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

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

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

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

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

Corresponding author: Maria Moiron, CEFE UMR 5175, 1919 route de Mende, 34293, Montpellier, France; Tel: +33(0)467613311; Fax: +33(0)467613336.

E-mail addresses: M. Moiron (mariamoironc@gmail.com), K.L. Laskowski (klaskowski@ucdavis.edu), P.T. Niemelä (niemela@biologie.uni-muenchen.de)

Running headline: meta-analysis of behaviour and survival

Keywords: among-individual variation, animal personality, bivariate model, fitness, longevity, repeatability, selection, systematic review

Type of article: Reviews and Syntheses

Authorship statement: 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 accessibility statement: Data will be available from the Dryad Digital Repository and data DOI will be included at the end of the article.

Word count in main text: 4347, **Number of figures:** 1, **Number of tables:** 3, **Number of references:** 77

ABSTRACT

Research focusing on among-individual differences in behaviour (“animal personality”) has been blooming for over a decade. One of the central theories explaining the maintenance of behavioural variation posits a trade-off between behaviour and survival with individuals expressing greater “risky” behaviours suffering 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 (4.4%) of the variance in survival. We also found that risky (versus “shy”) behavioural types live 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 implies that individual differences in behaviour explain important differences in survival but not in the direction predicted by theory. Importantly, this suggests that the models predicting survival trade-offs may need revision and/or empiricists may need to reconsider their proxies of risky behaviours when testing such theory.

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 among-individual variation in behavioural expression (also termed "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 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 as mechanisms explaining 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 2008a; 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 2008a; 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 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 mean behavioural expression, while, at the same time, change their behavioural expression from one instance to the next, respectively (Dingemanse & Dochtermann 2013). Both individual differences and reversible plasticity in the expression of labile traits are predicted to be independently associated with survival (Sih *et al.* 2004b; Ratikainen & Kokko 2019). Moreover, the direction of the associations between traits often differs at the among- versus within-individual levels (Adolph & Hardin 2007; Brommer 2013; Niemelä & Dingemanse 2018b). The models predicting a negative association between survival and risky behavioural types explicitly state that those traits covary at the among-individual level of variation (Stamps 2007; Biro & Stamps 2008a; Réale *et al.* 2010). Thus, unbiased testing of the theoretical prediction at the among-individual level of variation requires study designs and statistical analyses that allow researchers to partition behavioural (co)variance to its among- and within-individual levels (Brommer 2013; Dingemanse & Dochtermann 2013; Niemelä & Dingemanse 2018a). Nevertheless, such partitioning is currently still rare in the empirical behavioural ecology literature (Niemelä & Dingemanse 2018a, b; Royauté *et al.* 2018). 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 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 2008a; 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. We tested three key predictions. 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 2008a; 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 the variance in behaviour (Tarka *et al.* 2018). Therefore, as a second step, we tested whether females differ in the strength of the correlation between behaviour and survival compared to males at the individual level. Finally, we explored whether the relationship between behaviour and survival was different when it was measured in the wild versus 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 not in the laboratory environments.

METHODS

(a) 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) and survival variables following the preferred reporting items for systematic reviews and meta-analyses (PRISMA) approach (Liberati *et al.* 2009; Moher *et al.* 2009) (electronic supplementary material, 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 electronic supplementary material, 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 2007-2018. 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 electronic supplementary material, Table S1). With all the collected datasets, we estimated (unpublished) among-individual correlations between behaviour and survival.

Our search retrieved a total of 125 estimates from 34 studies with primary datasets collected (plus estimates from one published study) from which we had to drop seven studies due to convergence problems (see below). From the remaining 27 studies with primary datasets collected (Table 1): five were fully unpublished, 20 were published but did not estimate among-individual correlations (rather they used the 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 re-analysed 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).

From each dataset we extracted the following information: type of behaviour (e.g. exploration, activity, boldness, aggression), type of fitness component (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/or survival estimates. Following Niemelä & Dingemanse (2018), 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 electronic supplementary material, Table S1 for which estimates were multipled by -1).

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

In order to collect 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, but repeatability estimates (R_y) for the all the behaviours were available for the focal dataset. Normally, it is not possible to estimate among-individual correlations in the absence of repeated measurements. However, since survival is a fixed trait ($R_z = 1 \; in \; Eqn. 1$), the residual part in the equation describing the association between different levels of correlations (Eqn.1) is dropped and, thus, simplified to Eqn.2. In this way, we can estimate the among-individual correlation by estimating the phenotypic correlation between behaviour and survival (i.e. r_{p_y,p_z}) and then, dividing the posterior distribution of r_{p_y,p_z} by $\sqrt{R_y}$ (Eqn.3).

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

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

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

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 to 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 2,000 iterations. We used four different parameter expanded priors tailored specifically for each of the four types of bivariate models used (electronic supplementary material, 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).

(c) Statistical methods for meta-analytic models

We estimated the i) average among-individual level correlation between behaviour and survival (i.e. r_{i_y,i_z}), ii) average absolute magnitude (i.e. $|r_{i_y,i_z}|$) and iii) squared average absolute magnitude of that correlation (i.e. $|r_{i_y,i_z}|^2$) of that correlation. 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 behaviour (i.e., animal personality) that is attributable (in a statistical sense) to among-individual variation in survival. We applied the "analyse-then-transform" approach (Morrissey 2016), consisting of estimating the posterior distribution of the average z-transformed correlation coefficient (r_{i_y,i_z}Z; Eqn. 4), back-transforming this posterior to standard correlation coefficients (r_{i_y,i_z}; Eqn. 5), folding the latter 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 transformed into absolute values prior to analysis. 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) and study heterogeneity (I^2 study) while statistically controlling for sampling error variance (Higgins & Thompson 2002) (Table 3). 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.

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

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

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). Sampling variance was calculated from the standard error (using Eqn. 6). Thus, the 95% Credible Intervals from each 125 correlation coefficient were transformed into standard errors prior to calculating sampling variance by using Eqn. 7. We included data set identity and phylogeny as random effects in all meta-analytic models. Our models are thus controlled for pseudo-replication caused by the inclusion of repeated correlation coefficients from the same data set and, for evolutionary divergence of the species. Our pooled data contained 28 data sets (27 data sets with published and unpublished primary data, plus one published study with published correlation coefficient estimates) and 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.

$$VarZ_r = SE^2\left(\frac{1}{(1+r)(1-r)}\right)^2 \qquad \text{Eqn. 6}$$

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

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

(d) 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 were included in the published (all three estimates came from a single study) studies we used, and so 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 and 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 different from zero (*r* = [mean, 95% CI] 0.072 (-0.105, 0.201)); that is, individuals that exhibited riskier behaviour did not suffer greater mortality. In regards to our second prediction, we did not find evidence that females differed in their strength of correlation compared to males (Table 2). However, we did find that the average correlation estimated from data collected in the wild was positive (*r* = 0.156 (0.019, 0.314)), while the correlation did not differ from zero when the data was collected in the laboratory environment (*r* = -0.043 (-0.284, 0.261)). 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 0.157–0.267) (Table 2), indicating that the correlation between behaviours and survival is on average different from zero (irrespective of the direction of the correlation). Finally, behaviours globally explained 4.4% of the variation in survival at the among-individual level ($|r|^2$ in global model= 0.044, Table 2). 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).

Sampling variance

We found no directional bias in our (mostly unpublished) correlation coefficients given that the funnel plot was symmetrical (Fig. 1) and the Egger's regression indicated lack of bias (*p*=0.218). The total heterogeneity was high (79%; 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. 21%). Study-level heterogeneity was moderate (36%), meaning that the magnitude and/or sign of correlations differed between studies (Table 3). Residual heterogeneity was moderate to small (27%; Table 3), indicating that within a study, the correlations were relatively similar. Phylogeny explained only a small amount of variation and had large standard deviation (16%; 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.

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 (i.e., negative association of survival with boldness, and positive with exploration), 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 one of the central theories explaining maintenance of behavioural variation at the among-individual level of variation (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) (Carter *et al.* 2013) and/or survival without bias (Biro & Dingemanse 2009; Biro 2012; Stuber *et al.* 2013; Niemelä *et al.* 2015). Nevertheless, the absolute magnitude of the correlation was different from zero (|r|~0.21), meaning that the direction of the correlation simply differs across studies (i.e.

large among-study heterogeneity, Table 3). Since behaviour explained around 4% of the variation in survival, our results indicate that behaviour is an important (although weak) predictor of survival, but not in the way predicted by 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 difference might occur because of (at least) three (non-exclusive) reasons. Firstly, the species composition in studies conducted in the wild versus 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 coefficients to differ substantially across environments. 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 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 (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 i) conducted in closed populations, ii) reported extremely high encounter rates or iii) 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 2008b; Réale *et al.* 2010).

However, in laboratory environments, those environmental factors determining the causes and consequences of the expression of risky behaviours are largely removed; 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 versus laboratory (i.e., intrinsic mortality in the laboratory and extrinsic mortality in the wild), making the correlations differ across environments. Nevertheless, given that we found a positive correlation between expressions of risky behaviours and survival in the wild, our results may actually indicate that risky behavioural types in the wild can avoid or reduce the costs associated with predation (compared to shy types), 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 the association of among-individual variation in 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. unpartioned 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., individual differences in behavioural expression (Niemelä & Dingemanse 2018a, b; Royauté *et al.* 2018). For example, a previous meta-analysis showed that ~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 among- and within-individual patterns of co-variation are similar in strength and direction (Brommer 2013; Dingemanse & Dochtermann 2013; Niemelä & Dingemanse 2018b). Partitioning behavioural variance into its among- and within-individual components not only provides important insights about the detailed biological mechanisms underlying behavioral expression (Dingemanse *et al.* 2010), but more importantly, if the models and predictions are developed at a specific level of variation (e.g., the focal theory tested in this work explicitly lays out among-individual level predictions), the unpartitioned phenotypic data can therefore not test theory in an unbiased manner. A remarkable example of individual-level study in the context of our meta-analysis is Boulton *et al.* (2018), where authors used bivariate mixed-effects models to estimate (unbiased) 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 apply 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 meta-analytic techniques, we were able to show that there is indeed a significant relationship between behaviour and survival, with behavioural variation explaining about 4% of the variance in survival. However, this relationship 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 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.

AKNOWLEDGEMENTS

We thank Alfredo Sánchez-Tójar and Raphaël Royauté for feedback in the methodological approach, all authors of Table 1 for sharing their raw data, and Jonathan Pruitt, Erik Mathyssen, Giovanni Polverino, Pavla Salandova, Lucas Wauters, Julia Greenberg, Anssi Vainikka, Bart Adriaenssens, Maren Vitousek, Chelsea Blake, Mark McCormick, Patricia Fleming, David Fisher, Francesca Santostefano, John Quinn, Simona Kralj-Fiser, Lundy Sparrow Project, Alfredo Sánchez-Tójar and Wolf Blanckenhorn for sharing the requested and/or unpublished data. M.M. was funded by a Marie Skłodowska-Curie Individual Fellowship (PLASTIC TERN, Grant Agreement Number 793550); P.T.N. was supported by the DFG (Deutsche Forschungsgemeinschaft; NI 1539/2-1).

REFERENCES

Adolph, S.C. & Hardin, J.S. (2007). Estimating phenotypic correlations: correcting for bias due to intraindividual variability. *Funct. Ecol.*, 21, 178–184.

Akçay, Ç., Campbell, S.E. & Beecher, M.D. (2015). The fitness consequences of honesty: Under-signalers have a survival advantage in song sparrows. *Evolution*, 69, 3186–3193.

Bell, A.M., Hankison, S.J. & Laskowski, K.L. (2009). The repeatability of behaviour: a meta-analysis. *Anim. Behav.*, 77, 771–783.

Bergeron, P., Montiglio, P.-O., Réale, D., Humphries, M.M., Gimenez, O. & Garant, D. (2013). Disruptive viability selection on adult exploratory behaviour in eastern chipmunks. *J. Evol. Biol.*, 26, 766–774.

Biro, P. a. (2012). Do rapid assays predict repeatability in labile (behavioural) traits? *Anim. Behav.*, 83, 1295–1300.

Biro, P.A. & Dingemanse, N.J. (2009). Sampling bias resulting from animal personality. *Trends Ecol. Evol.*, 24, 66–67.

Biro, P.A. & Stamps, J.A. (2008a). Are animal personality traits linked to life-history productivity? *Trends Ecol. Evol.*, 23, 361–368.

Biro, P.A. & Stamps, J.A. (2008b). Are animal personality traits linked to life-history productivity? *Trends Ecol. Evol.*, 23, 361–8.

Boulton, K., Walling, C.A., Grimmer, A.J., Rosenthal, G.G. & Wilson, A.J. (2018). Phenotypic and genetic integration of personality and growth under competition in the sheepshead swordtail, Xiphophorus birchmanni. *Evolution*, 72, 187–201.

Brommer, J.E. (2013). On between-individual and residual (co)variances in the study of animal personality: are you willing to take the "individual gambit"? *Behav. Ecol. Sociobiol.*, 67, 1027–1032.

Carere, C. & Gherardi, F. (2013). Animal personalities matter for biological invasions. *Trends Ecol. Evol.*, 28, 5–6.

Carter, A.J., Feeney, W.E., Marshall, H.H., Cowlishaw, G. & Heinsohn, R. (2013). Animal personality: what are behavioural ecologists measuring? *Biol. Rev. Camb. Philos. Soc.*, 88, 465–75.

Chapple, D.G., Simmonds, S.M. & Wong, B.B.M. (2012). Can behavioral and personality traits influence the success of unintentional species introductions? *Trends Ecol. Evol.*, 27, 57–64.

Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, A. (2010). Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philos. Trans. R. Soc. B Biol. Sci.*, 365, 4065–4076.

Dall, S.R.X., Bell, A.M., Bolnick, D.I. & Ratnieks, F.L.W. (2012). An evolutionary ecology of individual differences. *Ecol. Lett.*, 15, 1189–98.

Dammhahn, M., Dingemanse, N.J., Niemelä, P.T. & Réale, D. (2018). Pace-of-life syndromes: a framework for the adaptive integration of behaviour, physiology and life history. *Behav. Ecol. Sociobiol.*, 72, 62.

Dingemanse, N.J. & Dochtermann, N. (2013). Quantifying individual variation in behaviour: mixed-effect modelling approaches. *J. Anim. Ecol.*, 82, 39–54.

Dingemanse, N.J., Kazem, A.J.N., Réale, D. & Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol. Evol.*, 25, 81–9.

Dingemanse, N.J. & Reale, D. (2005). Natural Selection and Animal Personality. *Behavior*, 142, 1159–1184.

DiRienzo, N., Pruitt, J.N. & Hedrick, A. V. (2013). The combined behavioural tendencies of predator and prey mediate the outcome of their interaction. *Anim. Behav.*, 86, 317–322.

Fisher, D.N., David, M., Tregenza, T. & Rodríguez-Muñoz, R. (2015). Dynamics of among-individual behavioral variation over adult lifespan in a wild insect. *Behav. Ecol.*, 26, 975–985.

Fogarty, S., Cote, J. & Sih, A. (2011). Social Personality Polymorphism and the Spread of Invasive Species: A Model. *Am. Nat.*, 177, 273–287.

Foster, W.C., Armstrong, C.M., Chism, G.T. & Pruitt, J.N. (2017). Smaller and bolder prey snails have higher survival in staged encounters with the sea star Pisaster giganteus. *Curr. Zool.*, 63, 633–638.

Frankham, R. (2008). Genetic adaptation to captivity in species conservation programs. *Mol. Ecol.*, 17, 325–333.

Hadfield, J. (2010). MCMC Methods for Multi-response Generalized Linear Mixed Models : The MCMCglmm R Package. *J. Stat. Softw.*, 33, 1–22.

Higgins, J.P.T. & Thompson, S.G. (2002). Quantifying heterogeneity in a meta-analysis. *Stat. Med.*, 21, 1539–1558.

Holtmann, B., Lagisz, M. & Nakagawa, S. (2017). Metabolic rates, and not hormone levels, are a likely mediator of between-individual differences in behaviour: a meta-analysis. *Funct. Ecol.*, 31, 685–696.

Hulthén, K., Chapman, B.B., Nilsson, P.A., Hansson, L.-A., Skov, C., Brodersen, J., *et al.* (2017). A predation cost to bold fish in the wild. *Sci. Rep.*, 7, 1239.

Jablonszky, M., Szász, E., Krenhardt, K., Markó, G., Hegyi, G., Herényi, M., *et al.* (2018). Unravelling the relationships between life history, behaviour and condition under the pace-of-life syndromes hypothesis using long-term data from a wild bird. *Behav. Ecol. Sociobiol.*, 72, 52.

Kain, M.P. & McCoy, M.W. (2016). Anti-predator behavioral variation among Physa acuta in response to temporally fluctuating predation risk by Procambarus. *Behav. Processes*, 133, 15–23.

Keiser, C.N., Ingley, S.J., Toscano, B.J., Scharf, I. & Pruitt, J.N. (2018). Habitat complexity dampens selection on prey activity level. *Ethology*, 124, 25–32.

Kralj-Fišer, S., Hebets, E.A. & Kuntner, M. (2017). Different patterns of behavioral variation across and within species of spiders with differing degrees of urbanization. *Behav. Ecol. Sociobiol.*, 71, 125.

Lapiedra, O., Schoener, T.W., Leal, M., Losos, J.B. & Kolbe, J.J. (2018). Predator-driven natural selection on risk-taking behavior in anole lizards. *Science (80-.).*, 360, 1017–1020.

Liberati, A., Altman, D.G., Tetzlaff, J., Mulrow, C., Gøtzsche, P.C., Ioannidis, J.P.A., *et al.* (2009). The PRISMA statement for reporting systematic reviews and meta-analyses of studies that evaluate health care interventions: explanation and elaboration. In: *Journal of clinical epidemiology*.

Marshall, H.H., Sanderson, J.L., Mwanghuya, F., Businge, R., Kyabulima, S., Hares, M.C., *et al.* (2016). Variable ecological conditions promote male helping by changing banded mongoose group composition. *Behav. Ecol.*, 27, 978–987.

Mathot, K.J. & Frankenhuis, W.E. (2018). Models of pace-of-life syndromes (POLS): a systematic review. *Behav. Ecol. Sociobiol.*, 72, 41.

McGhee, K.E., Pintor, L.M. & Bell, A.M. (2013). Reciprocal Behavioral Plasticity and Behavioral Types during Predator-Prey Interactions. *Am. Nat.*, 182, 704–717.

Moher, D., Liberati, A., Tetzlaff, J. & Altman, D.G. (2009). Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement. *J. Clin. Epidemiol.*, 62, 1006–1012.

Monceau, K., Dechaume-Moncharmont, F.-X., Moreau, J., Lucas, C., Capoduro, R., Motreuil, S., *et al.* (2017). Personality, immune response and reproductive success: an appraisal of the pace-of-life syndrome hypothesis. *J. Anim. Ecol.*, 86, 932–942.

Morales, J.A., Cardoso, D.G., Della Lucia, T.M.C. & Guedes, R.N.C. (2013). Weevil x Insecticide: Does 'Personality' Matter? *PLoS One*, 8, e67283.

Morrissey, M.B. (2016). Meta-analysis of magnitudes, differences and variation in evolutionary parameters. *J. Evol. Biol.*, 29, 1882–1904.

Nakagawa, S. & Lagisz, M. (2016). Visualizing unbiased and biased unweighted meta-analyses. *J. Evol. Biol.*, 29, 1914–1916.

Nakagawa, S. & Santos, E.S.A. (2012). Methodological issues and advances in biological meta-analysis. *Evol. Ecol.*, 26, 1253–1274.

Niemelä, P.T. & Dingemanse, N.J. (2014). Artificial environments and the study of "adaptive" personalities. *Trends Ecol. Evol.*, 29, 245–247.

Niemelä, P.T. & Dingemanse, N.J. (2018a). Meta-analysis reveals weak associations between intrinsic state and personality. *Proc. R. Soc. B Biol. Sci.*, 285, 20172823.

Niemelä, P.T. & Dingemanse, N.J. (2018b). On the usage of single measurements in behavioural ecology research on individual differences. *Anim. Behav.*, 145, 99–105.

Niemelä, P.T., Lattenkamp, E.Z. & Dingemanse, N.J. (2015). Personality-related survival and sampling bias in wild cricket nymphs. *Behav. Ecol.*, 26, 936–946.

Niemelä, P.T., Niehoff, P.P., Gasparini, C., Dingemanse, N.J. & Tuni, C. (2019). Crickets become behaviourally more stable when raised under higher temperatures. *Behav. Ecol. Sociobiol.*, 73, 81.

van Overveld, T., Adriaensen, F. & Matthysen, E. (2015). No evidence for correlational selection on exploratory behaviour and natal dispersal in the great tit. *Evol. Ecol.*, 29, 137–156.

Pettorelli, N., Hilborn, A., Duncan, C. & Durant, S.M. (2015). Individual Variability. In: *Advances in Ecological Research*. pp. 19–44.

Piquet, J.C., López-Darias, M., van der Marel, A., Nogales, M. & Waterman, J. (2018). Unraveling behavioral and pace-of-life syndromes in a reduced parasite and predation pressure context: personality and survival of the Barbary ground squirrel. *Behav. Ecol. Sociobiol.*, 72, 147.

van de Pol, M. & Wright, J. (2009). A simple method for distinguishing within- versus between-subject effects using mixed models. *Anim. Behav.*, 77, 753–758.

Pruitt, J.N., Stachowicz, J.J. & Sih, A. (2012). Behavioral Types of Predator and Prey Jointly Determine Prey Survival: Potential Implications for the Maintenance of Within-Species Behavioral Variation. *Am. Nat.*, 179, 217–227.

Quinn, J.L., Patrick, S.C., Bouwhuis, S., Wilkin, T.A. & Sheldon, B.C. (2009). Heterogeneous selection on a heritable temperament trait in a variable environment. *J. Anim. Ecol.*, 78, 1203–1215.

R Core Team. (2017). A language and environment for statistical computing. *R Found. Stat. Comput.*, Vienna, Austria.

Ratikainen, I.I. & Kokko, H. (2019). The coevolution of lifespan and reversible plasticity. *Nat. Commun.*, 10, 538.

Réale, D. & Festa-Bianchet, M. (2003). Predator-induced natural selection on temperament in bighorn ewes. *Anim. Behav.*, 65, 463–470.

Réale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V. & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philos. Trans. R. Soc. B Biol. Sci.*, 365, 4051–4063.

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.

Royauté, R., Berdal, M.A., Garrison, C.R. & Dochtermann, N.A. (2018). Paceless life? A meta-analysis of the pace-of-life syndrome hypothesis. *Behav. Ecol. Sociobiol.*, 72, 64.

Sánchez-Tójar, A., Winney, I., Girndt, A., Simons, M.J.P., Nakagawa, S., Burke, T., *et al.* (2017). Winter territory prospecting is associated with life-history stage but not activity in a passerine. *J. Avian Biol.*, 48, 407–416.

Santicchia, F., Gagnaison, C., Bisi, F., Martinoli, A., Matthysen, E., Bertolino, S., *et al.* (2018). Habitat-dependent effects of personality on survival and reproduction in red squirrels. *Behav. Ecol. Sociobiol.*, 72, 134.

Santostefano, F., Wilson, A.J., Niemelä, P.T. & Dingemanse, N.J. (2017). Behavioural mediators of genetic life-history trade-offs in field crickets. *Proc. R. Soc. B Biol. Sci.*, 26, 15–17.

Schuett, W., Dall, S.R.X., Kloesener, M.H., Baeumer, J., Beinlich, F. & Eggers, T. (2015). Life-history trade-offs mediate “personality” variation in two colour morphs of the pea aphid, Acyrthosiphon pisum. *J. Anim. Ecol.*, 84, 90–101.

Shackleton, M.A., Jennions, M.D. & Hunt, J. (2005). Fighting success and attractiveness as predictors of male mating success in the black field cricket, Teleogryllus commodus: the effectiveness of no-choice tests. *Behav. Ecol. Sociobiol.*, 58, 1–8.

Sih, A., Bell, A. & Johnson, J.C. (2004a). Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.*, 19, 372–8.

Sih, A., Bell, A.M., Johnson, J.C. & Ziemba, R.E. (2004b). Behavioral Syndromes: An Integrative Overview. *Q. Rev. Biol.*, 79, 241–277.

Sih, A., Mathot, K.J., Moirón, M., Montiglio, P.-O., Wolf, M. & Dingemanse, N.J. (2015). Animal personality and state–behaviour feedbacks: a review and guide for empiricists. *Trends Ecol. Evol.*, 30, 50–60.

Smith, B.R. & Blumstein, D.T. (2008). Fitness consequences of personality: a meta-analysis. *Behav. Ecol.*, 19, 448–455.

Stamps, J.A. (2007). Growth-mortality tradeoffs and “personality traits” in animals. *Ecol. Lett.*, 10, 355–363.

Stearns, S.C. (1992). *The evolution of life histories*. Oxford University Press, New York.

Stuber, E.F., Araya-Ajoy, Y.G., Mathot, K.J., Mutzel, A., Nicolaus, M., Wijmenga, J.J., *et al.* (2013). Slow explorers take less risk: A problem of sampling bias in ecological studies. *Behav. Ecol.*, 24, 1092–1098.

Stuck, A.E., Rubenstein, L.Z., Wieland, D., Vandenbroucke, J.P., Irwig, L., Macaskill, P., *et al.* (1998). Bias in meta-analysis detected by a simple, graphical. *BMJ*, 316, 469–469.

Tarka, M., Guenther, A., Niemelä, P.T., Nakagawa, S. & Noble, D.W.A. (2018). Sex differences in life history, behavior, and physiology along a slow-fast continuum: a meta-analysis. *Behav. Ecol. Sociobiol.*, 72, 132.

Viechtbauer, W. (2010). Conducting Meta-Analyses in R with the metafor Package. *J. Stat. Softw.*, 36.

Wilson, D.S., Clark, A.B., Coleman, K. & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends Ecol. Evol.*, 9, 442–446.

Wolf, M. & Weissing, F.J. (2010). An explanatory framework for adaptive personality differences. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*, 365, 3959–68.

TABLES

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*	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	10
(Niemelä *et al.* 2015)	*Gryllus campestris*	wild	2
(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
Niemela (unpublished)	*Gryllus campestris*	wild	4
Pruitt (unpublished)	*Strongylocentrotus purpuratus*	lab	4
Salandova (unpublished)	*Pisaura mirabilis*	lab	4
Lundy sparrow project (unpublished)	*Passer domesticus domesticus*	wild	4

***footnote:** 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.

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. 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.

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)

Table 3. Heterogeneity estimates (I^2) with the associated standard deviation (in brackets) for the global meta-analytic model. 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 and phylogeny and, the residual and total 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)

FIGURES

Figure 1. Funnel plot of precision for z-transformed among-individual correlation coefficients (*r*Z) 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 *r*Z from the zero effect.