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Meta-analysis reveals weak associations between intrinsic state and personality

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Individual differences in behaviour characterize humans and animals alike. A hot field in behavioural ecology asks why this variation in ‘personality’ evolved. Theory posits that selection favours the integration of ‘intrinsic state’ and behaviour. Metabolism, hormones, energetic reserves and structural size have particularly been proposed as states covarying with behaviour among-individuals, either genetically or through plasticity integration. We conducted a meta-analysis estimating the amount of among-individual variation in behaviour attributable to variation in state. Our literature search showed that only 22% of the studies claiming to estimate individual-level associations between state and behaviour actually did so. Our meta-analysis revealed that relatively aggressive, bold, explorative and/or active individuals had relatively high metabolic rates, hormone levels, body weights and/or body sizes. The proportion of among-individual variation common to state and behaviour was nevertheless small (approx. 5%). This means that (i) adaptive explanations involving intrinsic states fail to explain much individual variation in behaviour, (ii) empiricists should consider nonlinear, additive or interactive effects of (multiple) intrinsic states, (iii) explanations not involving intrinsic states might be important, or (iv) empirical tests of state-dependent personality theory were inappropriate. Our meta-analysis highlights the importance of feedback between empiricists and theoreticians in the study of adaptive behavioural variation.

1. Introduction

Over the past decade, it has become evident that repeatedly expressed behaviours differ more substantially among individuals than previously assumed [1,2]. Evidence is also accumulating that individuals differ in whole suites of behaviours [3], similar to how humans vary in personality [4]. Current research is further revealing individual variation in behaviour as a key factor in many ecological [5–9] and evolutionary processes [10–13]. Despite this progress, we still have limited understanding of *why* repeatable individual variation in behaviour has evolved. This is not due to a lack of adaptive theory but rather to empiricists long lagging behind in putting model assumptions and predictions to the test [14–16]. Recently, however, empirical tests have accumulated in the literature (e.g. [17,18]), implying that formal meta-analytical reviews can now be conducted to summarize available data, and elicit productive feedback between empiricists and theoreticians [14,16].

Behavioural ecologists have developed a body of theory explaining individual behaviour from an adaptive perspective. Many theoretical [19–24] and conceptual [25–31] models explain individual differences in behaviour as resulting from individual differences in intrinsic ‘state’ (defined as internal features of the individual affecting optimal behaviour [32]) or from adaptive positive feedback loops between state and behaviour [15], in both cases implying that selection may favour the adaptive integration of state and behaviour. Empirical tests of theory have recently focused on measuring behavioural and intrinsic state variables within the same set of individuals, typically focusing on ‘risky’ behaviours (defined as behaviours affecting resource acquisition at the cost of increased mortality [20,33]) and state variables such as metabolic

Table 1. Data transformations and sampling variance calculations applied to published data; r represents the focal correlation coefficient, n the number of individuals, SE the standard error, and 95% CI the 95% confidence or credible interval.

description	equation	equation
Fisher's r to Z transformation (Z_r)	$Z_r = \frac{1}{2} \ln \frac{1+r}{1-r}$	equation (2.1)
back-transformation Z to r (r)	$r = \frac{\exp(2Z_r) - 1}{\exp(2Z_r) + 1}$	equation (2.2)
SE-based calculation of sampling variance ($\text{Var}Z_r$)	$\text{Var}Z_r = \text{SE}^2 \left(\frac{1}{(1+r)(1-r)} \right)^2$	equation (2.3)
95% CI to SE transformation	$\text{s.e.} = \frac{(\text{upper} - \text{lower CI})}{2t_{n-3}}$	equation (2.4)

rate (e.g. [34–37]), plasma hormone levels (e.g. [38–41]), body mass (e.g. [42–45]) or body size (e.g. [46,47]).

The idea that individual differences in above-mentioned intrinsic states underpin or have coevolved with individual variation in behaviour is extremely popular in the behavioural ecology literature, yet an authoritative review of empirical evidence is missing. Key questions are whether these state variables harbour repeatable individual variation (a key assumption), and whether such repeatable differences in state are in turn—regardless of presumed cause–effect relationships—important statistical predictors of repeatable differences in behaviour (a key prediction). A recent meta-analysis has already verified the assumption that many intrinsic state variables are—like behavioural traits [1]—individually repeatable [48]. This means that if such among-individual differences in state and behaviour are strongly integrated, we would predict strong among-individual correlations between states and behaviours.

Behavioural and intrinsic state variables do not harbour just among-individual variation, but typically also substantial within-individual variation [49–51], which represents an important obstacle in addressing this hot question. The ‘state-dependent personality’ hypothesis explicitly posits that state and behaviour covary *among* individuals. By contrast, state and behaviours also covary *within* individuals due to other processes such as plasticity integration or correlated measurement errors [51]. This implies that a firm test of theory requires datasets that unambiguously partition among- from within-individual patterns of covariance between state and behaviour. Appropriate tests of theory therefore must present repeated measures data for both state and behaviour, and apply advanced multi-level statistical techniques to partition among- from within-individual patterns of covariance between state and behaviour [51]. We present here a meta-analysis that uses such high-quality data, thereby firmly evaluating empirical evidence for state-dependent personality theory.

2. Methods

(a) Collection of meta-analytical data

We conducted a literature search in the Web of Science and Scopus on 23 November 2017 to retrieve papers presenting among-individual correlations between behaviours and internal state variables playing a key role in adaptive state-dependent

personality theory (metabolic rate, hormone levels, body mass and body size) using the PRISMA (i.e. preferred reporting items for systematic reviews and meta-analyses) method [52] (electronic supplementary material, figure S1). Body mass and body size were treated as distinct state variables (i) because the former is influenced both by structural size *and* the amount of energetic reserves [53] while the latter is not, and (ii) because adaptive behaviour models imply that energetic reserves and size have distinct effects on behaviour [32]. We used a broad range of search terms to identify papers focusing on among-individual associations between mentioned intrinsic state variables and behaviour (search terms detailed in electronic supplementary material, text S1). We primarily focused on terms like ‘animal personality’, ‘behavioural syndrome’, ‘pace-of-life’ and ‘coping style’ since studies using those terms generally present among-individual rather than unpartitioned (‘raw’) phenotypic correlations. Notably, more general search terms (e.g. ‘behavior’ or ‘behaviour’) typically instead retrieved unpartitioned estimates, and this was also generally the case for studies published prior to the year (approx. 2010) when multivariate mixed-effect modelling approaches (enabling the unbiased estimation of among-individual correlations) were becoming established in behavioural ecology [51,54]. We also screened papers cited in table 1 of each of two key review papers [27,30] to retrieve additional studies documenting individual-level correlations between behaviour and metabolism. In our Web of Science search, we used ‘Behavioral sciences’, ‘Ecology’, ‘Endocrinology and metabolism’, ‘Evolutionary biology’, ‘Physiology’ and ‘Zoology’ as topic fields. In our Scopus search, we used ‘Agricultural and Biological Sciences’ as topic field. These searches altogether retrieved 1086 papers. We also acquired information from an additional 16 studies from other sources. Those included re-analyses (either by P.T.N. or the authors of the focal study) of five unpublished and six published datasets to acquire estimates of among-individual correlations not presented in the original publications. We excluded two published estimates of among-individual correlations that were $>|1|$ [42], because such values are outside the natural range and cannot be z-transformed (a requirement for inclusion in our meta-analysis, detailed below). Our searches retrieved a total of 146 among-individual correlations between state and behaviour (detailed in electronic supplementary material, table S1).

We changed the sign of 25 correlation coefficients (for 13 positive and 12 negative correlations; electronic supplementary material, table S1) to ensure that higher values indicated more ‘proactive’ behaviour (*sensu* [55]), higher levels of boldness, activity, exploration or aggressiveness, and lower levels of docility. By doing so, we ensured that the sign of the untransformed correlation coefficients was biologically interpretable. Adaptive

Table 2. Estimates (mode) of r (correlation coefficient), $|r|$ (absolute value of correlation coefficient) and $|r|^2$ (squared absolute value of correlation coefficient) between behaviour and state (all states combined) and between behaviour and the four state variables separately from models controlling for study identity. We present here point mode estimates with 95% CIs (in brackets) derived from standard multilevel meta-analytic models.

	r	$ r $	$ r ^2$
all states combined	0.101 (0.011; 0.185)	0.216 (0.168; 0.278)	0.047 (0.028; 0.076)
body mass	0.074 (−0.056; 0.210)	0.215 (0.149; 0.335)	0.039 (0.018; 0.107)
body size	0.018 (−0.062; 0.127)	0.132 (0.077; 0.201)	0.017 (0.005; 0.039)
metabolic rate	0.226 (−0.057; 0.439)	0.337 (0.205; 0.545)	0.113 (0.039; 0.290)
hormone levels	0.064 (−0.139; 0.234)	0.141 (0.042; 0.316)	0.020 (0.001; 0.097)

theory notably predicts that both the sign and direction of correlations between state and behaviour may vary as a function of ecological conditions [15]; our statistical analyses (detailed below) both estimated and controlled for such biological variation in effect sizes ('heterogeneity analyses', detailed below). Our main interest was in estimating the fraction of among-individual variance common to state and behaviour (see Introduction), and we therefore focused on absolute values of (squared) correlations. Biological variation in sign of correlations would be indicated by absolute values having greater effect sizes compared to untransformed ones.

(b) Statistical methods

We focused on estimating the squared average absolute magnitude of the among-individual correlation ($|r|^2$) between state and behaviour, as this metric represents the proportion of among-individual variance in behaviour ('personality') that is attributable (in a statistical sense) to among-individual variation in state. To achieve this, we applied the 'analyse-then-transform' approach [56], consisting of estimating the posterior distribution of the average z -transformed correlation coefficient (r_Z ; equation (2.1), table 1), back-transforming this posterior to normal correlation coefficients (r ; equation (2.2), table 1), folding the latter posterior to return the absolute average magnitude of the correlations ($|r|$) (eq. (7) in [56]), and squaring the folded posterior distribution to estimate $|r|^2$. This approach is more accurate than the alternative 'transform-then-analyse' approach [56,57], where correlations are transformed into absolute values prior to analysis. For each focal posterior distribution (i.e. of r , $|r|$ or $|r|^2$), we estimated the mode and 95% credible intervals (95% CIs). We also estimated total heterogeneity (I^2 total), residual heterogeneity (I^2 residual) and study heterogeneity (I^2 study; the proportion of variance among effect sizes explained by a study identity variance component) while statistically controlling for sampling error variance [58] (electronic supplementary material, table S2).

We applied standard multilevel meta-analytic models (i.e. intercept models) to estimates of among-individual correlations between behaviour and each of the four types of state-variable (metabolic rate, hormone levels, body mass and body size) separately, estimating their global effect sizes. We controlled for sampling variance in all models as doing so controls for statistical noise (e.g. differences in sample size across estimates) and thereby greatly increases the precision of estimated effect size [56,57]. Sampling variance was calculated (using equation (2.3), table 1) from the standard error reported for each correlation estimate (95% confidence/credible Intervals were transformed into standard errors prior to calculating sampling variance if reported instead using equation (2.4), table 1). The following random effects were considered in our models: study identity ($n = 30$ studies), species identity ($n = 21$ species) and phylogeny. Unfortunately, we were unable to simultaneously include all of these effects into

our statistical models as this led to model convergence issues. This was probably the case because 71% (15/21) of the studies had unique species (electronic supplementary material, table S1). Reassuringly, models fitting only study, species or phylogeny produced the same general results (electronic supplementary material, table S3). In the main text, we arbitrarily chose to present the model controlling for study identity effects. This model suitably avoids pseudo-replication caused by the inclusion of repeated observations of estimates within the same study. The standard meta-analytical models were run using the MCMCglmm package [59] in the statistical environment R 3.1.3. [60]. We ran 3 300 000 iterations per model, from which we discarded the initial 300 000 (burn-in period). Each iteration chain was sampled at an interval of 1000 iterations, which resulted in a low autocorrelation among samples (always ≤ 0.04). Estimates with 95% credible intervals (CIs) not overlapping with zero were viewed as indicating statistically significant effects.

(c) Publication bias

We constructed funnel plots, fitting precision (i.e. the inverse of sampling variance) versus meta-analytic residuals (derived from our standard meta-analytical model that was conditioned for sampling variance and study identity), to test for publication bias in correlation coefficients [61]. We used Egger's regression analysis to test whether the distribution of estimates was more asymmetrical than expected by chance [62]. Following [61], meta-analytic residuals were calculated using the MCMCglmm R package [59], and Egger's regression conducted using the R package *metaphor* [63]. Funnel plot was symmetrical, suggesting no publication bias (electronic supplementary material, figure S2), which Egger's regression confirmed statistically ($p = 0.904$). Moreover, a trim-and-fill test [64] indicated no missing studies on either side of the funnel plot ($p = 0.500$).

3. Results

The average among-individual correlation between intrinsic state and behaviour differed from zero ($r = [\text{mean}, 95\% \text{ CIs}]$ 0.101, 0.011; 0.185) (table 2). The positive value implied that relatively aggressive, bold, explorative and/or active (i.e. 'pro-active') individuals had relatively high metabolic rates, hormone levels, body weights and/or body sizes. This assessment was confirmed when we ran analyses for each of the four types of intrinsic state variable separately: their point estimates were all positive (table 2). The absolute average correlation was significant and (by definition) positive ($|r| = 0.216, 0.168; 0.278$) providing conclusive evidence for the existence of 'state-dependent personality'. The estimate of $|r|$ was about twice as high as the estimate of r owing to substantial among-study heterogeneity (see below) in the

sign of state-behaviour correlations (electronic supplementary material, table S2). Among-individual variation in intrinsic state, importantly, explained (in a statistical sense) only a very minor proportion of the among-individual variation in behaviour ($|r|^2 = 0.047, 0.028; 0.076$) (table 2). This meta-analytical finding implies that repeatable variation in intrinsic state and behaviour overlap only to a minor extent (i.e. 4.7%).

Neither type of correlation coefficient (r , $|r|$) differed between the four types of state-variable (metabolism, hormones, body mass, body size), nor did the proportion of among-individual variation common to both state and behaviour ($|r|^2$) differ between classes of state. Large credible intervals associated with each of the four point estimates (table 2), notably, indicated that subtle differences would not have been detectable.

The total heterogeneity was 'high' (80%; electronic supplementary material, table S2) following Higgins & Thompson [58] classification (i.e. 25%: small, 50%: medium, 75%: high). Our estimate was thus well within the limits of total heterogeneity expected in ecological studies [65]. Statistical noise or sampling error, (i.e. sampling variance) explained 20% (total variance – total heterogeneity; 100% – 80%) of the total variance in estimates of r . Study-level heterogeneity was at the medium level (46%), indicating that estimates (i.e. the strength and/or sign of correlations) differed, on average, between studies (electronic supplementary material, table S2). Residual heterogeneity was small (34%; electronic supplementary material, table S2) indicating that the variation in r was relatively small within studies. Moreover, phylogeny explained relatively much variation in state-behaviour correlations among studies (65%; electronic supplementary material, table S2), indicative of evolutionary signals on associations between state and behaviour. This finding implies, as predicted by ecological theory [15], the existence of genetic variation among species in either phenotypic plasticity (underpinning positive state-behaviour feedback loops) or genetic correlations between state and behaviour.

4. Discussion

Our study supports predictions of state-dependent personality theory as our meta-analysis showed that intrinsic state explained significant variation in behaviour among individuals. Our meta-analysis revealed that relatively aggressive, bold, explorative and/or non-docile (i.e. 'pro-active') individuals were also characterized by relatively high metabolic rates, hormone levels, body weights and/or structural body sizes. This finding does not suggest any specific cause-effect relationship (e.g. state affecting behaviour). Instead, it demonstrates that intrinsic state and behaviour are, on average, integrated among individuals, whether proximately underpinned by phenotypic plasticity (e.g. positive feedback loops) or by genetic correlations between intrinsic states and behaviour. Variation in intrinsic state thus 'explains' variation in personality in a statistical sense. Our meta-analysis also showed that each intrinsic state variable explained at best 3–8% (95% CIs) of the variation in 'personality' (*sensu* [51]). This implies either (i) that intrinsic states explain only a modest portion of the standing individual variation in behaviour, (ii) that nonlinear, additive or interactive effects of (multiple) intrinsic state variables are (as predicted by

theory) instead important, (iii) that other explanations (e.g. extrinsic states) should be considered, or (iv) that empirical tests of theory are somehow inappropriate [66,67]. Our study thereby represents an important first step in furthering productive interactions between empiricists and theoreticians in explaining repeatable individual variation in behaviour from an adaptive perspective.

Our meta-analysis focused on among-individual correlations between behaviour and circulating hormones, metabolism, body weight, or structural body size. While we demonstrated that these types of intrinsic state variables individually did not explain much variation in 'personality', this does not mean that explanations involving state are unimportant. First, other state variables, whether intrinsic (e.g. immune defence, morphology) or extrinsic (e.g. behaviour of conspecifics, competitive regimes, predation risk), may need to be considered. Second, theory often predicts threshold effects, or other nonlinear relationships, between state and behaviour [19,68–71]. Empiricists instead primarily estimate linear associations (possibly because bivariate mixed effects models only enable the estimations of linear covariances). Effect sizes based on correlation coefficients reviewed here may thus underestimate true effect sizes. Therefore, in some cases proper testing of the theory might require estimating nonlinear associations between state and behaviour. Third, the combined ('additive') effects of the four intrinsic state variables studied here may actually explain as much as 18.8% of the variation in personality (i.e. $4 \times 4.7\%$), though this would require that the four types of intrinsic state variable varied independently (which may be unlikely). A test of this idea would necessitate studies, few of which exist to date, quantifying various intrinsic state variables simultaneously. Studying multiple intrinsic state variables simultaneously would also enable testing a third explanation, positing that internal state variables interactively affect individual-level behaviour. Finally, there is considerable debate in the literature on whether the proxies of intrinsic states reviewed here are appropriate proxies of the intrinsic state variables considered by adaptive theory. For example, hormone receptor density, affinity, or specificity, greatly influence the effects of circulating hormone levels on the phenotype and may represent better proxies for hormonal state [72–74]. Similarly, body mass is often used as a measure of body reserves but is often also conflated with aspects of physiological condition and structural size.

The measurement theoretical arguments made above are also applicable to the choice of behaviour measured as part of empirical tests of state-dependent personality theory [66,67]. State-dependent personality models, for example, largely focus on 'risky' behaviours (i.e. behaviours that facilitate the acquisition of resources at the cost of increased mortality [20,22,33]). Our meta-analysis instead included estimates of among-individual correlations between intrinsic state variables and any empirically studied behaviour. This was not the cause of the low effect size because there was no notable increase in the proportion of among-individual variance in behaviour explained by state when we only included studies of risky behaviours (i.e. exploration, activity, boldness and aggression; $n = 112$ estimates) in our standard meta-analytic model ($|r|^2 = 0.053, 0.030–0.091$). In summary, an important role for individual variation in intrinsic state in explaining personality variation would require more complex explanations

than empiricists currently tend to consider. At the same time, our findings may also imply that alternative, state-independent, explanations for personality (e.g. mutation-selection balance), are more important than currently appreciated.

Our literature search also brought to the foreground a somewhat worrying pattern of scientific conduct that has repeatedly been highlighted in the personality literature [14,16] but has largely been ignored, and thereby obstructs scientific progress. That is, despite the huge amount of empirical literature on the topic of ‘animal personalities’ and ‘behavioural syndromes’, we found surprisingly few studies presenting appropriate empirical tests of theory. Unfortunately, this was not due to a paucity of empirical studies claiming to report relationships between intrinsic state and ‘personality’: our search identified 145 of such studies. Instead, the vast majority of studies claiming to report among-individual level estimates (113 out of 145 studies; 78%) reported unpartitioned phenotypic associations instead. These estimates were typically based on intrinsic states and/or behaviours measured once or, if repeated measures of traits existed, using state as a model covariate in a way that does not allow the separation of among- and within-individual level effects. Only a minority (32 out of 145 studies; 22%) used a combination of sampling design (i.e. repeated measures design) and statistical methods that allowed for the calculation of among-individual correlations indicative of associations between state and personality. Making matters worse, half of those latter studies (16 out of 32; 50%) reported simplistic statistical approximations of among-individual correlations that are known to be biased towards within-individual correlations [75–77]. Two types of approximations were used in particular: (i) correlations between individual-mean values or best linear unbiased predictors (BLUPs), or (ii) mean values or BLUPs of state fitted as a covariate explaining variation in behaviour. Consequently, only about 11% of the studies (16 out of 147) reported among-individual correlations unambiguously indicative of state-dependent personality. Fortunately, there are specific situations where unpartitioned phenotypic correlations, or statistical approximations of among-individual correlations (detailed above), provide unbiased estimates of among-individual correlations, namely when within- and among-individual correlations are identical [51]. We tested

this assertion by additionally applying our meta-analysis to estimates of within-individual correlations. These analyses confirmed our suspicion that studies reporting phenotypic correlations cannot be used to test adaptive state-dependent personality theory: absolute within-individual correlations between intrinsic state and behaviour were significantly weaker than their among-individual counterparts (electronic supplementary material, text S2). This implies that phenotypic correlations represent biased, attenuated, estimates of among-individual correlations between state and behaviour [51,78], and highlights the importance of estimating the appropriate parameters for testing theory [16].

In conclusion, our meta-analysis supports adaptive personality theory predicting the adaptive integration of intrinsic state and behaviour among individuals. Our meta-analysis also showed that each intrinsic state variable explained (in a statistical sense) relatively little variation in ‘personality’. Finally, our meta-analysis revealed that much of the current empirical work (unknowingly) fails to appropriately test adaptive personality theory. A revival of interactions between empiricists and theoreticians seeking to explain individual behaviour from an adaptive perspective is therefore required to further this hot area in evolutionary behavioural ecology.

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors’ contributions. P.T.N. and N.J.D. designed the study, and drafted the manuscript, together. P.T.N. collected the data and carried out the statistical analysis. Both authors approved publication.

Competing interests. We declare we have no competing interests.

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