some of the central theories explaining the maintenance of behavioural variation at the among-individual level (e.g. Sih *et al.* 2004a; Stamps 2007; Biro & Stamps 2008; Réale *et al.* 2010; Dammhahn *et al.* 2018) and, thus, suggests that theory might need to be revised. Alternatively, theory might still be valid but empiricists are not testing it correctly either by failing to measure the correct behaviours (e.g. truly risky behaviours) and/or survival without bias (Biro & Dingemanse 2009; Biro 2012; Carter *et al.* 2013; Stuber *et al.* 2013; Niemelä *et al.* 2015). Nevertheless, the absolute magnitude of the correlation was different from zero (|r|˜0.24), meaning that the direction of the correlation simply differs across studies (i.e. moderate among-study heterogeneity, Table 3). Since behaviour explained around 6% of the variation in survival, our results indicate that behaviour is indeed an important (although weak) predictor of survival, but not in the way predicted by the predominant theory.

Interestingly, our meta-analysis revealed that individuals that displayed risky behavioural types live longer in the wild but this association was absent under laboratory conditions. This pattern might occur because of, at least, three (non-exclusive) reasons. Firstly, the species composition in studies conducted in the wild vs. in the laboratory may differ systematically. If species differ in the strength of among-individual correlation between behaviours and survival, this could cause the correlation to be significant in one environment and non-significant in the other. Indeed, studies carried out in the wild focused almost solely on birds and small mammals while studies conducted in the laboratory used almost entirely invertebrates (Table 1, Fig. S2). However, our results do not provide strong support for this interpretation; variance explained by the phylogeny in our global model was small (and with a large error term, Table 3). Secondly, the positive association between risky behaviours and survival in the wild could have been partly caused by higher encounter rates of risky

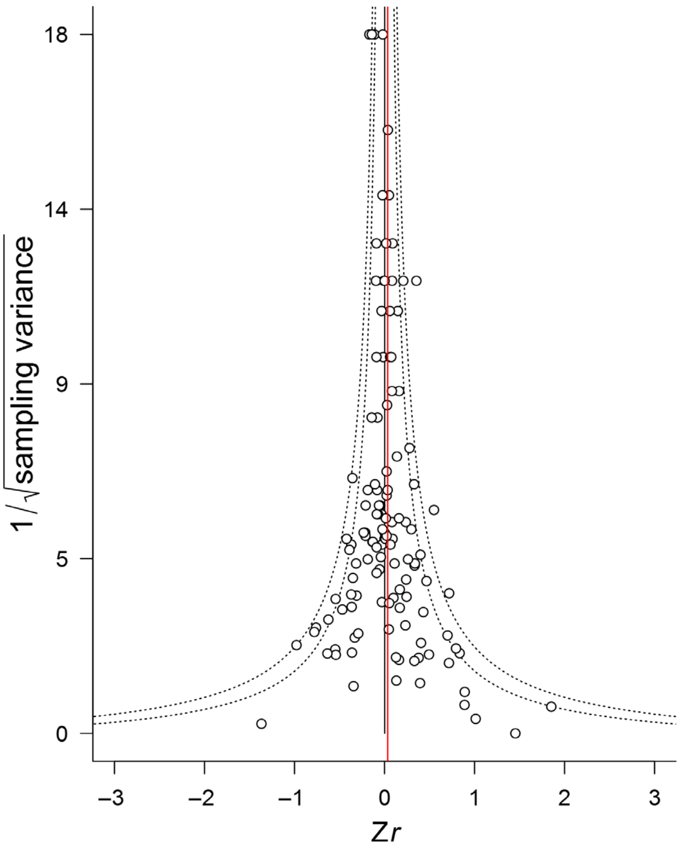

Figure 2 Funnel plot of precision for Z-transformed among-individual correlation coefficients (*Zr*) between survival and behavioural traits. Inner and outer dashed lines indicate pseudo- 95% and 99% confidence intervals, respectively. The solid red vertical line indicates the deviation of the distribution of *Zr* from the zero effect.

(compared to shy) behavioural types. Indeed, there is increasing evidence for sampling bias towards risky behavioural types in the wild (Stuber *et al.* 2013; Niemelä *et al.* 2015). We, however, excluded data sets where the survival estimates could have been biased by higher encounter rates of risky behavioural types. All the wild studies included in our meta-analysis were either (1) conducted in closed populations, (2) reported extremely high encounter rates or (3) were studies where direct mortality was observed. Thus, our meta-analytic estimate is most likely representing true variation in survival rates rather than variation in encounter rates. The third, and we argue most likely, explanation is that the selection pressures differ across the two environments (Frankham 2008; Niemelä & Dingemanse 2014). Risky behaviours are predicted to facilitate higher resource acquisition in the wild, potentially leading to a subsequent increase in body condition, but at the cost of higher predation risk (Stamps 2007; Biro & Stamps 2008; Réale *et al.* 2010). However, in laboratory environments, those environmental factors determining the consequences of the expression of risky behaviours are largely absent; i.e. risky behaviours do not facilitate higher resource acquisition nor lead to higher mortality due to predation, breaking the functional association between behaviour and survival. This means that empiricists are most likely measuring biologically different phenomena in the wild vs. laboratory (i.e. intrinsic mortality in the laboratory and extrinsic mortality in the wild), making the correlations significant in one but not the other environment. Nevertheless, we found a significant positive correlation between expressions of risky behaviours and survival in the wild. This finding may indicate that risky behavioural types in the wild can avoid or reduce the costs associated with predation, potentially because they are able to acquire better or more resources, and therefore, present greater body condition and competitive abilities.

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

Table 3 Heterogeneity estimates (I^2) with the associated standard deviation (in brackets) for all meta-analytic models

	I^2 Study	I^2 Group	I^2 Phylogeny	I^2 Residual	I^2 Total
Global model	0.28 (0.16)	0.16 (0.13)	0.15 (0.16)	0.21 (0.09)	0.80 (0.06)
Wild model	0.10 (0.11)	0.22 (0.17)	0.08 (0.09)	0.35 (0.17)	0.76 (0.07)
Laboratory model	0.30 (0.25)	0.06 (0.08)	0.39 (0.30)	0.11 (0.08)	0.86 (0.07)
Female model	0.12 (0.11)	0.12 (0.12)	0.14 (0.14)	0.16 (0.14)	0.54 (0.16)
Male model	0.32 (0.22)	0.19 (0.18)	0.14 (0.14)	0.20 (0.11)	0.85 (0.05)

I^2 refers to the proportion of variance among effect sizes explained by a focal variance component after excluding the total sampling error variance. We present heterogeneity estimates for study identity, group identity and phylogeny and, the residual and total heterogeneity.

survival are similar in strength and direction (Brommer 2013; Dingemanse & Dochtermann 2013; Niemelä & Dingemanse 2018b). Partitioning behavioural variance into its among- and within-individual components provides relevant insights about the detailed biological mechanisms underlying behavioural expression (Dingemanse *et al*. 2010). More importantly, if the models and predictions are developed at a specific level of variation (e.g. the focal theory tested in this work), the unpartitioned phenotypic data cannot test theory in an unbiased manner. A remarkable example of truly individual-level study in the context of our meta-analysis is Boulton *et al*. (2018), where authors used bivariate mixed-effects models to estimate among-individual level correlations between behaviour and longevity. Generally, information about appropriate data collection designs and statistical tools to test (among-) individual level theory is widely available (e.g. van de Pol & Wright 2009; Dingemanse & Dochtermann 2013). In the future, we hope that empiricists increasingly adopt these tools to expand the proportion of studies that firmly test the focal theory at the appropriate level of variation.

CONCLUSION

Individual variation in behaviour is predicted to be related to differences in individual fitness components such as survival and longevity. Using a meta-analytic approach, we were able to show that behavioural variation explained about 6% of the variance in survival. However, the relationship between survival and behaviour was not in the direction predicted by the key models, implying that current theoretical predictions are not capturing the whole complexity of the phenomenon. Current theory suggesting negative associations between among-individual level expression of risky behaviours and survival is almost solely based on verbal models (Mathot & Frankenhuis 2018). We therefore need more formal mathematical models that assess under which conditions risky behavioural types would or would not incur a survival cost, encouraging further theoretical work on developing environmental-specific hypothesis and empirical work on testing the validity of those predictions.

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AUTHORSHIP

M.M., K.L.L. and P.T.N. designed the study, performed the literature review and estimated correlation coefficients; P.T.N. ran meta-analytical models; and all authors wrote the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cvdncjt0c (Moiron *et al*. 2019).

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