Causes and Consequences of Among-Individual Variation in Behaviour in Animal Populations

by

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Abstract

The field of animal personality, the study of adaptive among-individual behavioural differences in animal populations, has both exploded in popularity in the last few decades and come under heavy scrutiny by behavioural ecologists. The sudden interest in the field stems from the widespread finding that individuals in populations often behave consistently differently from one another, even across contexts, while the criticism stems from the lack of ecological relevance of many studies on the topic and the lack of grounding in testable theoretical predictions. My thesis is centered on 1) testing current theory about the mechanisms maintaining adaptive behavioural variation in populations over generations and 2) evaluating the fitness consequences of behavioural differences in an understudied, yet ecologically relevant, behaviour: sampling. First, I conducted a systematic review and meta-analysis to test the hypothesis that among-individual differences in behaviour are maintained because they reflect differences in the allocation toward survival versus reproduction, effectively a trade-off between survival and reproduction mediated by behaviour. My study was comprised of 760 estimates from 194 studies, and I found that contrary to predictions, the relationship between behaviour and fitness could not be explained by trade-offs between survival and reproduction, pointing to the potential role of individual differences in resource acquisition in mediating the relationship between behavioural expression and fitness outcomes in animal populations. Second, I conducted a field study using a model system, the black-capped chickadee (*Poecile atricapillus*), to assess whether there are among-individual differences in sampling behaviour (i.e., gathering information about a resource patch to assess its profitability to manage uncertainty about resource availability), and whether such differences predict annual survival in the population. In our sample of 132 individually marked chickadees, we found that chickadees sample under two distinct sets of conditions— when the risk of starvation was high and when the risk of starvation was low—and adjusted their sampling behaviour under these two sets of conditions in response to ambient temperature as predicted by existing models of optimal sampling. Interestingly, there was a very strong among-individual covariance between the two types of sampling, and we found moderate support that individuals that invest more in sampling overall also had higher annual survival. The positive covariance between the two types of sampling can only be understood in light of individual differences in access to resources, and I discuss how resource heterogeneity, which I identified as being a key mediator in the relationship between individual behaviour and fitness using meta-analysis, needs to be a central focus in future work addressing adaptive behavioural differences in animal populations.

Preface

Chapter 2 of this thesis has been submitted to the journal *Biological Reviews* and is a collaboration with co-authors Anne A. Besson, Shinichi Nakagawa, and Kimberley J. Mathot. KJM and I (EHA) developed the study, and AAB and myself completed the article screening and data extractions. I completed the statistical analyses with input from SN and KJM. I wrote the first draft of the manuscript with significant input from KJM; all co-authors provided editorial feedback.

Chapter 3 of this thesis was conducted in accordance with the Canadian Council on Animal Care (CCAC) guidelines with ethics approval granted by the University of Alberta Animal Care and Use Committee (AUP00002210). Banding was conducted with approval from the Bird Banding Office in Canada (permits: 10936 and 10936 A). Field studies were conducted with approval from Alberta Fish and Wildlife Capture and Research (17658720). The study was conceived by myself (EHA) and Kimberley J. Mathot. Equipment for the study was designed and constructed by Jan J. Wijmenga, and fieldwork was conducted by myself and JJW. Molecular sexing of the individuals included in the study was conducted by Sheeraja Sridharan.

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Chapter 1: General Introduction

Individuals in animal populations often show consistent and repeatable differences in behaviour, which is known as ‘animal personality’ (Dall et al. 2004; Sih et al. 2004; Réale et al. 2007). Animal personality is significant, because it challenges the classic view in behavioural ecology that only the mean values of phenotypic traits are adaptive, while variation in traits is not (Wilson 1998). Although trait variation is an integral component of natural selection, and thus adaptive evolution, the field of animal personality endeavors to understand how phenotypic variation, specifically behavioural variation, is maintained over generations, rather than decreasing around one or a few adaptive means. In the early days of this emergent field in behavioural ecology, several independent examples highlighted this phenomenon that is now integral in behavioural ecology, showing that repeated testing of an individual’s behaviour, a labile trait, yielded similar values when individuals were tested multiple times, even across contexts, and that among-individuals, different behavioural phenotypes were maintained in the population across generations (e.g., Wilson et al. 1993; Verbeek et al. 1994; Réale et al. 2000; Dingemanse et al. 2004). This had a cascading effect on the field of behavioural ecology, and there is now clear evidence that repeatable behavioural variation exists across taxa (Bell et al. 2009), and there is much interest in understanding whether this variation is adaptive.

Theory has been developed to explain the presence of adaptive among-individual behavioural variation, creating testable predictions for the field of animal personality. Explanations for among-individual differences in behaviour include trade-offs between survival and reproduction, state-dependence, fluctuating selection, and negative frequency dependent selection (Dingemanse & Wolf 2010; Luttbeg & Sih 2010; Wolf & Weissing 2010). The trade-off explanation posits that different levels of behavioural expression favour either an individual’s investment in survival (i.e., longevity) or reproduction (Luttbeg & Sih 2010). For example, behavioural expression that increases access to resources, such as foraging in the presence of a predator, allows an individual to invest the resources it immediately gains into reproduction, however at the cost of longevity due to repeated exposure to predation risk. Conversely, an individual that opts not to forage in the presence of a predator will not gain immediate resources to invest in reproduction, but may survive longer relative to “riskier” individuals, such that over a lifetime, reproductive output is the same across all individuals in the population (Wolf et al. 2007; Luttbeg & Sih 2010). Although this is an intuitive explanation for consistent among-individual differences in behaviour, there is little evidence to suggest that behavioural variation is maintained primarily via trade-offs (Smith & Blumstein 2008; Moiron et al. 2020a; Haave-Audet et al, *Submitted*).

Contrary to the trade-off explanation, state-dependent behavioural variation does not posit that relative fitness will be equal among members of a population. State-dependent behavioural variation arises because individuals vary in state in the population (e.g., dominance, metabolism, territory quality, attractiveness to potential mates, etc.), and individuals behave in a way that maximizes fitness given the individuals’ current state (Wolf & Weissing 2010). Because individuals differ in state (such as in metabolic rate or dominance rank), they must adjust their behaviour relative to others in the population to match their current state, which results in differences in behaviour that may have different fitness outcomes. Behavioural differences related to both stable (e.g., organ size) and labile (e.g., dominance rank) states can maintain consistent differences in behaviour between individuals over time. Further, when differences in individual state are environmentally induced (e.g., an individual’s early environment was more resource rich than another’s), behavioural variation can exist in the population even if fitness outcomes are unequal, because individuals are forced to make ‘the best of a bad job’. For example, theory predicts that individuals require some level of energy reserves before they can afford to invest in sampling, which provides information on the current profitability of a resource option, and that by sampling, these individuals are better able to maintain higher energy reserves due to the information about, and access to, resources accrued through sampling (Dall & Johnstone 2002; Mathot et al. 2012).

Like the trade-off explanation, and unlike state-dependence, fluctuating selection predicts that net long-term fitness in a population is the same across phenotypes, because different behavioural types are selected under different conditions. In this scenario, changing environmental conditions ensure that under changing contexts, no single behavioural type has an adaptive advantage (Dingemanse & Wolf 2010). For example, empirical tests in great tits (*Parus major*) suggest that high and low exploratory behaviour are selected for in different years (Dingemanse et al. 2004), that corresponded with changes in environmental conditions. That is, in years where food is scarce and/or hard to find, there is a net benefit to investing in sampling and, conversely, in years where food is abundant and/or predictable, there is a net cost of investing in sampling. Finally, under negative frequency dependence, the adaptive value of a behavioural type changes as a function of the frequency of that behavioural type relative to others in the population (Dingemanse & Wolf 2010). For example, in a population of producers—individuals that gather information about the profitability of a resource—scrounger individuals, those that rely on producers to assess profitability without gathering information themselves, have a fitness advantage over producers because they can spend their energy exploiting resources rather than spending it on gathering information. However, once the frequency of scroungers in the population reaches a tipping point, it is no longer profitable to scrounge because there are insufficient producers to scrounge from, and it becomes profitable to be a producer, continuing the fluctuating cycle based on density of behavioural types in the population (Barnard & Sibly 1981).

While the evidence for consistent behavioural differences in animal personality is vast and increasing, the field is lagging in testing the predictions outlined by the theory presented above. Specifically, explicit investigation of the mechanisms through which adaptive behavioural variation persists are needed. The field has been criticized for remaining largely descriptive rather than being grounded in testing ecological predictions (DiRienzo & Montiglio 2015; David & Dall 2016), and many behavioural tests lack sufficient ecological construct to provide insight into the evolutions of adaptive behavioural variation (Carter et al. 2013; Niemelä & Dingemanse 2014). While individual examples outlining each of the mechanisms presented above exist, critical gaps in theory have recently been highlighted, and some theory remains untested empirically.

In Chapter 2 of my thesis, I evaluate support for one such gap in the theory of adaptive behavioural variation, recently articulated by Laskowski et al. (2020); while theory has tried to bridge the gap between life-history trade-offs and state-dependent behaviour to explain among-individual differences in behaviour, the field does not consider how differences in resource acquisition may play a role in mediating the relationship between behaviour and an individual fitness outcome. The pace-of-life syndrome (POLS) framework attempts to bridge the mechanisms of trade-offs between longevity and reproductive output and state-dependence using behavioural expression as the state that mediates how individuals should invest in one of survival or reproduction (Réale et al. 2010). However, evidence of POLS as a mechanism maintaining behavioural variation is limited (Royauté et al. 2018), and behavioural ecologists have posited that some other mechanism may be masking the among-individual differences in investment toward one of survival or reproduction, specifically when differences in resource acquisition are stronger than differences in resource allocation among-individuals (Laskowski et al. 2020). Using meta-analysis, I evaluated support for trade-offs between longevity and reproduction as a mechanism maintaining behavioural variation versus the role that differences in resource acquisition may play in influencing the relationship between behaviour and fitness. This thesis chapter provides evidence that variation in resource acquisition is a key mechanism influencing the observed effect of individual behaviour and fitness, and we outline how the field must account for differences in access to resources in order to get at the underlying mechanisms maintaining behavioural variation.

In Chapter 3 of my thesis, I present a study where we empirically tested model predictions of the conditions under which sampling behaviour should occur in the field. Specifically, I investigated sampling behaviour, a trait that is expected to have fitness consequences in populations because it allows individuals to gather information about the profitability of different options of a particular resource (Dall 2010). I studied sampling behaviour in a population of black-capped chickadees (*Poecile atricapillus*), because chickadees are wintering resident birds that experience temperatures well below their thermo-neutral zone, which places significant energetic constraints on them. Under these conditions, we were able to test theory regarding the effects of varying energetic demands on sampling behaviour and observe whether repeatable individual differences in sampling behaviour predicted annual survival in the population. My experimental study is the first to empirically test the predictions for the conditions under which sampling should take place and is the first to assess the survival consequences of this behaviour. Together, each component of my thesis plays a role in advancing theory and understanding about adaptive behavioural variation in populations.

Finally, in Chapter 4, I provide a general discussion that synthesizes the results from Chapters 2 and 3. I discuss the overarching conclusion drawn from both of my thesis chapters: the fitness consequences of among-individual differences in behaviour appear to be heavily related to variation in resource availability and/or acquisition across individuals. I conclude with suggestions for future work in this area and discuss its importance to the study of adaptive behavioural differences in animal populations.

Chapter 2: Differences in resource acquisition, not allocation, mediate the relationship between behaviour and fitness: A systematic review and meta-analysis

Introduction

Individuals in populations often differ consistently in behaviour, a phenomenon known as animal personality (Dall et al. 2004). For example, when predator cues are presented, some individuals will consistently be among the first to resume feeding, while others are consistently among the last (e.g., Arteaga-Torres et al. 2020). Much contemporary work in the fields of behavioural and evolutionary ecology has been dedicated to detecting and quantifying repeatable among-individual differences in behaviour, leading to an explosion of studies on the topic over the last few decades (reviewed in Smith & Blumstein 2008; Bell et al. 2009; Moiron et al. 2020a). Consistent among-individual differences in behaviour have now been documented across numerous taxa, and there is growing interest in understanding why this behavioural variation exists in populations (Dingemanse & Réale 2005; Dingemanse & Wolf 2010; Wolf & Weissing 2010). Formal theoretical models have demonstrated that trade-offs between different fitness components (survival and reproduction) and state-dependent behaviour can both favour the maintenance of animal personality (Dall et al. 2004; Wolf et al. 2007; Sih et al. 2015).

The notion of trade-offs between survival and reproduction as being a potentially important mechanism favouring animal personality is intuitive. Under such trade-offs, all else being equal, different levels of behavioural expression reflect alternative routes to equal fitness (Wolf et al. 2007; Dingemanse & Wolf 2010). Trade-off models, which were developed from life-history theory, predict that behaviours that are associated with increased investment in one fitness component, reproduction, are simultaneously associated with decreased investment in an alternative fitness component, survival. The rationale for trade-offs is that resources are limited, and resources invested in reproduction cannot be invested in survival, and vice versa (Stearns 1989; Stearns 1992). On the other hand, state-dependent models of animal personality assume that the optimal behavioural expression by an individual depends on its state (e.g., morphology, physiology, etc.; Wolf & Weissing 2010). If individual differences in state are stable, either intrinsically (Dingemanse & Wolf 2010; Wolf & Weissing 2010) or via stabilizing feedbacks (Sih et al. 2015), then this can lead to individuals consistently exhibiting different levels of behaviour. Under state-dependent behaviour, different levels of behavioural expression do not necessarily lead to the same fitness outcomes, as some individuals may be in better states than others.

Trade-offs and state dependence are not mutually exclusive. Models developed under the pace-of-life syndrome framework attempt to bridge these two mechanisms (Réale et al. 2010; Dammhahn et al. 2018). Taking life-history trade-offs as a starting point, individuals can exhibit a pace of life anywhere along a continuum from fast to slow. Individuals with a fast pace of life have high reproduction and low survival, while individuals with a slow pace of life have low reproduction and high survival. These differences in life history strategies are taken to be the state that shape the optimal expression of suites of other behaviours (Réale et al. 2010). For example, fast life histories might favour a higher expression of risk-taking behaviours, while slow life histories might favour greater investment in learning (Réale et al. 2010). However, this framework blends mechanisms acting at two distinct levels of biological organization: trade-offs occurring at the within-individual level and state-dependence occurring at the among-individual level (Laskowski et al. 2020). When the mechanism mediating the relationship between two traits is different at different levels, such as when trade-offs shape relationships within-individuals, but differences in individual quality or access to resources shape the relationship across individuals (see Figure 2.1), the observed relationships at the phenotypic level represent a blend of the patterns expected at either level on their own (Dingemanse et al. 2012; Brommer 2013; Dingemanse & Dochtermann 2013; Niemelä & Dingemanse 2018b). Although this point has been appreciated for some time in classic life-history theory (van Noordwijk & de Jong 1986; Metcalf 2016), it has not been fully appreciated in the animal personality field until recently (Mathot & Frankenhuis 2018; Montiglio et al. 2018; Laskowski et al. 2020).

While numerous empirical studies have assessed the links between behaviour and fitness in recent years (reviewed in Smith & Blumstein 2008; Moiron et al. 2020a), there has not yet been an evaluation of the relative importance of among-individual differences in resource allocation (i.e., resolving trade-offs between survival and reproduction) and resource acquisition (i.e., how individuals differ in resources available to allocate toward survival and reproduction) in generating these relationships (Laskowski et al. 2020). Differences in resource acquisition could arise via multiple, non-exclusive processes including inherent differences in individual quality (i.e., genetic differences), permanent environment effects (e.g., food availability during early development), and/or environmental differences that facilitate resource acquisition (e.g., high versus low food availability). Assessing the roles of differences in resource allocation versus resource acquisition requires comparisons of the correlations between a given behaviour and both survival and reproduction, and analysis of these relationships at the correct level (within- versus among-individuals; Figure 2.1).

Here, we conducted a systematic review and meta-analysis to assess the relative importance of individual differences in resource allocation and resource acquisition in mediating the relationship between repeatable among-individual differences in behaviour and fitness components. To do this, we investigated the relationship between behaviour and reproduction and between behaviour and survival. If behaviour mediates a trade-off in allocation of resources, then behaviours associated with increased reproduction should be associated with decreased survival, and vice versa. However, if behaviour mediates differences in acquisition of resources, then behaviours that increase reproduction should also increase survival (Figure 2.1). Additionally, we test whether the role of behaviour in mediating differences in resource allocation versus resource acquisition differ across different levels of biological organization by contrasting relationships at the within-individual, among-individual, and phenotypic levels. Current conceptual frameworks predict that variation in resource acquisition govern relationships between behaviour and fitness among-individuals, but trade-offs govern relationships within individuals

(Figure 2.1c). We also consider the moderating effects of testing conditions (field versus lab) and behaviour type on these relationships. We expected the relative importance of resource acquisition to be greater under field conditions, where individuals compete for limited resources compared to the lab, where resources are often provided *ad libitum*. We also expected that the relationship between behaviour and fitness components may differ for different behaviours, because some behaviours (e.g., foraging, boldness) are more intuitively linked to resource acquisition than others (e.g., sociability, stress responsiveness).

Methods

Data collection and inclusion/exclusion criteria

To carry out our systematic review and meta-analysis, we used the reporting guidelines recommended by the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA; Moher et al. 2009). We verified the reporting of our study items using the PRISMA-EcoEvo guidelines outlined by O'Dea et al. (2021; Table A1.1). We conducted our literature search in two databases, *Scopus* and *Web of Science*. We included all available years up to the time at which the search was conducted (January 2019). Our search terms included a behavioural and a fitness component. The search terms were based on the terms included in the meta-analysis conducted by Smith & Blumstein (2008), with two key differences; we expanded our terms to include more current terminology in the field of animal personality and removed those that were targeting specific behavioural traits (e.g., exploration, aggression, etc.). The behaviour-related terms were: personalit*, temperament, "individual difference", "coping style", "coping strateg*", "among individual", "individual specialization", "behavio$ral type", "behavio$ral syndrome", "behavio$ral strateg*", "behavio$ral difference*", "behavio$ral response*", and "behavio$ral style". The fitness related terms included: fitness, survival, "reproductive success", mortality, reproduction, longevity, "clutch size", "litter size", fecundity, and survivorship. We searched for articles with these terms in ‘Topic’. Articles needed to include at least one behavioural and one fitness search term. Because the focus of our meta-analysis was on non-human animals, we excluded articles that contained any of the following terms in ‘Topic’: child*, human, infant, patient*, participant*, m?n, wom?n, public, job*, employment, disorder*, mood*, politic*, student, elderly, adolescent, socioeconomic, and people.

We performed the literature search on January 25th, 2019. The literature search produced a total of 8001 unique references. We also screened for articles in Table 1 of Smith & Blumstein (2008) and in Table 1 of Moiron et al. (2020a) and added any articles that were missed by our initial query. The title and abstract of each article were screened by two authors (E.H.A and A.A.B.) independently using the Raayan online application (Ouzzani et al. 2016). Where the two authors did not reach the same conclusion about inclusion/exclusion of an article, the title and abstract were discussed jointly with K.J.M. to reach consensus. We selected studies based on the following criteria:

1. Some behaviour of the focal individuals was measured as a continuous variable or as a binary categorical variable. We did not include studies that treated behaviour as categorical and included > 2 levels, because this would preclude calculating a correlation coefficient (see 3, below). We also did not consider performance traits (e.g., escape speed) to be behavioural traits, and did not include them in our extractions.
2. A direct proxy of individual fitness was given (i.e., survival or some measure of reproduction). Measures of survival included longevity (in hours, days, months, or years), and apparent survival (e.g., probability of recapture [yes/no]). Measures of reproduction in females included clutch size, brood size, litter size, number of fledglings, offspring survival during period of maternal care, and age at first reproduction. Measures of reproduction in males included number of eggs fertilized, number of offspring sired, brood size or number of fledglings with social partner, selection for mating by a female in a choice test, offspring survival during period of parental care (when male is involved in parental care), and number of extra-pair offspring. We did not

consider reproductive tissue size or individual body size as a measure of reproductive output, nor were mate guarding or levels of filial cannibalism considered fitness outcomes. In instances where similar or non-independent fitness proxies were presented (in the case of reproduction) from the same set of individuals in a study, we extracted the estimate for the longest period of parental involvement. For example, if studies included estimated relationships between behaviour and clutch size and between the same behaviour and number of young fledged, we only extracted the latter estimate since our aim was not to isolate the timing of the observed effect, but whether there was an effect overall.

3. The study analyzed the direct correlation between individual behaviour and fitness outcome (survival or reproduction), included statistics that allowed the correlation to be estimated indirectly, or presented the raw data in either figures or supplementary material such that the correlation could be estimated directly. Correlations were not included if the direction of the relationship could not be determined.
4. The study had to include extractable information on sample size, an estimate of effect size from descriptive or inferential statistics, and a measure of uncertainty. In some cases, this information was not published in the study, but was available in supplementary material, in the accompanying published dataset, extractable from figures or obtained directly from the authors.

Following our criteria, 194 studies were retained for analysis (Figure 2.2; Table A1.2). Articles that were selected based on title/abstract, but which subsequently did not meet one of our four criteria when reading the full text are listed in Table A1.3 along with the reason for their exclusion. From the retained articles, we extracted 760 estimates. Estimates were extracted by two authors (E.H.A and A.A.B.); 127 estimates were reviewed by three authors to ensure consistency (E.H.A., A.A.B., K.J.M.), and an additional 36 estimates were checked by K.J.M. We did not assess or rank the quality of the extracted estimates (e.g., whether data collection was blind, the quality of the reporting, etc.).

Data coding and calculation of effect sizes

For each estimate extracted, we noted the year the study was published, and the species name of the focal organism (to allow us to control for phylogeny in the meta-regression). For each extracted dataset, we also indicated the type of behaviour (see Table A1.4 for definitions and directional coding), the type of fitness measure (survival or reproduction), the environment in which behaviour and fitness were measured (artificial/lab or natural/field), the sex (male, female, both, unknown) and age (juvenile, adult, both, unknown) of the focal individuals, and the level of the correlation between behaviour and fitness (phenotypic, within-, or among-individual; genetic correlations were coded as among-individual). We also extracted the direction of the relationship between behaviour and fitness by assigning behavioural types that could *a priori* be conceived to increase resources for reproduction and/or decrease survival with increasing level of expression as the reference type for coding direction (Table A1.4). Many of these were consistent with the expected traits for "fast" pace of life according to the Pace-of-Life-Syndrome hypothesis (Réale et al. 2010), however, there were exceptions. For example, contrary to the POLS framework, we coded parental care such that higher investment in parental care was positive (see Table A1.4).

Since we were interested in investigating the relationship between two variables—individual behaviour and fitness—we converted all estimates to *r* (Nakagawa et al. 2017). We extracted descriptive statistics over inferential statistics when possible, as recommended by Noble et al. (2017). We used descriptive and inferential statistics to obtain estimates of *r* using Calculation of Effect Size, and Practical Meta-Analysis Effect Size Calculator (Wilson 2001a; Lenhard & Lenhard 2016) and from formulae obtained from Nakagawa & Cuthill (2007).

When the raw data were available for repeated observations, we obtained an estimate for the unpartitioned phenotypic correlation between behaviour and fitness, and further partitioned variation into its among- and within-individual components using Bayesian mixed effect models (Dingemanse &

Dochtermann 2013), using the package *MCMCglmm* (Hadfield 2010). We used the priors provided in the supplementary material from Moiron et al. (2020a). When the fitness outcome presented in the study was a metric of reproductive success, and repeated individual measures for reproduction were available, we also partitioned variation of the fitness metric into its among- and within-individual components. Since survival and longevity are only expressed once per individual, it was not possible to partition realized survival or longevity into among- and within-individual components, even if survival probability may itself be labile. In these cases, we used the approach used by Moiron et al. (2020a), and only estimated the among-individual correlation by constraining the within-individual variance to zero. Data extractions and variance partitioning analyses are provided by Haave-Audet et al. (2021).

Meta-analysis and meta-regression analysis

We conducted all statistical analyses in the program R version 3.6.1 and RStudio version 1.2.1335 (RStudio Team 2018; R Core Team 2019). To evaluate whether the relationship between behaviour and fitness is mediated by variation in resource acquisition and/or allocation (i.e., trade-offs), we used the subset of the data that included matching estimates of focal individuals that had an estimate of the effect of behaviour on survival and an estimate of the effect of the same behaviour on reproduction. First, we calculated the Pearson correlation coefficient using estimates partitioned at the among-individual level. To determine the pattern at the within-individual level, we calculated the Pearson correlation coefficient using phenotypic estimates, since phenotypic estimates are generally better estimates of within- rather than among-individual patterns of co-variation (Dingemanse & Dochtermann 2013; Niemelä & Dingemanse 2018a).

Next, we looked at the moderating effect of the type of behaviour and the conditions in which fitness was measured on the relationship between individual behaviour and fitness. We conducted phylogenetic multilevel meta-analysis and meta-regressions (Nakagawa & Santos 2012) using the function rma.mv in the R package *metafor* (Viechtbauer 2010). We split the dataset by fitness proxy (survival versus reproduction) and level of partitioning (among-individual, within-individual, or phenotypic) to investigate whether patterns in the relationship between behaviour and fitness differed across the different combinations of level of partitioning and fitness proxy. We did not include a within-individual-survival dataset since variation in the fitness proxy cannot be partitioned into its within-individual component (because an individual can only die once). Potentially important random effects that we considered for inclusion in models were the phylogenetic effect of species, the non-phylogenetic effect of species, the study ID, the group of organisms tested, and the observation level ID. To assess which random effects to include in the models, we ran null meta-regression models with no predictor variables and all the potential random effects on each of the five separate fitness-proxy – level of partitioning datasets and calculated the amount of heterogeneity (I^2) explained by each (Higgins et al. 2003; Nakagawa & Santos 2012). We retained the following random effects: a phylogenetic correlation matrix, species' common name (for non-phylogenetic effect of species), study ID and observation ID, but dropped the group of organisms ID, since it explained less than 0.01% of heterogeneity in each of the datasets.

We constructed phylogenies using the package *rotl* and the Open Tree of Life Synthetic Tree (Michonneau et al. 2016; OpenTreeOfLife et al. 2019). We were unable to extract phylogenetic distances for some species, due to unresolved lineages. To solve this issue, we replaced the problematic species' names with closely related species already in the dataset as proxies for the broken lineages. The unresolved species and replacements were *Aquarius remigis* (replaced with *Gerris remigis*), *Zootoca vivpara* (replaced with *Lacerta vivipara*), *Pomacentrus wardi* (replaced with *Pomacentrus moluccensis*), *Poecilia reticulata* (replaced with *Gambusia geiseri*) and *Pan troglodytes* (replaced with *Pan troglodytes troglodytes*). To control for non-independence among sampling errors (since multiple estimates were obtained using the same cohort of individuals in many cases), we used a variance-covariance matrix of V*Zr* as the measure of variance in meta-regression (Noble et al. 2017).

To determine the amount of heterogeneity that could be explained by the two moderators of interest— behaviour and fitness condition— we first calculated heterogeneity (I^2) on null models using each of the five split datasets, which only contained random effects. We then ran two separate models using each of the five split datasets, one with behaviour and the other with fitness condition as fixed effects and assessed the contribution of the fixed effects to heterogeneity by calculating marginal R^2 (sensu Nakagawa & Schielzeth 2013). We visualized effect sizes using the R packages *ggplot2* and *orchaRd* (Wickham 2016; Nakagawa et al. 2020). Data and reproducible analyses are provided by Haave-Audet et al. (2021).

Publication bias analysis and sensitivity analysis

We evaluated evidence for publication bias by assessing funnel plot asymmetry and tested the significance of the asymmetry using a multilevel version of Egger regression, which is essentially a meta-regression model (Nakagawa et al. 2021). We included the following fixed effects in the Egger regression to control for variables that we found to be important in the previous analyses (see Sections 1-3 above): the square root of VZr (the sampling variance of Zr), the type of behaviour, the fitness proxy, and the level of partitioning. We also included the following random effects in the Egger regression model, based on the variables that contributed most to heterogeneity in the null models described above (see Section 3): non-phylogenetic effect of species, study ID, and observation ID. We assessed the presence of a time lag effect in the publication of negative results by regressing standardized effect sizes (Zr) against publication year (Jennions & Moller 2002), also known as a decline effect (Koricheva & Kulinskaya 2019), with the same random effects as the Egger regression model (non-phylogenetic effect of species, study ID, observation ID).

Results

Our extraction criteria resulted in 760 estimates from 194 studies (Figure 2.2), which included 126 species across 10 classes (Figure 2.3). Most of the estimates that we extracted were phenotypic correlations (*k*= 457); we obtained 286 estimates partitioned at the among-individual level and only 17 estimates partitioned at the within-individual level. Estimates were relatively evenly distributed across the two fitness proxies (*k*= 400 for reproduction and *k*= 360 for survival). Fitness testing conditions were also relatively evenly represented across lab (*k*= 361) and field (*k*= 399) testing conditions. However, behavioural categories were not evenly represented across estimates (see section 2 below). The behavioural category with the most estimates was *Exploration* (*k*= 244), followed by *Boldness* (*k*= 153 estimates), *Aggression* (*k*= 129 estimates) and *Stress* (*k*= 95 estimates). The behaviour with the fewest estimates was *Courtship* (*k*= 16), followed by *Foraging* (*k*= 23), *Activity* (*k*= 34), *Parental care* (*k*= 25), and *Social behaviour* (*k*= 41).

Relationships between behaviour and fitness: differences in acquisition or allocation?

We assessed whether differences in resource acquisition or resource allocation mediate the relationship between behaviour and fitness by calculating the correlation between estimates using survival as a fitness proxy and those using reproduction as a fitness proxy. Positive correlations would be consistent with variation in acquisition as the major driver of the patterns, while negative correlations would be consistent with differences in allocation (i.e., trade-offs) as the major driver of the patterns. We evaluated this at both the among-individual level and the phenotypic level using two datasets. The first dataset included 18 pairs of estimates partitioned at the among-individual level from five studies. There was some support for a positive correlation between paired estimates of survival and reproduction, although this effect was not statistically significant (r = 0.206, 95% confidence interval [-0.288-0.614]; Figure 2.4a). The second dataset used 63 pairs of unpartitioned phenotypic estimates from 15 studies and there was strong statistically significant support for a positive correlation between estimates using survival as a fitness proxy and reproduction as a fitness proxy at this level (r = 0.387, 95% confidence interval [0.154-0.579]; Figure 2.4b).

Do the type of behaviour and the testing conditions contribute to heterogeneity?

As a secondary analysis, we assessed whether the relationship between behaviour and fitness differed based on the type of behaviour at the among-individual, within-individual, and phenotypic levels. We used the following datasets to assess the contribution of the type of behaviour to heterogeneity using meta-regression: phenotypic-survival (*k*= 218 estimates), phenotypic-reproduction (*k*= 239 estimates), among-individual-survival (*k*= 142 estimates), among-individual-reproduction (*k*= 144 estimates), and within-individual-reproduction (*k*= 17 estimates). Heterogeneity (I^2) was high for the null models of each of the datasets, except for within-individual-reproduction, which was moderate (Table 2.1): phenotypic-survival (I^2 = 95%), phenotypic-reproduction (I^2= 97%), among-individual-survival (I^2= 96%), among-individual-reproduction (I^2= 91%), within-individual-reproduction (I^2= 57%). In each dataset, the estimated mean of the relationship between individual behaviour and fitness was not statistically different from zero, before considering the effect of moderators on the relationship between behaviour and fitness: the overall mean estimate of the effect size for the phenotypic-survival data was Z*r*= 0.048 (r= 0.048, 95% CI [-0.045-0.140]), Z*r*= 0.057 (r= 0.057, 95% CI [-0.072-0.188]) for the phenotypic-reproduction data, Z*r*= -0.021 (r= -0.021, 95% CI [-0.203-0.161]) for the among-individual survival data, Z*r*= -0.014 (r= -0.014, 95% CI [-0.104-0.076]) for the among-individual reproduction data, and Z*r*= -0.0007 (r= -0.0007, 95% CI [-0.086-0.085]) for the within-individual-reproduction data (Figure 2.5). Behaviour types explained between 0.9% and 57% of variation across each of the five datasets (Table 2.2). The effect of field versus laboratory conditions for measuring fitness explained between 0.04% and 13% of variation across the five datasets (Table 2.2; Figure 2.6).

Publication bias

Visual assessment of the funnel plot did not provide evidence for publication bias (Figure 2.7a). Results of the Egger regression also indicated no evidence of publication bias since the intercept (Z*r*= 0.108, 95% CI [-0.035-0.252]) and slope (Z*r*= 0.217, 95% CI [-0.271-0.701]) of the regression were not significantly different from zero (Figure 2.7b; Table A1.5). Similarly, we found little evidence of a time lag effect by conducting a regression of effect sizes against year of publication; both the intercept (Z*r*= 4.419, 95% CI [-10.88-19.712]) and slope (Z*r*= -0.002, 95% CI [-0.01-0.01]) did not significantly differ from zero (Figure 2.7c; Table A1.6).

Discussion

Using meta-analysis, we evaluated the relationship between individual behaviour and fitness. Our results were consistent with variation in resource acquisition as a key mediator of the relationship between behaviour and fitness components (survival and reproduction) because the estimates for the relationship between behaviour and reproduction and between behaviour and survival were positively correlated. Further, this relationship held at both the phenotypic and among-individual levels. This was surprising, because the expectation based on current theory, is that while there can be among-individual differences in resource acquisition that obscures the trade-off between allocation toward survival and reproduction, allocation trade-offs should still be detected at the within-individual level if among-individual variance in resource acquisition has been accounted for (Figure 2.1c). We also found little support that the relationship between behaviour and fitness proxies varied as a function of behaviour type, and there was no evidence that the testing context (i.e., field or lab) affected the relationship. Taken together, our results suggest a key role of variation in resource acquisition in mediating relationships between behaviour and survival, not only among-individuals, but also within-individuals. This unexpected result warrants further investigation, and we discuss the implications of this finding for understanding and evaluating the role of trade-offs in maintaining consistent among-individual differences in behaviour.

Is the relationship between behaviour and fitness mediated by variation in resource acquisition or resource allocation?

Differences in resource allocation toward survival versus reproduction is widely cited as a key mechanism explaining consistent among-individual differences in behaviour (Wolf et al. 2007; Biro & Stamps 2008; Dingemanse & Wolf 2010). Models of trade-offs predict that traits that are associated with high survival are also associated with low reproduction, and vice versa. More recently, differences in resource acquisition have been proposed to contribute to fitness differences associated with different behavioural types (Laskowski et al. 2020). Under variation in resource acquisition, traits that are positively associated with survival are also positively associated with reproduction (Figure 2.1c). In our systematic review and meta-analysis, we detected a non-significant positive correlation between among-individual estimates of the relationship between behaviour and survival and between behaviour and reproduction, suggesting that differences in resources acquisition, not allocation, mediate the relationship between individual fitness and behaviour among-individuals. This result is in line with two previous meta-analyses, both of which failed to find consistent support for trade-offs as an explanation for adaptive behavioural differences (Smith & Blumstein 2008; Moiron et al. 2020a).

Furthermore, our analyses suggest that variation in acquisition is operating at both the within- and among-individual levels. First, we demonstrated that in our dataset, phenotypic correlations better captured within-individual correlations, as has been suggested by earlier theoretical work (Dingemanse & Dochtermann 2013), and empirically demonstrated using meta-analysis (Niemelä & Dingemanse 2018a). We did this by showing that the statistically significant correlation between among-individual estimates and phenotypic estimates was weakly positive (r= 0.228, 95% CI [0.042-0.399]), while the statistically significant correlation between within-individual estimates and phenotypic estimates was strongly positive (r= 0.804, 95% CI [0.538-0.951]; Figure A1.1). In other words, the phenotypic correlation more closely mirrored the within-individual correlation than the among-individual correlation. This allowed us to use phenotypic correlations as proxies for within-individual correlations when considering survival effects, a necessary approach given that survival cannot be measured repeatedly within individuals. These analyses are consistent with the interpretation that within individuals, variation in resource acquisition mediates the relationship between behaviour and fitness, since the correlation between phenotypic estimates using both survival and reproduction as fitness proxies was positive, in the same way that it was at the among-individual level.

The absence of detectable trade-offs within individuals was unexpected and implies that there is an axis of variation that we are not capturing in this analysis. We suggest that there are at least two additional axes of variation that may be important in shaping within-individual variation in behaviour, survival, and reproduction: age and resources. In some species, both annual survival probability and reproductive success increase with increasing age/experience (e.g., Lunn et al. 1994; Martin 1995), while in others, as older individuals senesce, both reproduction and survival begin to decline (e.g., Bérubé et al. 1999; Bouwhuis et al. 2012; Han & Yang 2021). Increasing reproductive success with age and/or experience would generate positive covariance between survival and reproduction. If behavioural expression is also age-dependent (Stamps & Groothuis 2010; Araya-Ajoy & Dingemanse 2017), it could account for the positive phenotypic correlation between survival and reproduction observed in the present study. Evaluating the relative importance of age and/or experience effects would be relatively straightforward but would require data on the relative age of subjects.

Another gradient likely to shape behaviour, survival, and reproduction within-individuals is access to resources. Resources and environmental conditions are likely to fluctuate across contexts (e.g., years, seasons), and may result in a positive covariance between an individual's investment toward survival and reproduction at any given time because when more resources are available, individuals can simultaneously increase their investment towards both reproduction and survival. For example, survival of both adult and juvenile great tits (*Parus major*) increases in beech-crop years (Perdeck et al. 2000), which would create a positive within-individual correlation between survival and reproduction (via juvenile survival). If behavioural expression is state- (i.e., resource-) dependent, this could generate positive within-individual correlations between behaviour and both survival probability and reproduction, as observed here. Although two recent meta-analyses have demonstrated that resource acquisition influences behavioural expression within individuals (Dougherty 2021a; Dougherty 2021b), empirical work estimating the relationships between behaviour, survival and reproduction simultaneously across environmental gradients of resource availability are needed to test this idea explicitly (Montiglio et al. 2018; Hämäläinen et al. 2021). Our results nonetheless indicate that variation in resource acquisition may play a more important role in shaping behaviour-fitness co-variances than currently captured by theory.

How do the type of behaviour and the fitness testing conditions affect the relationship between behaviour and fitness?

In a recent perspective paper, Laskowski and colleagues (2020) argued that more explicit consideration of how behaviours are functionally linked to resource acquisition versus resource allocation are required to generate *a priori* predictions about how specific behaviours should be associated with fitness. Although we did not directly assess this in our meta-analysis, we did assess whether there was evidence that the relationship between behaviour and fitness differed for different types of behaviours, because we expected that certain behaviours would be more strongly associated with variation in resource acquisition than others. There was no significant relationship between the type of behaviour and the relationship between behaviour and fitness at any of the "fitness proxy – level of organization" combinations, except in the phenotypic-reproduction dataset. This appeared to be driven by the behaviour *courtship*, which had the strongest mean response, though was also only based on seven estimates. The lack of an effect of behavioural type on fitness was surprising, since, for example, foraging and boldness should both intuitively bring in more resources with increasing behavioural expression (Stamps 2007; Biro & Stamps 2008). However, if the expression of these behaviours is state-dependent along multiple dimensions of state (e.g., animals experiencing a state of hunger have higher behavioural expression, but expression is also higher when there is low predation risk), also called multidimensional reaction norms (Westneat et al. 2011; Westneat et al. 2015), failing to account for the multidimensionality of behavioural expression within-individuals might obscure the relationship between behaviour and fitness.

High unexplained heterogeneity in our meta-analysis indicated that there is much unaccounted context-dependency in the relationship between behaviour and fitness. Our meta-analysis undoubtedly combines estimates across gradients of resource availability; if the within-individual variation in resource availability present in our study exceeds the within-individual variation in resource allocation, then within-individual trade-offs will not be detected even if they are occurring, and it is thus not possible to unambiguously separate the roles of resource acquisition and resource allocation in maintaining among-individual differences in behaviour. However, if resource acquisition is a key mediator of the relationship between behaviour and fitness, the strength of relationships should be stronger when behaviours are coded such that higher levels reflect higher resource acquisition, as verified by empirical studies. We attempted to accomplish this in our study by coding behaviours in a way that reflected that increasing behavioural expression increased resource acquisition. While we did not find a global effect of behavioural type on the relationship between behaviour and fitness, adding a moderator characterizing the resource landscape or resource heterogeneity could highlight contexts in which resource acquisition is important and others where it is not. For example, we could not predict how sociability would influence resource acquisition, because in certain contexts social behaviour may increase access to resources (e.g., Carter & Wilkinson 2013), while in others it may not (e.g., Bruintjes et al. 2010), thus we coded the direction of sociability in line with the Pace-of-Life Syndrome framework, which predicts that increasing social behaviour is related to a slow a pace of life (Réale et al. 2010). Even behaviours that are clearly predicted to be positively associated with resource acquisition may have a relationship with fitness components that depends on the resource landscape; for example, increasing foraging to increase resource acquisition in a hungry individual will be allocated toward survival, but once the individual is satiated, resources can then be allocated to reproduction (Houston & McNamara 2014). For this reason, Laskowski and colleagues (2020) urge that studies are needed that carefully control for and measure resource acquisition as a function of behaviour among individuals. Our meta-analysis suggests that such an approach is also warranted at the within-individual level. For example, controlled lab experiments can observe how behavioural expression, and the relationship between behaviour and fitness, change as a function of resource availability, in a system where individuals can uptake resources proportionally to their availability.

Resource availability should have a strong effect on fitness outcomes, regardless of the relationship between resource acquisition and behaviour (van Noordwijk & de Jong 1986; Stearns 1989). In our meta-analysis, we expected resource availability at the time the study was conducted to affect the relationship between behaviour and fitness; we thus assessed the effect of measuring fitness in the lab versus in the field on this relationship. We expected that testing conditions would matter because in the lab, variation in resource acquisition can be controlled. Specifically, we expected there to be no within-individual variation in resource acquisition, or at least less compared with field observations, where environmental conditions fluctuate, leading to a smaller estimated relationship between behaviour and fitness at the within-individual and phenotypic levels. This was not the case: estimated effect sizes between field and lab studies were broadly overlapping at all levels. Interestingly, Moiron et al. (2020b) also failed to detect an effect of testing location on the relationship between the expression of risky behaviour and survival. However, in our meta-analysis, differences in the types of behaviours measured and the taxonomic representation in lab versus field studies limit the inferences that we can draw from these comparisons. For example, studies measuring fitness in the field were mostly conducted on birds and mammals (331 estimates out of 361), while those conduced in the lab were primarily on invertebrates (198 estimates out of 221). Thus, in addition to the potential differences due to taxa specific effects, the effect of within-individual variation in age was also likely greater in the lab studies, given that taxa most commonly represented in the lab studies have shorter lifespans on average relative to the species that were most commonly represented in field studies. To determine whether there is an effect of resource availability, age/experience, and predation limitation on the relationship between behaviour and fitness, ideally, studies would need to assess the relationship both in the lab and in the field for the same focal organism and the same behaviour, similar to the approach that we took to assess whether there were trade-offs between survival and reproduction.

Limitations and future directions

Our meta-regression revealed significant heterogeneity that was primarily explained at the level of the observation (i.e., single estimates), indicating that there was substantial variation that was not explained by the four factors that we assessed: fitness proxy (survival or reproduction), hierarchical level (among-individual, within-individual, and phenotypic levels), type of behaviour, and testing condition. This demonstrates that the relationship between behaviour and fitness is largely context specific. We did not investigate the effect of other state variables such as population density, sex, and age in our meta-analyses, though other studies have found these to be important predictors of the relationship between behaviour and fitness (e.g., Kilgour et al. 2018; Santicchia et al. 2018; Dingemanse et al. 2020), and which undoubtedly contributed to some of the observed heterogeneity in our study. Although we did not detect a phylogenetic effect of species, in certain cases the non-phylogenetic effect of species explained some heterogeneity; this may be due to the over-representation of certain taxa in our study (Figure 2.3). Some animals are amenable to a particular type of testing, for example using standardized assays; behaviours measured in this manner may reflect unique functional traits that are commonly tested in a small number of model species, rather than effects due to species identity *per se*. Finally, the way our study was conducted assumed a linear relationship between behaviour and fitness, and thus we could not account for fluctuating selection or other non-linear relationships between behaviour and fitness, although there are examples of both fluctuating selection and disruptive selection on behaviour (e.g., Dingemanse et al. 2004; Bergeron et al. 2013).

The obvious next step for the field of animal personality is to address the lack of understanding of how resource acquisition affects behavioural expression (and vice versa), and in turn how this mediates fitness outcomes. Although this point has recently been raised by Laskowski and colleagues (2020), their call was focused on among-individual variation. Our analyses suggest that variation in resource acquisition may also be important toward understanding the co-variance between behaviour and fitness proxies at the within-individual level. Studies need to explicitly evaluate the relationship between behavioural expression and resource acquisition, for example by observing whether individuals adjust behavioural expression along gradients of resource availability (within-individual effect) as well as whether repeatable among-individual differences in behaviour are associated with repeatable among-individual differences in resource acquisition (among-individual effect). Our study contributes to the accumulating evidence that trade-offs between survival and reproduction may not be as important for maintaining behavioural variation among individuals in populations as previously thought. Our study also highlights the interesting and unexpected pattern of resource acquisition potentially shaping the relationship between behaviour and fitness within-individuals.

Conclusions

1) Variation in how individuals allocate limited resources to survival versus reproduction (i.e., trade-offs) is a leading explanation for consistent differences in behaviour in the field of animal personality. However, we found that behaviours associated with increased survival were also associated with increased reproduction, suggesting that differences in resource acquisition are more important in mediating these relationships than differences in resource allocation.

2) Contrary to what we expected, the relationship between behaviour and fitness were similar at both the within- and among-individual levels and were consistent with variation in resource acquisition as a potential mediator of the relationship a across both these levels.

3) Overall, the type of behaviour was not a strong predictor of the direction of the relationship between behaviour and fitness at any level (among and within individuals). This could be the result of differences in how the behaviours are defined and tested in different studies, meaning that within a behavioural category there may be functional differences of the behaviour on the focal organisms.

4) Although access to resources is expected to differ between field and lab studies, we found no effect of testing condition on the direction and strength of the relationship between behaviour and fitness proxies. This may be due to differences in taxa and/or behaviours represented in lab studies, and/or due to differences in the relative importance of within-individual variation in age captured in lab studies compared to field studies.

5) Taken together, our results provide strong support that trade-offs are not a key mechanism linking behaviour and fitness at either the among- or within-individual levels, but instead, indicate that variation in resource acquisition may be more important than previously thought. Empirical studies are needed that explicitly test the link between behavioural expression and resource acquisition both within and among individuals to allow a stronger predictive framework to be developed.

Acknowledgements & Data Availability

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Discovery Grant (DP200100367) and KJM was supported by University of Alberta Startup funds and an NSERC Discovery Grant (RGPIN-2018-04358). Data and reproducible analyses are provided at http://doi.org/10.5281/zenodo.5111893 (Haave-Audet *et al.*, 2021).

Tables & Figures

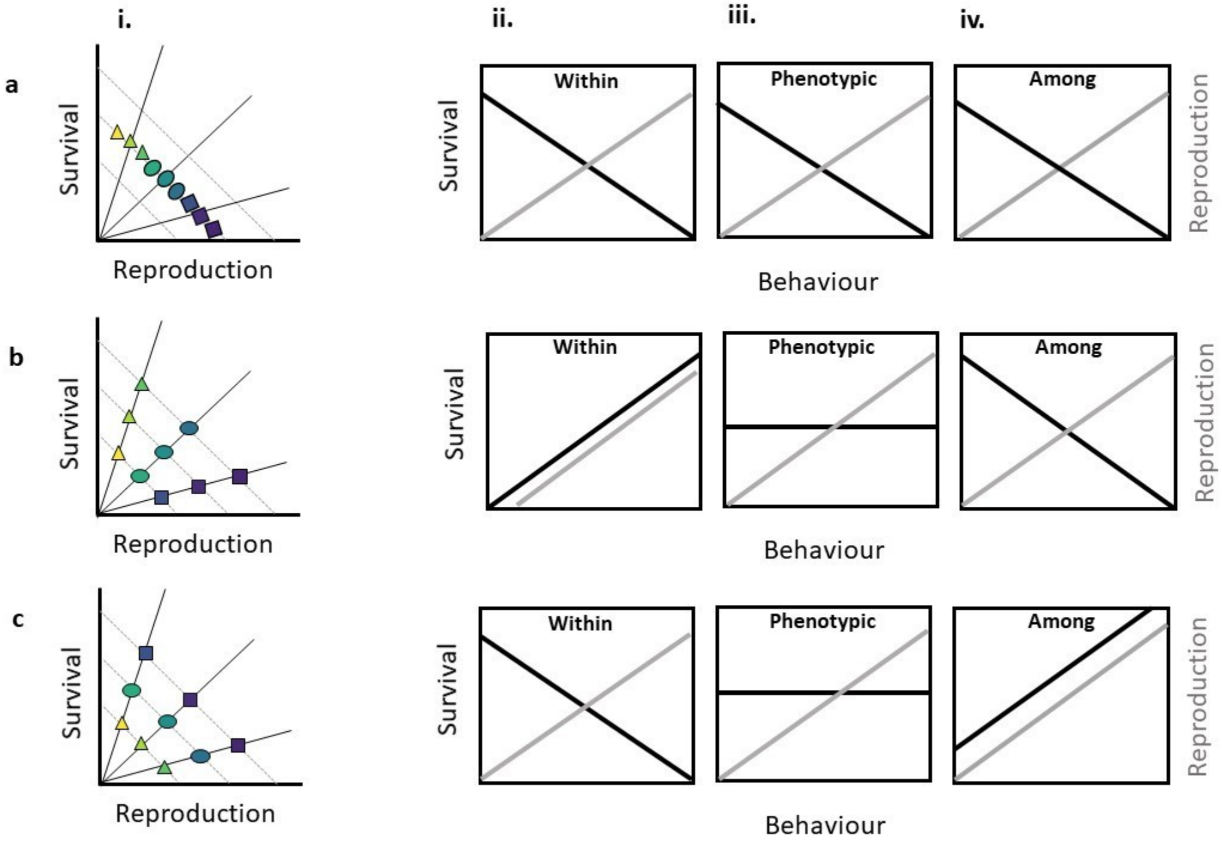

Figure 2.1. The relationship between behaviour and survival and between behaviour and reproduction depends on the relative importance of variation in resource allocation versus resource acquisition at the within- and among-individual levels. We illustrate this using three hypothetical individuals (denoted by symbol shape) with three different combinations of variation in resource acquisition and resource allocation. Variation in behavioural expression is illustrated by the colour and saturation of the symbols (darker, more saturated colours = higher level of expression). In panel i), the solid lines represent a specific allocation between survival and reproduction (i.e., points falling on the same solid line have the same relative allocation to survival versus reproduction). Parallel dotted lines denote differences in total resources available (i.e., acquisition). The remaining panels (ii-iv) show how the specific combination of variation in allocation and acquisition illustrated in panel i) generate different ii) within-individual, iii) phenotypic, and iv) among-individual correlations between behaviour and survival (black lines) and between behaviour and reproduction (grey lines). In a) resource allocation varies both within- and among-individuals, but there is no variation in resource acquisition either within- or among-individuals. All individuals have access to the same total resource and differ in how they allocate resources to

survival versus reproduction. The individual illustrated by the triangle consistently allocates more to survival (and less to reproduction) compared to the individual illustrated by the circle, who in turn allocates more to survival compared to the individual illustrated by the square. Higher behavioural expression is associated with higher allocation to reproduction both within-individuals and among-individuals. Consequently, correlations between behaviour and fitness are identical both within- and among-individuals, and the phenotypic correlation provides an unbiased estimate of either level. In b) individuals vary in patterns of allocation at the among- but not within-individual level, but behaviour also varies as a function of acquisition within-individuals. The individual illustrated by the square consistently invests more toward reproduction than the individual illustrated by the circle, while the individual illustrated by the circle consistently invests more toward reproduction than the individual illustrated by the triangle. Across individuals, higher expression is associated with higher allocation to reproduction. This results in the detection of trade-offs at the among-individual level because patterns of allocation differ among-individuals. However, within-individuals, increasing behavioural expression increases resource acquisition, which means that investment toward both survival and reproduction increases as behavioural expression increases. At the phenotypic level, higher behavioural expression is associated with higher reproduction. However, there is no detectable relationship between behavioural expression and survival since the phenotypic level averages the opposing patterns at the within- and among-individuals levels. In c) Individuals vary in resource acquisition, but allocation varies as a function of behaviour within individuals. The individual illustrated by the square consistently acquires more resources than the individual illustrated by the circle, while the individual illustrated by the circle consistently acquires more resources than the individual illustrated by the triangle. Across individuals, higher behavioural expression is associated with greater acquisition, while within-individuals, higher behavioural expression is associated with higher allocation toward reproduction. Here, the phenotypic correlation has a positive slope when reproduction is used as a fitness proxy, because at both the within- and among-individual levels, behaviour positively covaries with investment into reproduction. However, since the patterns of within and among-individual covariances are different when survival is used as a fitness proxy, there is no relationship detected at the phenotypic level. Figure inspired by van Noordwijk and de Jong (1986) and Laskowski et al. (2020). Behavioural expression depicted using the viridis colour palette (Garnier, 2018). Note that the relationships depicted in panel c) are the ones predicted by current theory in animal personality (Laskowski et al., 2020).

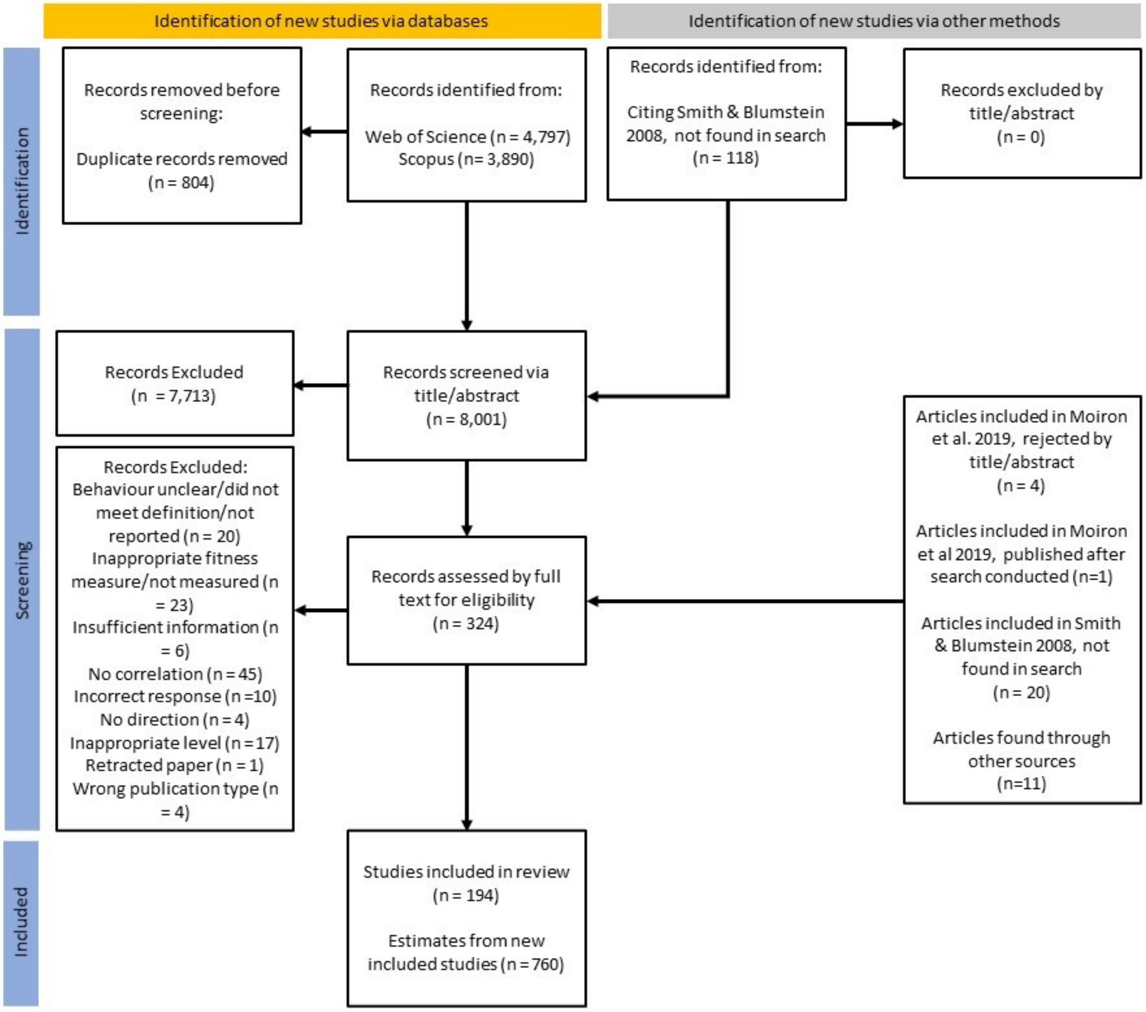

Figure 2.2. PRISMA flow-chart indicating the number of articles retained at each phase of the systematic review. The list of included studies can be found in Table A1.1 and the list of rejected studies and the reason for rejection can be found in Table A1.2.

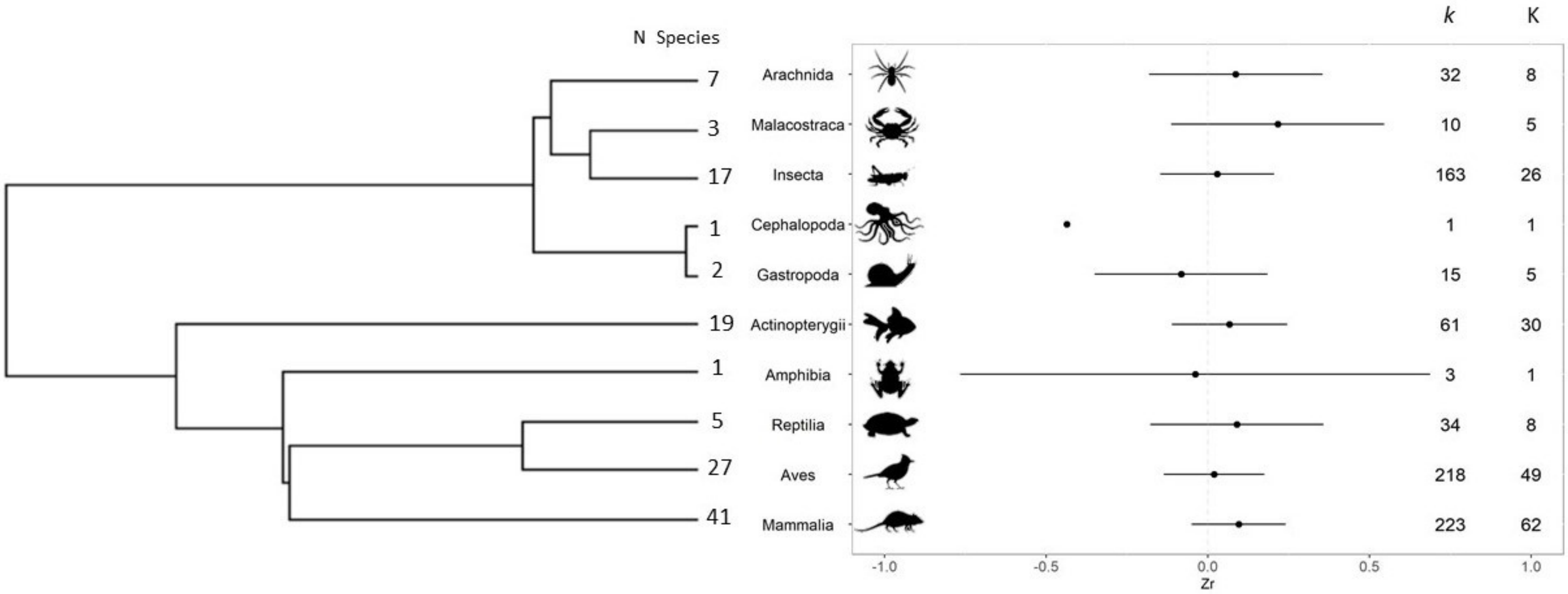

Figure 2.3. Phylogenetic relationships used in the meta-regression, grouped by class, and the accompanying mean effect size of the relationship between behaviour and fitness for k estimates from K studies. Animal icons modified from Wikimedia Commons: Tris T7 - Own work, CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=76188736.

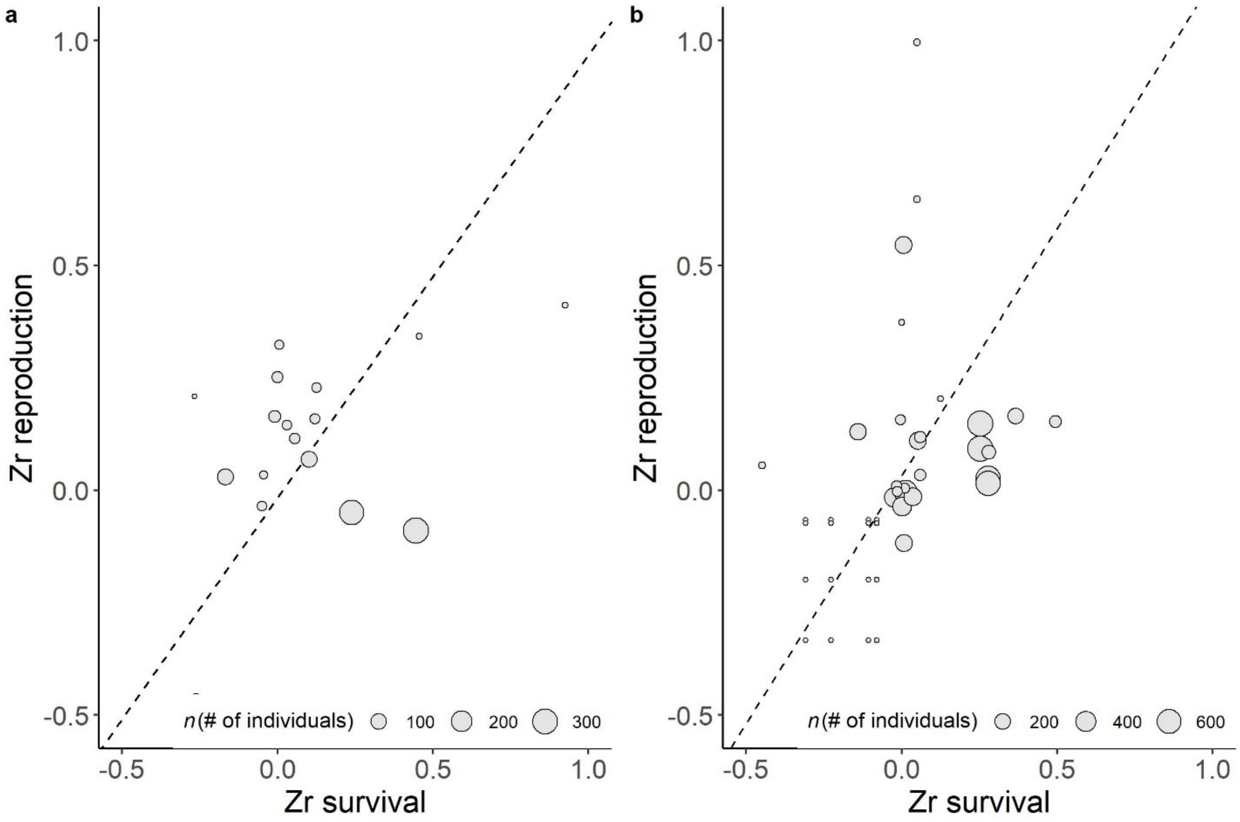

Figure 2.4. Correlation between standardized effect sizes of paired estimates of the relationship between individual behaviour and fitness (survival and reproduction) using a) estimates partitioned among-individuals (k=18 pairs), and b) unpartitioned phenotypic estimates (k= 63).

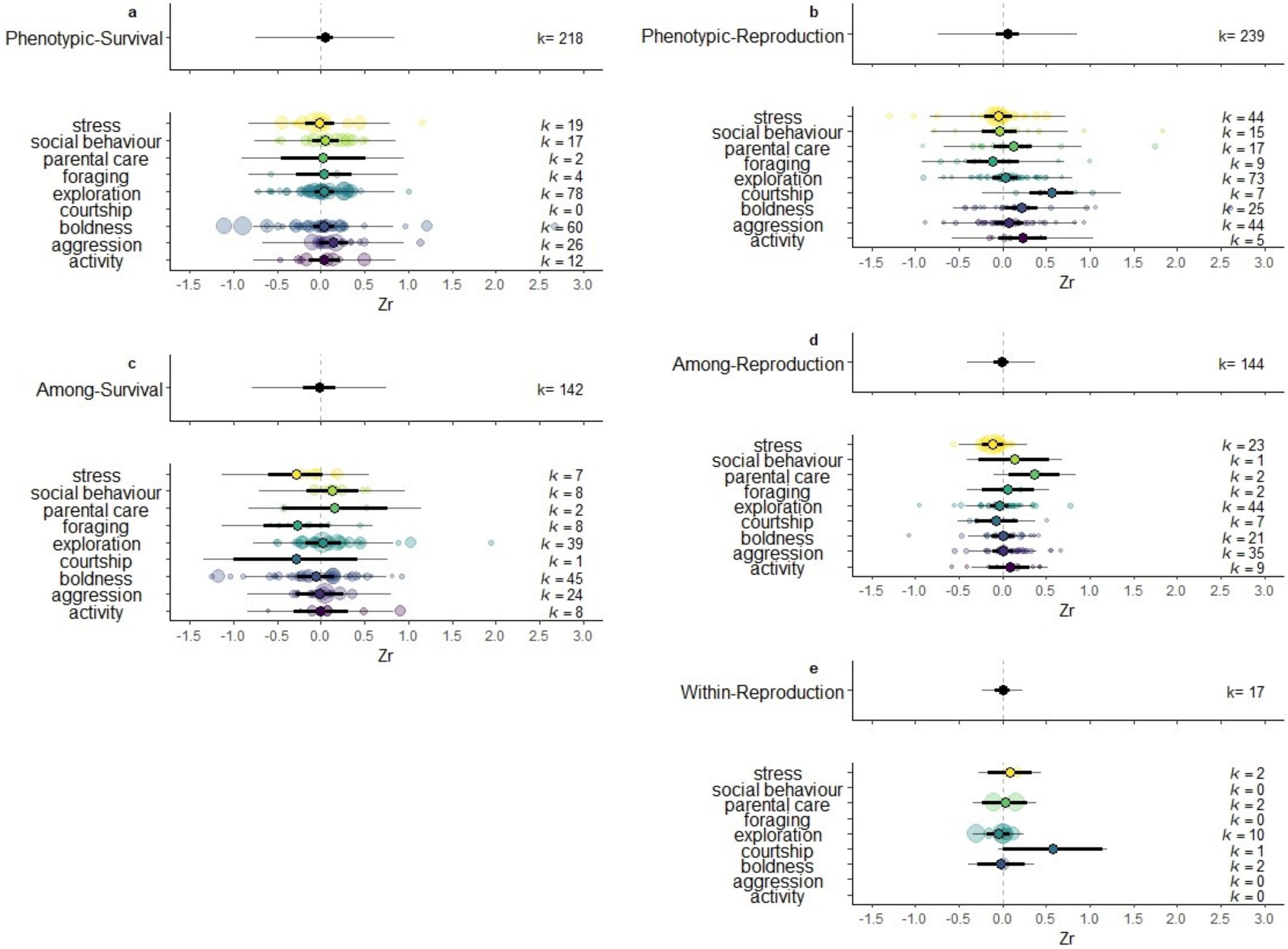
a
Phenotypic-Survival
k= 218
stress
social behaviour
parental care
foraging
exploration
courtship
boldness
aggression
activity
k = 19
k = 17
k = 2
k = 4
k = 78
k = 0
k = 60
k = 26
k = 12
-1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0
Zr
b
Phenotypic-Reproduction
k= 239
stress
social behaviour
parental care
foraging
exploration
courtship
boldness
aggression
activity
k = 44
k = 15
k = 17
k = 9
k = 73
k = 7
k = 25
k = 44
k = 5
-1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0
Zr
c
Among-Survival
k= 142
stress
social behaviour
parental care
foraging
exploration
courtship
boldness
aggression
activity
k = 7
k = 8
k = 2
k = 8
k = 39
k = 1
k = 45
k = 24
k = 8
-1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0
Zr
d
Among-Reproduction
k= 144
stress
social behaviour
parental care
foraging
exploration
courtship
boldness
aggression
activity
k = 23
k = 1
k = 2
k = 2
k = 44
k = 7
k = 21
k = 35
k = 9
-1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0
Zr
e
Within-Reproduction
k= 17
stress
social behaviour
parental care
foraging
exploration
courtship
boldness
aggression
activity
k = 2
k = 0
k = 2
k = 0
k = 10
k = 1
k = 2
k = 0
k = 0
-1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0
Zr

Figure 2.5. Mean estimates (Zr) of the relationship between individual behaviour and fitness. The top panels of each quadrant depict the overall mean, and bottom panels show the effect moderated by the type of behaviour, at the a) phenotypic level with survival as a fitness proxy, b) phenotypic level with reproduction as a fitness proxy, c) among-individual level with survival as a fitness proxy, d) among-individual level with reproduction as a fitness proxy, and e) within-individual level with reproduction as a fitness proxy. Opaque circles represent the mean effect size, and translucent circles represent individual estimates, where the size of the circle represents the number of individuals tested. Bold lines depict 95% confidence intervals and thin lines depict 95% prediction intervals.

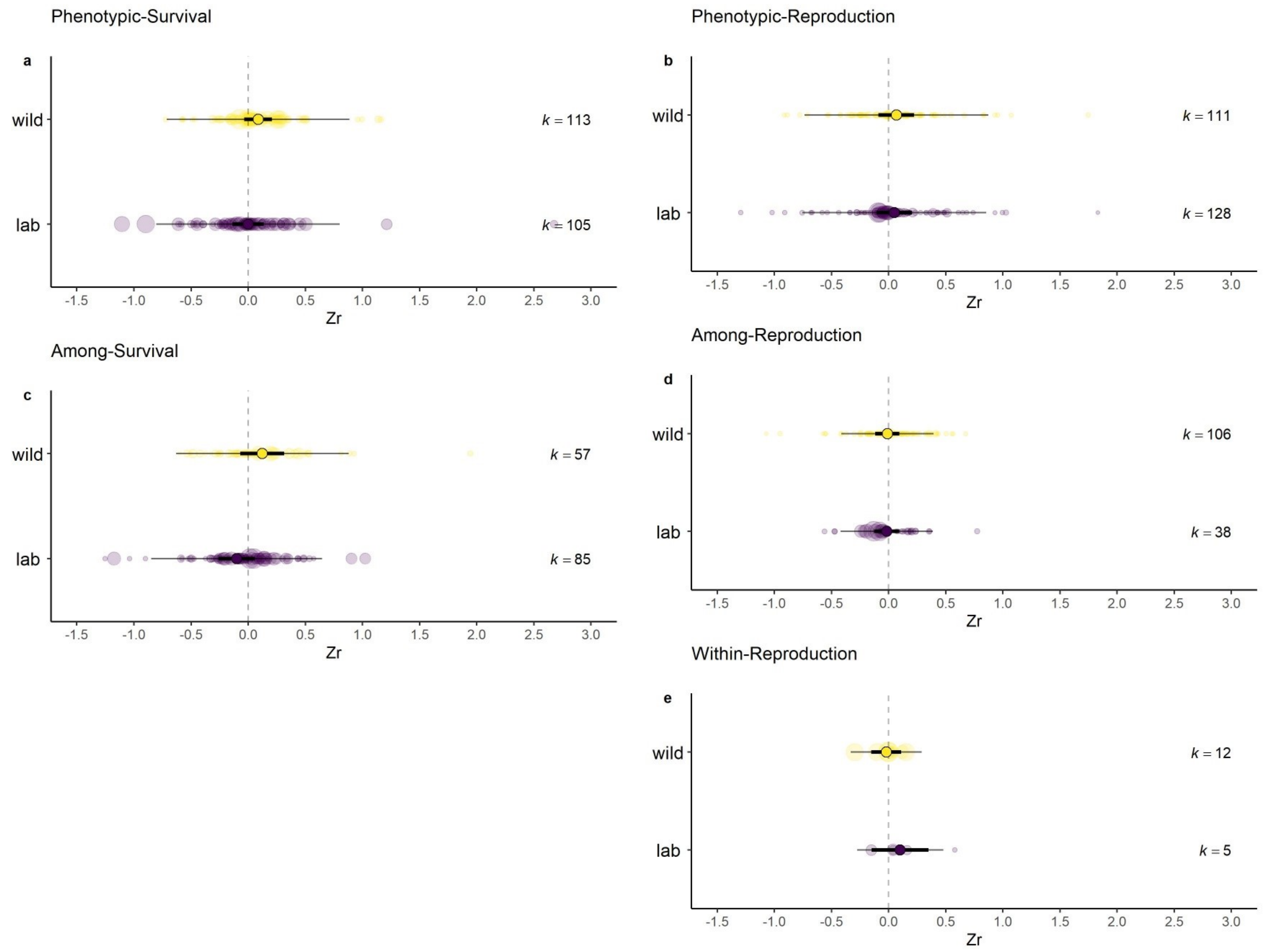
Phenotypic-Survival
a
wild
lab
k = 113
k = 105
-1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0
Zr
Phenotypic-Reproduction
b
wild
lab
k = 111
k = 128
-1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0
Zr
Among-Survival
c
wild
lab
k = 57
k = 85
-1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0
Zr
Among-Reproduction
d
wild
lab
k = 106
k = 38
-1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0
Zr
Within-Reproduction
e
wild
lab
k = 12
k = 5
-1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0
Zr

Figure 2.6. Mean estimates (Zr) of the relationship between individual behaviour and fitness moderated by the testing conditions under which behaviour was measured, at the a) phenotypic level with survival as a fitness proxy, b) phenotypic level with reproduction as a fitness proxy, c) among-individual level with survival as a fitness proxy, d) among-individual level with reproduction as a fitness proxy, and e) within-individual level with reproduction as a fitness proxy. Opaque circles represent the mean effect size, and translucent circles represent individual estimates, where the size of the circles represent the number of individuals tested. Bold lines depict 95% confidence intervals and thin lines depict 95% prediction intervals.

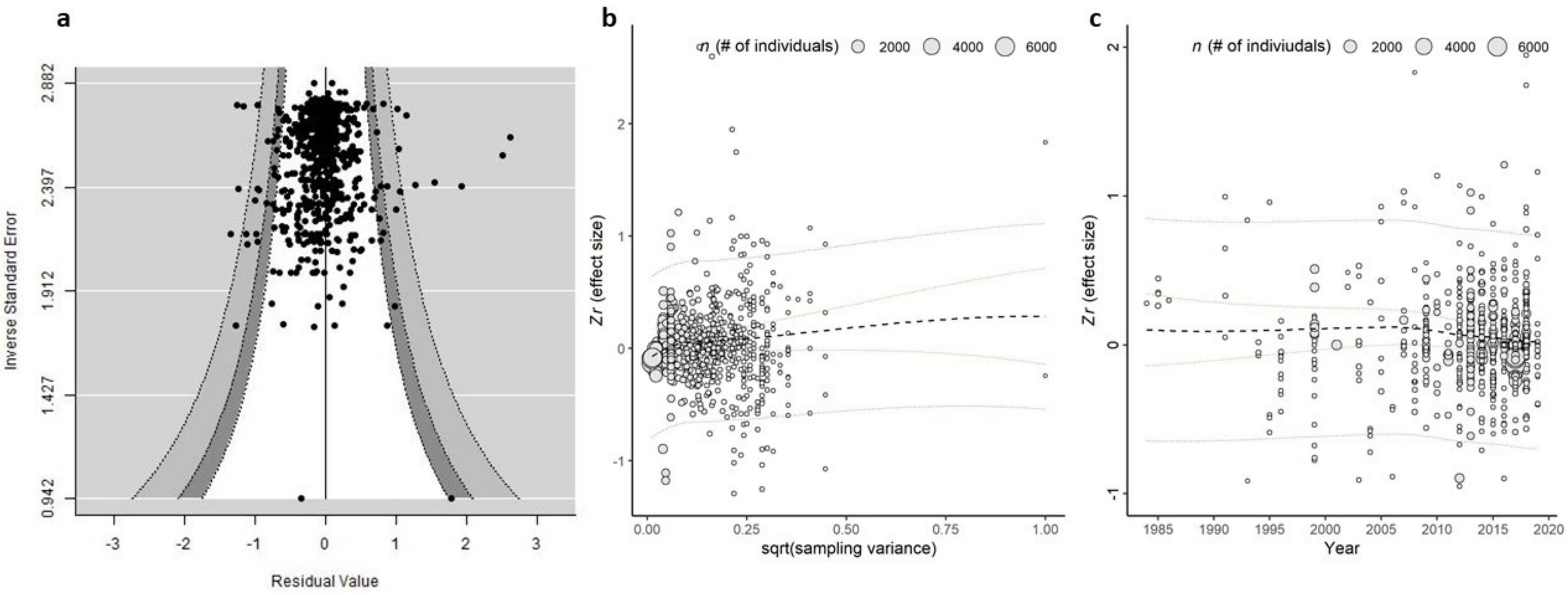
a
Inverse Standard Error
2.882
2.397
1.912
1.427
0.942
-3
-2
-1
0
1
2
3
Residual Value
b
n (# of individuals)
2000
4000
6000
Zr (effect size)
2
1
0
-1
0.00
0.25
0.50
0.75
1.00
sqrt(sampling variance)
c
n (# of indiviudals)
2000
4000
6000
Zr (effect size)
2
1
0
-1
1985
1990
1995
2000
2005
2010
2015
2020
Year

Figure 2.7. Assessing publication bias. a) Funnel plot (from inside the funnel (x-axis =0) outwards, shading depicts significance, where 1) $0.1 < p \leq 1$, 2) $0.05 < p \leq 0.1$, 3) $0.01 < p \leq 0.05$, 4) $0.0 < p \leq 0.01$). b) Egger regression to assess funnel asymmetry, with 95% confidence intervals depicted by the orange (inner) dotted lines and 95% prediction intervals depicted by the blue (outer) dotted lines. c) Regression testing time lag effect of published effect sizes, with 95% confidence intervals depicted by the orange (inner) dotted lines and 95% prediction intervals depicted by the blue (outer) dotted lines (these are non-linear as they are predictions from multi-moderator models).

Table 2.1. Heterogeneity (I^2) calculated on the null meta-regression models for five fitness-variance-partitioning datasets.

	Phenotypic-survival	**Phenotypic-reproduction**	**Among-survival**	**Among-reproduction**	**Within-reproduction**
Total I^2	95.5%	97.4%	95.6%	91.5%	56.6%
Phylogenetic effect of species	0%	0%	6.8%	0%	0%
Non-phylogenetic effect of species	19.2%	6.2%	15.5%	22.1%	0%
Study ID	56.8%	70.8%	15.1%	0%	0%
Observation ID	19.2%	20.4%	58.1%	69.4%	56.6%

Table 2.2. Variation explained by behaviour and the condition in which fitness was measured as moderators in meta-regression in each of five partitioning-fitness proxy datasets.

Moderator	**Dataset**	**R^2**	***Q***	***p*-value**	***df***
Behaviour	Phenotypic-survival	0.009	3.388	0.908	8
	Phenotypic-reproduction	0.091	32.840	0.0001*	9
	Among-survival	0.062	9.975	0.353	9
	Among-reproduction	0.117	12.464	0.188	9
	Within-reproduction	0.573	5.707	0.336	5
Fitness Condition	Phenotypic-survival	0.012	1.908	0.385	2
	Phenotypic-reproduction	0.0004	0.794	0.672	2
	Among-survival	0.081	4.492	0.106	2
	Among-reproduction	0.0001	0.094	0.954	2
	Within-reproduction	0.135	0.774	0.679	2

*Denotes statistical significance at alpha = 0.05.

Chapter 3: Sampling to survive: energetic constraints shape sampling decisions in black-capped chickadees (*Poecile atricapillus*)

Introduction

Animals are faced with uncertainty in virtually every decision they make, including who to mate with to maximize reproduction, where to roost to avoid predation and the elements, and which food patches to exploit to maximize energy intake (Dall 2010). Uncertainty exists because animals are limited in the time and energy they can invest learning about their environment, and because the environment can change unpredictably (i.e., stochastically). Uncertainty can have critical fitness consequences, and thus strategies for managing uncertainty are predicted to be under strong selection pressure (Dall et al. 2005). There are two main options for managing uncertainty: insurance and sampling. Individuals can mitigate the negative consequences of uncertainty by investing in insurance. For example, a forager can cache food or build energy reserves to buffer themselves against unpredictable foraging failures (Dall & Johnstone 2002). When uncertainty is not solely attributed to stochasticity, individuals can reduce uncertainty by sampling the environment. Sampling allows individuals to update their information about the availability and state of resources (Stephens 1987; Dall & Johnstone 2002).

Theory predicts that insurance and sampling should depend on the level of resource predictability and individual energy requirements relative to food availability (Mathot & Dall 2013). More specifically, sampling behaviour is predicted to occur under two distinct sets of conditions: 1) when the risk of starvation is great, sampling maximizes the probability of survival and 2) when the risk of starvation is low, sampling maximizes expected intake rate (Mathot & Dall 2013). At intermediate starvation risk, sampling is not expected. Sampling under these two distinct sets of conditions is referred to as "sampling out of necessity" and "sampling as a luxury", respectively (Mathot & Dall 2013). The key determinant of whether sampling will occur out of necessity or as a luxury is starvation risk, which itself is affected by food availability relative to energy requirements and current state (Stephens 1981). For example, for a given food availability, higher basal metabolic rate, lower ambient temperature, or lower energy reserves (i.e., body fat), would all increase the risk of starvation. Thus, sampling as a luxury is expected to decrease as conditions become more challenging, while sampling as a necessity should increase as conditions become more challenging (e.g., lower ambient temperatures).

Empirical work has highlighted that within-populations, individuals often show repeatable variation in the use of both insurance and sampling. For example, some individuals invest more in fat stores as a form of insurance against the risk of starvation (Bednekoff & Krebs 1995). In some species, among-individual differences in fat stores can only be understood in light of uncertainty reduction, because subordinate individuals, which experience greater food uncertainty compared to dominant individuals, are the ones to carry more fat (e.g., Witter & Swaddle 1995; Gosler 1996; Pravosudov et al. 1999).This is contrary to what would be predicted based on priority access to food, which would predict that dominants should carry more fat (Ekman & Lilliendahl 1993; Pravosudov & Lucas 2000). In other studies, it has been shown that some individuals consistently spend more time sampling potential food patches (e.g., Morand-Ferron et al. 2011; Rosa et al. 2012; Arvidsson & Matthysen 2016). For example, some studies have demonstrated that certain individuals consistently discover new food patches or novel food sources before other members in the population (van Overveld & Matthysen 2010; Rojas-Ferrer et al. 2019). Others have demonstrated that some individuals consistently track patches that vary in quality more closely than others (Krebs et al. 1978; Shettleworth et al. 1988; Morand-Ferron et al. 2011). In another example, van Overveld & Matthysen (2013) observed a population of great tits (*Parus major*) in a system of randomly fluctuating “all-or-nothing” food patches and found that individuals displayed differences in their tendency to re-visit patches that were no longer profitable, and that individuals that sampled the empty patches returned to those patches more rapidly once they had been re-baited.

Given the potential fitness consequences of investing in sampling, it may appear maladaptive that some individuals consistently display less sampling behaviour than others in a population (or vice versa). However, and when considering survival as a component of fitness specifically, sampling behaviour should have different effects on survival depending on whether sampling is occurring out of necessity or as a luxury. If sampling behaviour is taking place out of necessity, then sampling and survival are expected to be negatively related. On the other hand, if sampling behaviour is occurring as a luxury, then sampling and survival should be positively related. If sampling as a necessity and sampling as a luxury occur at the same time in a given population, sampling may have no overall relationship with survival compared with not sampling, but greater variance, with sampling being done by the individuals in both the best condition (high survival probability) and worst condition (low survival probability) in a given population.

Although it is now clear that consistent among-individual differences in sampling behaviour are often present within populations, there are no explicit tests of the key theoretical prediction that sampling behaviour can take place as a luxury or out of necessity. Here, we evaluated support for these two distinct types of sampling, and their associated survival effects. To do this, we performed field experiments in free-living black-capped chickadees (*Poecile atricapillus*) where we manipulated the availability of predictable food sources. Food uncertainty provides a good system for investigating sampling behaviour and its fitness consequences, especially in environments where conditions are harsh. This is because harsh conditions, including temperatures well outside the thermoneutral zone of the organism and/or food scarcity, are expected to strongly influence starvation risk. Black-capped chickadees overwinter in central to northern North America and must forage at a time of year when natural food availability and quality are low (Smith 1992), making them vulnerable to starvation and energy shortfalls for thermoregulation in below-freezing environments. Further, black-capped chickadees readily visit artificial feeders, making them amenable to studies with food availability manipulations.

In this study, we experimentally manipulated food availability throughout the winter in a population of black-capped chickadees and tracked individual visits to feeders to quantify sampling behaviour. We quantified sampling behaviour over a three-month period for 132 chickadees and recorded survival over the subsequent 12 months. We measured sampling behaviour both when predictable, alternative food sources were available (sampling as a luxury) and when alternative predictable food sources were not available (sampling as a necessity). Further, we assessed sampling behaviour over a range of below-freezing temperatures, to assess how the use of sampling as a necessity versus sampling as a luxury changed as a function of temperature. Previous theoretical work predicts that sampling as a luxury increases with decreasing energetic costs, while sampling as a necessity increases with increasing energetic costs (Mathot & Dall 2013). We predicted that sampling as a luxury should increase with increasing temperature, while sampling as a necessity should increase with decreasing temperature based on the relationship between ambient temperature and costs of thermoregulation (Broggi et al. 2004). We also evaluated support for consistent among-individual differences in sampling, and asked whether these differences were related to sex, since in chickadees, males are dominant over females (Smith 1992), and we would predict that subordinate (i.e., female) individuals would have an overall higher sampling rate than dominant (i.e., male) individuals, because they are faced with higher uncertainty around access to food (Koivula et al. 1994). Finally, we assessed whether among-individual differences in sampling behaviour predicted annual survival in the population. Since sampling as a luxury and sampling as a necessity are expected to have different relationships with survival, we assessed the strength and the direction of the relationship between survival and sampling when an alternative food source was available (sampling as a luxury) and when an alternative food source was not available (sampling out of necessity).

Methods

Field site and study organisms

We studied a population of black-capped chickadees (hereafter *BCCH*) at the University of Alberta Botanic Garden, located near Devon, Alberta, Canada (53° 24' 27'' N, 113° 45' 41'' W) between November 2019 and March 2020. BCCH are small passerines (~ 12 g) that form stable winter flocks (Smith 1992). To track individual foraging, we installed eight feeding stations (at least 270 m apart to approximate BCCH flock territory size) with radio-frequency identification (RFID) boards, which recorded birds with passive-integrated transponder (PIT) tags (see Arteaga-Torres et al. 2020 for detailed description). We first installed the feeding stations at our field site in the fall of 2017. To identify individuals in the population, we captured individual BCCH at the eight feeding stations using mist nets in fall 2018, spring 2019 and fall 2019, prior to experiments. Feeding stations were baited with black oil sunflower seeds, and we made food available approximately one month prior to mist-netting, to allow birds time to discover the feeders. PIT tags were affixed on leg bands (8 mm x 2mm, EM4102 frequency, Eccel Technology Ltd, UK). At capture, we took individual standard morphometric measurements, including body mass, wing length, tarsus length, bill depth, and bill length. Because BCCH are sexually monomorphic (Smith 1992), we also took a blood sample from the brachial vein to molecularly sex individuals. For individuals for which we could not obtain a blood sample, we assigned sex using a discriminant function analysis based on body mass, wing length and tarsus length (S. Sridharan*, Personal communication*).

Sampling experiments

Following mist netting in fall 2019, we left the eight feeding stations baited with sunflower seeds for two weeks prior to beginning the information sampling experiment to avoid carryover effects from catching. At the onset of the experiments, we introduced a second RFID-enabled feeder ~ 10-15 m away from the first feeder at each of the eight feeding stations; this distance was selected to ensure that birds would easily find the new feeder and that the new feeder was within the foraging territory of a given flock. Once the second feeder was installed, we left both feeders empty for one week prior to starting food manipulations. At the onset of the food manipulations, both feeders were filled with black oil sunflower seeds, marking the start of the experiment. We then ran the following experimental treatments four times over of the course of the season at each of the eight feeding stations in the following order: 1) *full-full*: both feeders at the station were full for four days, 2) *full-empty*: one feeder was randomly emptied at each station while the other remained full for four days, 3) *empty-full:* the opposite feeder was emptied and the other filled for four days, 4) *empty-empty:* both feeders at each station were emptied for 12 days (Figure 3.1; detailed timeline in Appendix 2). We ran the *empty-empty* treatment for 12 days, to reduce the effects of supplemental feeding on inflating overwinter survival (Wilson 2001b; Robb et al. 2008). Conducting the *full-full* treatment following the *empty-empty* treatment in each replicate ensured that birds resumed using the feeders following a prolonged period without food. Including treatments with an alternative available food source (one feeder full, one feeder empty) and without an alternative food source (both feeders empty) allowed us to assess sampling behaviour with changing food availability. We considered sampling behaviour when an alternative food source was available to be sampling as a luxury, and sampling when no alternative food source was available to be sampling as a necessity. Throughout the experimental period, daily average temperature ranged from -36.56°C to 1.60°C (mean= -8.51°C ± 5.71°C, s.d.); assessing sampling behaviour over a temperature gradient allowed us to investigate the effect of environmentally induced changes in energetic requirements on sampling. We matched RFID board battery changes with treatment changes every four days. During the 12-day *empty-empty* treatments, we continued to change the batteries every four days. During the experimental period, the RFID boards at feeders recorded the visits of PIT-tagged individuals in the population, giving us instantaneous visit records (i.e., date-time of the visit and individual ID).

Data selection and analysis

We conducted data selection and analyses using R version 3.6.1 (R Core Team 2019) and RStudio version 1.2.1335 (RStudio Team 2018). Using the individual detection data at the 16 feeders, we calculated individual inter-visit interval (IVI) as a measure of feeder visits; IVI represents the time between two subsequent feeder visits by an individual at the same feeder on the same day. The RFID system used in the present study has a potential read frequency of 25 Hz (i.e., up to 25 detections of a PIT tag can be registered per 1 sec assuming the PIT tag is within the detection radius of the antenna). Based on video recordings at the feeders and field observations (see Arteaga-Torres et al. 2020 for details), we removed visits that had an IVI < 12 seconds, as they cannot represent two unique visits to the feeder, but rather, reflected repeated recordings of the same individual during the same visit. We quantified sampling behaviour by determining IVI at feeders that individuals had previously encountered in an empty state, indicating that individuals were updating their information about food availability at a patch that was known to be empty (Shettleworth et al. 1988). Sampling behaviour was operationally defined as a visit to a feeder that was experienced as unrewarding on the visit immediately preceding the current visit, following Stephens (1987). As such, sampling behaviour was measured at empty feeders during the *full-empty* and *empty-full* treatments, and during the *empty-empty* treatment at the feeder that was full prior to the treatment change (Figure 3.1).

We evaluated whether the tendency to sample empty feeders was repeatable at the level of the individual, assessed the within-individual effects of environmental conditions on sampling behaviour, and evaluated whether sampling under different conditions of alternative food availability predicted annual survival. To quantify sampling behaviour, we determined which individuals were present at a feeder at any point during the four days prior to emptying the feeder, when the feeder was profitable, and determined which of those birds returned to sample once the feeder was emptied (yes/no). Based on our operational definition presented above, an individual was considered to have sampled if it returned to the unprofitable (empty) feeder at least once after experiencing the unprofitable state; that is, a bird sampled if it visited the empty feeder more than once, and did not sample if it visited the empty feeder once or not at all. We divided instances of sampling behaviour (i.e., an individual was detected more than once after the feeder was emptied) into sampling as a luxury, when a predictable alternative food source was available (i.e., the second feeder at the feeder station was full), and sampling out of necessity, when there was no alternative food source (i.e., the second feeder at the feeder station was empty). To determine apparent annual survival (yes/no), we used redetection data at the RFID enabled feeders in the period between January and March 2021, one year after the end of the sampling experiment. Individuals that were detected at least once during this period were considered alive (survival = 1), while individuals that were not redetected during this period were considered dead (survival = 0). Since individuals vary in energetic demand, which may alter the costs/benefits of sampling, we also quantified the number of times an individual visited feeders on the day before the sampling treatments (hereafter referred to as *baseline foraging*), as a proxy for energetic demand, under the assumption that the number of visits to full feeders is related to an individual's energetic requirement under the current environmental conditions.

We analyzed sampling behaviour using Bayesian multivariate mixed effects models using the R package *MCMCglmm* (Hadfield 2010). Although we were specifically interested in testing the relationship between sampling behaviour and survival, we recognized that our operational definition of sampling might also capture among-individual differences in propensity to visit feeders. For example, some individuals might have higher overall activity, and consistently visit feeders more often regardless of whether they are currently rewarding. To evaluate this possibility, we additionally included baseline foraging behaviour as a response variable to allow us to assess its within- and among-individual covariance with our two types of sampling. Using the method outlined in Houslay & Wilson (2017), we constructed a four trait model with baseline foraging (continuous variable), sampling out of necessity (yes/no), sampling as a luxury (yes/no) and survival (yes/no) as responses. We included the effect of (scaled) average temperature during the four-day sampling period as a predictor of sampling behaviour and (scaled) average temperature as a predictor of baseline foraging on the day it was quantified. This allowed us to test the prediction that within-individuals, sampling as a luxury increases with increasing temperature, while sampling out of necessity decreases with increasing temperature. We also included sex as a predictor of sampling, baseline foraging and survival, which allowed us to test for sex-related differences in sampling, foraging and survival. Priors and model structure are outlined in Appendix 2. This approach allowed us to test for the correlation between foraging and sampling as a luxury and between baseline foraging and sampling out of necessity, as well as to evaluate whether sampling under different conditions and baseline foraging had different effects on apparent survival. We included individual ID as a random effect, allowing us to quantify the among-individual relationship between sampling behaviour and survival, and baseline foraging and survival. We could not assess within-individual correlations between our two measures of sampling because they were not measured during the same instances (see Dingemanse & Dochtermann 2013, Table 2, scenario 4), nor any within-individual correlations involving survival, as this did not vary at the within-individual level. We used point estimates and 95% credible intervals to evaluate support for a given effect. We describe estimates with credible intervals that did not overlap zero as providing strong support for an effect, while estimates that centered on zero are described as providing no support for an effect, or strong support for lack of an effect. For estimates that were not centered on zero, but whose credible intervals overlapped zero, we calculated Bayesian p-values based on the proportion of counts of estimates that were above or below zero, depending on the direction of the estimated mean. Estimates with Bayesian p-values < 0.15 are referred to as showing moderate support for an effect because this corresponds to 5.7 times greater support for the interpretation of an effect compared to the interpretation of no effect.

Results

Over the course of the experimental period (29 November 2019 through 4 March 2020) 135 leg-banded black-capped chickadees were detected using the feeders at least once, while 132 chickadees (62 females, 67 males, 3 unknown) were detected at the RFID enabled feeders during the four-day periods that feeders were full prior to emptying (the experimental sampling period, and thus included in analyses). On average, individuals visited 2.54 out of the eight feeding sites at least once (s.d. 1.71, range: 1-8 sites), and on average, individuals were detected during 3.45 replicates out of four (s.d. 0.97, range: 1-4) during the experiment. The average temperature over the four-day sampling period affected the probability of sampling as a luxury and out of necessity. Consistent with predictions, there was strong support that sampling as a luxury increased with increasing temperature, and strong support that sampling out of necessity decreased with increasing temperature (Table 3.1; Figure 3.2). Further, there was also strong support that males had a lower probability of both sampling as a luxury and sampling out of necessity (Table 3.1). There was also strong support that baseline foraging was negatively affected by the average temperature on the day that foraging was measured, and males also had lower baseline foraging on average than females, though this difference was weak (Bayesian p-value=0.504; Table 3.1).

We verified that our measure of sampling did not merely reflect propensity to visit feeders irrespective of their current state by comparing among-individual correlations between sampling and baseline feeding. Sampling as a luxury and sampling out of necessity both had positive among-individual correlations with baseline foraging (luxury: mean= 0.378, 95% CrI: [0.174-0.571]; necessity: mean= 0.515, 95% CrI: [0.304-0.700]; Figure 3.3), however, a large proportion of the variance in sampling could not be explained by variation in baseline foraging, suggesting that our sampling measure captured a different trait than baseline foraging.

For survival effects of sampling, we predicted that among-individuals, sampling as a luxury would be positively related to survival, while sampling as a necessity would be negatively associated with survival. In contrast, we found that both types of sampling had similarly positive relationships with survival (luxury: mean: 0.126, 95% CrI: [-0.081-0.335], Bayesian p-value= 0.1182; necessity: mean= 0.123, 95% CrI: [-0.084-0.335], Bayesian p-value= 0.1262). By comparison, baseline foraging was only weakly correlated with survival (baseline foraging: mean= 0.066, 95% CrI: [-0.127-0.254], Bayesian p-value= 0.2511; Figure 3.3), further supporting the notion that baseline foraging was a distinct trait from sampling.

Finally, we observed a strong positive correlation between sampling as a luxury and sampling out of necessity at the among-individual level, which means that individuals that on average had a higher probability of sampling as a luxury also had a higher probability of sampling out of necessity, and vice versa (mean= 0.891, 95% CrI: [0.784-0.989]; Figure 3.3). The repeatability at the individual level was over 40% for both types of sampling (Table 3.1).

Discussion

Our field experiment in black-capped chickadees provides the first empirical support for theoretical predictions that sampling behaviour occurs under two distinct circumstances— sampling as a luxury and sampling out of necessity— and that increasing energy expenditure has opposite effects on each of these two types of sampling. Within-individuals, sampling as a luxury increased with increasing temperature and sampling out of necessity decreased with increasing temperature. Although we also show that sampling is repeatable, we found no evidence for among-individual differences in the propensity to sample as a luxury versus to sample out of necessity. Both types of sampling were strongly positively correlated, such that individuals that invest more in sampling as a luxury also invest more in sampling out of necessity. We also found moderate support that higher sampling was associated with higher annual survival. We discuss the significance of this work for our understanding of the adaptive value of sampling under variable environmental conditions.

Models of sampling behaviour predict that, all else being equal, greater energy requirement should lead to a lower occurrence of sampling as a luxury, and greater occurrence of sampling out of necessity (Mathot & Dall 2013). While the models predicting under which conditions each type of sampling will take place use metabolic rate as a measure of energetic requirement, here we used the average temperature over the four-day sampling period as a proxy for energetic demand faced by organisms, because previous work has demonstrated that decreasing temperature increases energetic demands in small birds via increased costs of thermoregulation (Broggi et al. 2004). We found that temperature had a significant effect on baseline foraging (i.e., the total number of visits to profitable feeders on the day prior to the sampling period) in our study; specifically, as temperature decreased, baseline foraging increased, providing further support for our assumption that ambient temperature can be used as a proxy of total energy requirement.

Our empirical results provide support for the prediction that sampling as a luxury and sampling out of necessity occur under distinct sets of energetic conditions (Mathot & Dall 2013). As predicted, when there was no alternative food source at the feeding site, and thus sampling was taking place out of necessity, temperature had a negative effect on the probability of sampling. In other words, sampling out of necessity increased with increasing energetic constraints. On the other hand, when there was an alternative predictable food source available, and thus sampling was taking place as a luxury, the probability of sampling was positively affected by temperature. A within-individual effect indicated that individual sampling behaviour was plastic—that is, individuals adjusted sampling behaviour to match current environmental conditions in relation to the energetic demands resulting from variation in temperature in relation to the availability of alternative foraging options.

Although individuals plastically adjusted their use of sampling, we also found that both types of sampling, sampling as a luxury and sampling out of necessity, were repeatable (r = 0.42 and r = 0.67, respectively). This repeatability is in line with other estimates for sampling behaviour in passerines. For example, the repeatability of exploration in a novel environment, often used as a proxy for information gathering, observed in another chickadee population was 0.39 (Devost et al. 2016), and the tendency to re-discover feeders that changed location in the field in zebra finches (*Taeniopygia guttata*) was 0.44 (McCowan et al. 2015). The repeatability of sampling observed in the present study might occur if individuals differ predictably in the type of sampling (i.e., luxury versus necessity) they engage in. This could take place if individuals with different dominance ranks invest in different types of sampling: for example, dominant individuals might be more likely to sample as a luxury while subordinate individuals are more likely to sample out of necessity. Under this scenario, we should expect a negative among-individual correlation between the two types of sampling. However, this was not the case in our study: instead, the two types of sampling were strongly positively correlated (r = 0.89). This indicates that individuals with a high propensity to sample under luxury conditions also had a high propensity to sample under necessity conditions (Table 3.1, Figure 3.3). Such a pattern could arise if our measure of sampling primarily captures activity or propensity to visit feeders. For example, other studies have found that activity predicted information gathering behaviour (Rojas-Ferrer et al. 2019) or a tendency to switch foraging patches when food availability is changed (van Overveld & Matthysen 2010). In our system, this might translate to some individuals having a higher tendency to visit feeders regardless of their profitability, simply because they are more active. Although we did find a positive correlation between baseline foraging and the two types of sampling, the correlation between the two types of sampling and baseline foraging were not nearly as strong as the correlation between sampling as a luxury and sampling out of necessity. Therefore, we conclude that among-individual variation in activity cannot fully account for the among-individual variation in sampling observed in our study population. Further, the very strong correlation between the two types of sampling is suggestive that they are two expressions of the same trait, “information gathering” or “sampling”, in the population.

Among-individual differences in overall sampling behaviour (combining both sampling as a luxury and sampling as a necessity) may arise via multiple, non-mutually exclusive mechanisms. For example, individuals with priority access to food may generally invest less in uncertainty reduction compared to individuals that do not have priority access to food (Ekman & Lilliendahl 1993). In chickadees, males are dominant over females (Smith 1992), which should translate to higher annual survival. Consistent with the notion that priority access to food may shape information gathering strategies, in our study, males sampled less than females and had higher survival. However, priority access to feeders cannot fully account for our results. Under the logic that subordinate birds sample more than dominant birds, we would expect a negative correlation between sampling and survival both within- and between-sexes, which was not the case. In contrast to the negative across-sex relationship between sampling and survival, within-sexes, we found moderate support for the interpretation that individuals that sampled more had higher survival.

What might account for the positive relationship between sampling and survival within sexes? Chickadees display more than one strategy for managing uncertainty: in addition to sampling, they insure themselves against unpredictable food supply in winter by caching (Smith 1992). We suggest that unaccounted differences in access to non-experimental food sources, specifically food caches, may underlie the patterns observed in the present study. Models predicting the conditions under which sampling should occur demonstrate that both sampling as a luxury and sampling out of necessity increase with increasing food availability (Mathot & Dall 2013); it is thus conceivable that differences in caching behaviour lead to differences in food availability among-individuals, accounting for the positive correlation between the two types of sampling. This is speculative and requires explicit empirical testing. Although there is some evidence from previous work in mountain (*Poecile gambeli*) and black-capped chickadees that caching effort and/or success differs across individuals (Pravosudov & Lucas 2000; Thompson & Morand-Ferron 2019), whether this affects sampling decisions has not been explicitly tested.

Current models of optimal sampling predict that variation in food availability can generate positive covariance between sampling as a luxury and sampling as insurance (Mathot & Dall 2013). Although the variation in food availability is envisioned as occurring within-individuals due to changes in environmental food availability, here, we propose that among-individual differences in resource availability in the form of food caches may also generate a positive among-individual covariance between sampling as a luxury and sampling out of necessity. This is consistent with a recent meta-analysis demonstrating that variation in resource acquisition is a key driver of among-individual differences in behaviour and the way in which behaviour relates to fitness components (Haave-Audet *et al*, *Submitted*). Thus, this work adds to the growing evidence that studies that explicitly account for heterogeneity in resource availability are needed to tease apart the mechanism driving individual differences in behaviour (Laskowski et al. 2020).

Tables and Figures

Table 3.1. The effect of temperature and sex on sampling (yes/no) as a luxury and out of necessity, and on baseline foraging and survival. Effect sizes represent posterior means from Bayesian mixed-effect models, with 95% credible intervals. Repeatability was obtained by calculating the proportion of variability in the sampling trait that was due to individual ID.

	Luxury	***Necessity***	***Baseline Foraging***	***Survival***
Fixed effects	**β (95% CrI)**	**β (95% CrI)**		
Temperature	0.332 (0.120-0.556)	-1.029 (-1.220- -0.804)	-5.514 (-7.255- -3.729)	*NA*
Sex (Male)	-0.820 (-1.645- -0.021)	-1.230 (-2.147- -0.307)	-4.090 (-15.856- 8.0125)	1.011 (-0.201- 2.168)
Repeatability				
Individual ID	0.415 (0.301-0.532)	0.669 (0.535-0.834)	0.408 (0.336-0.480)	*NA*

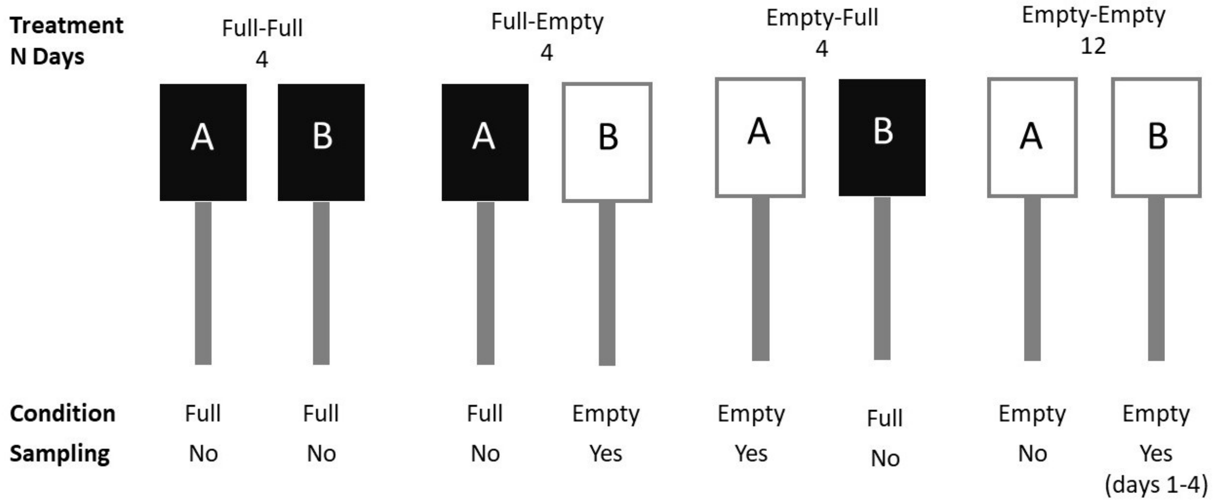

Figure 3.1. Experimental set-up to quantify sampling behaviour in black-capped chickadees. The study was composed of eight feeding sites distributed across the study area, with two feeders per site (A and B). The four treatments were run consecutively, and the entire sequence was replicated four times. Full feeders were supplied with unlimited black-oil sunflower seeds, which were completely removed when the feeders were emptied. We indicate when sampling could be quantified at a specific feeder for a specific treatment (sampling = yes) and when it could not (sampling = no). Sampling could only be quantified at newly emptied feeders because our operational definition of sampling was a visit to a feeder that had previously been experienced as unrewarding (empty), within four days of the feeder being emptied.

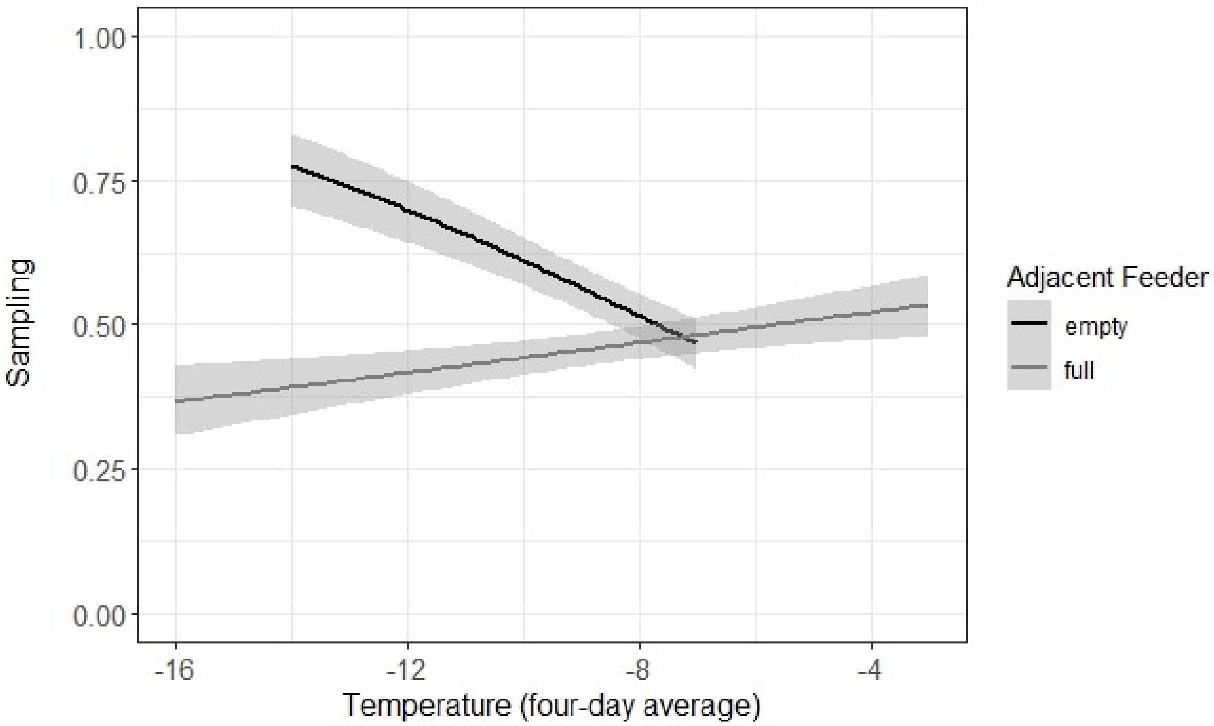

Figure 3.2. Effect of temperature and status of the adjacent feeder on the probability of sampling. Temperature in degrees Celsius. The graph was plotted using a generalized linear mixed-effect model, with an interaction between the status of the adjacent feeder and temperature. When the adjacent feeder was empty, sampling was considered to be out of necessity, and when the adjacent feeder was full, sampling was considered to be a luxury.

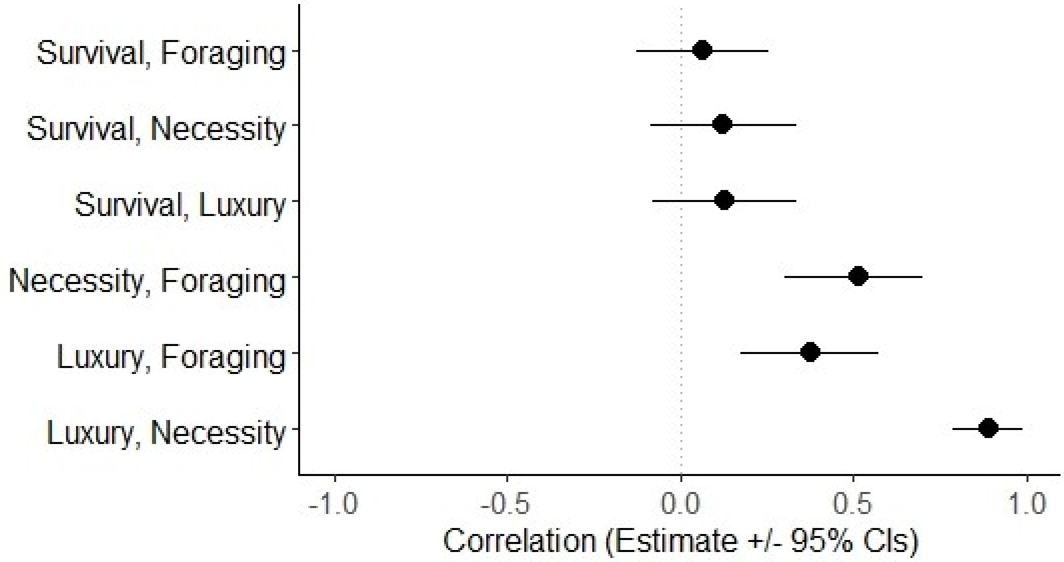

Figure 3.3. Among-individual relationships between sampling as luxury and out of necessity, baseline foraging, and survival, extracted from Bayesian mixed-effect models, with 95% credible intervals.

Chapter 4: Conclusions

My thesis explores the causes and consequences of among-individual differences in behaviour, using two distinct, but complementary approaches. In Chapter 2, I used meta-analysis to assess the strength and direction of the fitness consequences of individual differences in behaviour, with the specific aim of assessing whether individual differences in resource allocation toward longevity versus reproduction (i.e., trade-offs) explained the relationship between behaviour and fitness outcomes, or whether the relationship between behaviour and fitness components was better explained by individual differences in resource acquisition (i.e., some types of individuals have both higher survival and higher reproduction). In Chapter 3, I took an experimental approach using a model organism in the field, black-capped chickadees (*Poecile atricapillus*), to assess whether there are consistent among-individual differences in an understudied but ecologically important behaviour, information sampling in an extreme environment, and assessed the impact of those behavioural differences on a component of fitness, annual survival.

Both these approaches point to the same major conclusion: that heterogeneity in resource availability— or individual differences in access to resources— is key to mediating the fitness consequences of among-individual differences in behaviour. Using meta-analysis, this was made apparent by a positive correlation between effect sizes of studies that observed the impacts of behavioural differences on both survival and reproduction; that is, the direction and strength of the impact of increasing or decreasing behavioural expression on longevity also had the same effect on reproductive output. This result refutes the intuitive explanation that behavioural differences are maintained in populations because different expressions of behaviour in different individuals will either be positively correlated with only one of longevity or reproduction, showing that trade-offs between survival and reproduction is not a key mechanism maintaining among-individual differences in behaviour. Furthermore, while this effect at the among-individual level is explained by differences in resource acquisition between individuals, what make this thesis chapter particularly impactful is that we detected the same effect within-individuals. This is contrary to predictions made from life-history theory, based on which we expect that behaviour will mediate a trade-off in resource allocation toward survival or reproduction. This unexpected and exciting result further highlights how crucial it is for behavioural ecologists to consider the resource landscape available to individuals, and how this will affect behavioural expression and fitness outcomes both within- and among-individuals.

My thesis also provides the first empirical evidence, using a field study, that sampling behaviour occurs under two distinct sets of conditions: sampling behaviour increases both under high and low starvation risk, and the energetic demands placed on organisms affects the probability of sampling under different risks of starvation. While we expected to detect among-individual differences in sampling behaviour, we expected those differences to emerge due to differences in individuals' propensity to display each of the two types of sampling (i.e., some individuals being consistently more likely to sample out of necessity, and others being consistently more likely to sample as a luxury). However, we found that those individuals that consistently sampled under high risk of starvation also consistently sampled under low risk of starvation, and that individuals adjusted their sampling behaviour in response to the energetic demands incurred by below-freezing temperatures as predicted by theoretical models. Consistent with the findings highlighted in Chapter 2, the results presented in Chapter 3 indicate that there is an axis of variation that we are not accounting for in the study, such as resource heterogeneity across individuals.

In Chapter 2, I described ways in which researchers studying adaptive behavioural differences may account for differences in resource acquisition when investigating the fitness consequences of among-individual differences in behaviour, specifically by ensuring that studies measure the effect of changing resource availability on behavioural expression, and the subsequent effect on fitness. The study I present in Chapter 3, and future directions revealed by this study, highlight how this might be accomplished. While we detected a positive covariance between sampling under two distinct sets of conditions in chickadees, we did not account for individual differences in food caches. Caching is an important strategy that chickadees use to manage unpredictable food shortages in winter, and among-individual differences in caches may result in heterogeneity in resources available to individuals in the population, altering the conditions under which individuals are sampling at any given time. Thus, to better understand the underlying mechanism driving sampling behaviour under different risks of starvation in our study system, it would be necessary to homogenize resource availability across individuals. One way to achieve this in the field would be to limit cacheable food before and during the sampling study. This would not, however, completely eliminate individual differences in caching behaviour. Field observations to quantify individual caching effort complemented by lab studies with carefully controlled food availability and temperature may thus be best for assessing whether among-individual differences in resource availability (caches) covary with sampling behaviour, as we proposed.

Research on among-individual differences in behaviour has been criticized by behavioural ecologists for lacking ecological relevance to the focal organisms that are being studied (Carter et al. 2013; Niemelä & Dingemanse 2014). My thesis highlights that it is possible to assess among-individual differences in behaviour in the field using behaviours that are ecologically relevant to the study organism, notably sampling behaviour in a context where individuals are faced with high environmental uncertainty about foraging resources. While my meta-analytic study did not reveal differences in the conclusions drawn between studies that were conducted in an artificial (i.e., lab) setting compared to a field/wild setting, I note that given the effect of access to resources on the relationship between behavioural expression and fitness, that designing studies where ecological context is considered will be important to disentangling the role of resource heterogeneity both on among-individual differences in behaviour and within-individual effects of behaviour on fitness. Together, my thesis chapters are among the first to answer the call to explore the potential role of differences in resource acquisition among-individuals in mediating behavioural variation, as outlined by Laskowski et al. (2020), and lends further support to the contribution that this research avenue will bring to behavioural ecology and the study of adaptive behavioural differences.

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Appendices

Appendix 1- Supplementary material for: Differences in resource acquisition, not allocation, mediate the relationship between behaviour and fitness: A systematic review and meta-analysis

Table A1.1. PRISMA Eco-Evo reporting checklist.

Checklist Item	Sub-item Number	Sub-item	Reported by Authors?	Notes
Title and abstract	1.1	Identify the review as a systematic review, meta-analysis, or both	Yes	
	1.2	Summarise the aims and scope of the review	Yes	
	1.3	Describe the data set	Yes	
	1.4	State the results of the primary outcome	Yes	
	1.5	State conclusions	Yes	
	1.6	State limitations	Yes	
Aims and questions	2.1	Provide a rationale for the review	Yes	
	2.2	Reference any previous reviews or meta-analyses on the topic	Yes	
	2.3	State the aims and scope of the review (including its generality)	Yes	
	2.4	State the primary questions the review addresses (e.g. which moderators were tested)	Yes	
	2.5	Describe whether effect sizes were derived from experimental and/or observational comparisons	Yes	This detail is provided in the methods section
Review registration	3.1	Register review aims, hypotheses (if applicable), and methods in a time-stamped and publicly accessible archive and provide a link to the registration in the methods section of the manuscript. Ideally registration occurs before the search, but it can be done at any stage before data analysis.	No	
	3.2	Describe deviations from the registered aims and methods	No	
	3.3	Justify deviations from the registered aims and methods	No	
Eligibility criteria	4.1	Report the specific criteria used for including or excluding studies when screening titles and/or abstracts, and full texts, according to the aims of the systematic review (e.g. study design, taxa, data availability)	Yes	
	4.2	Justify criteria, if necessary (i.e. not obvious from aims and scope)	Yes	
Finding studies	5.1	Define the type of search (e.g. comprehensive search, representative sample)	Yes	

	5.2	State what sources of information were sought (e.g. published and unpublished studies, personal communications)	Yes	
	5.3	Include, for each database searched, the exact search strings used, with keyword combinations and Boolean operators	Yes	
	5.4	Provide enough information to repeat the equivalent search (if possible), including the timespan covered (start and end dates)	Yes	
Study selection	6.1	Describe how studies were selected for inclusion at each stage of the screening process (e.g. use of decision trees, screening software)	Yes	
	6.2	Report the number of people involved and how they contributed (e.g. independent parallel screening)	Yes	
Data collection process	7.1	Describe where in the reports data were collected from (e.g. text or figures)	Yes	
	7.2	Describe how data were collected (e.g. software used to digitize figures, external data sources)	Yes	
	7.3	Describe moderator variables that were constructed from collected data (e.g. number of generations calculated from years and average generation time)	NA	No moderator variables were calculated from other values
	7.4	Report how missing or ambiguous information was dealt with during data collection (e.g. authors of original studies were contacted for missing descriptive statistics, and/or effect sizes were calculated from test statistics)	Yes	
	7.5	Report who collected data	Yes	
	7.6	State the number of extractions that were checked for accuracy by co-authors	Yes	
Data items	8.1	Describe the key data sought from each study	Yes	
	8.2	Describe items that do not appear in the main results, or which could not be extracted due to insufficient information	Yes	
	8.3	Describe main assumptions or simplifications that were made (e.g. categorising both ‘length’ and ‘mass’ as ‘morphology’)	Yes	
	8.4	Describe the type of replication unit (e.g. individuals, broods, study sites)	Yes	
Assessment of individual study quality	9.1	Describe whether the quality of studies included in the systematic review or meta-analysis was assessed (e.g. blinded data collection, reporting quality, experimental vs. observational)	No	
	9.2	Describe how information about study quality was incorporated into analyses (e.g. meta-regression and/or sensitivity analysis)	No	Information on quality was not incorporated into analyses

Effect size measures	10.1	Describe effect size(s) used	Yes	
	10.2	Provide a reference to the equation of each calculated effect size (e.g. standardised mean difference, log response ratio) and (if applicable) its sampling variance	Yes	
	10.3	If no reference exists, derive the equations for each effect size and state the assumed sampling distribution(s)	NA	A reference for the effect size and its sampling variance was available, so no derivation was required
Missing data	11.1	Describe any steps taken to deal with missing data during analysis (e.g. imputation, complete case, subset analysis)	NA	There were no missing data
	11.2	Justify the decisions made to deal with missing data	NA	There were no missing data
Meta-analytic model description	12.1	Describe the models used for synthesis of effect sizes	Yes	
	12.2	The most common approach in ecology & evolution will be a random-effects model, often with a hierarchical/multilevel structure. If other types of models are chosen (e.g. common/fixed effects model, unweighted model), provide justification for this choice	Yes	
Software	13.1	Describe the statistical platform used for inference (e.g. *R*)	Yes	
	13.2	Describe the packages used to run models	Yes	
	13.3	Describe the functions used to run models	Yes	
	13.4	Describe any arguments that differed from the default settings	Yes	
	13.5	Describe the version numbers of all software used	Yes	
Non-independence	14.1	Describe the types of non-independence encountered (e.g. phylogenetic, spatial, multiple measurements over time)	Yes	
	14.2	Describe how non-independence has been handled	Yes	
	14.3	Justify decisions made	Yes	
Meta-regression and model selection	15.1	Provide a rationale for the inclusion of moderators (covariates) that were evaluated in meta-regression models	Yes	
	15.2	Justify the number of parameters estimated in models, in relation to the number of effect sizes and studies (e.g. interaction terms were not included due to insufficient sample sizes)	Yes	
	15.3	Describe any process of model selection	Yes	
Publication bias and	16.1	Describe assessments of the risk of bias due to missing results (e.g. publication, time-lag, and taxonomic biases)	Yes	

sensitivity analyses	16.2	Describe any steps taken to investigate the effects of such biases (if present)	Yes	
	16.3	Describe any other analyses of robustness of the results, e.g. due to effect size choice, weighting or analytical model assumptions, inclusion or exclusion of subsets of the data, or the inclusion of alternative moderator variables in meta-regressions	Yes	
Clarification of post hoc analyses	17.1	When hypotheses were formulated after data analysis, this should be acknowledged.	Yes	
Metadata, data, and code	18.1	Share metadata (i.e. data descriptions)	Yes	
	18.2	Share data required to reproduce the results presented in the manuscript	Yes	
	18.3	Share additional data, including information that was not presented in the manuscript (e.g. raw data used to calculate effect sizes, descriptions of where data were located in papers)	Yes	
	18.4	Share analysis scripts (or, if a software package with graphical user interface (GUI) was used, then describe full model specification and fully specify choices)	Yes	
Results of study selection process	19.1	Report the number of studies screened	Yes	
	19.2	Report the number of studies excluded at each stage of screening	Yes	
	19.3	Report brief reasons for exclusion from the full text stage	Yes	
	19.4	Present a Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA)-like flowchart (www.prisma-statement.org).	Yes	
Sample sizes and study characteristics	20.1	Report the number of studies and effect sizes for data included in meta-analyses	Yes	
	20.2	Report the number of studies and effect sizes for subsets of data included in meta-regressions	Yes	
	20.3	Provide a summary of key characteristics for reported outcomes (either in text or figures; e.g. one quarter of effect sizes reported for vertebrates and the rest invertebrates)	Yes	
	20.4	Provide a summary of limitations of included moderators (e.g. collinearity and overlap between moderators)	Yes	
	20.5	Provide a summary of characteristics related to individual study quality (risk of bias)	NA	The quality of studies included in the meta-analysis was not assessed
Meta-analysis	21.1	Provide a quantitative synthesis of results across studies, including estimates for the mean effect size, with confidence/credible intervals	Yes	

Heterogeneity	22.1	Report indicators of heterogeneity in the estimated effect (e.g. I2, tau2 and other variance components)	Yes	
Meta-regression	23.1	Provide estimates of meta-regression slopes (i.e. regression coefficients) and confidence/credible intervals	Yes	
	23.2	Include estimates and confidence/credible intervals for all moderator variables that were assessed (i.e. complete reporting)	Yes	
	23.3	Report interactions, if they were included	NA	No interactions were included
	23.4	Describe outcomes from model selection, if done (e.g. R2 and AIC)	Yes	
Outcomes of publication bias & sensitivity analyses	24.1	Provide results for the assessments of the risks of bias (e.g. Egger's regression, funnel plots)	Yes	
	24.2	Provide results for the robustness of the review's results (e.g. subgroup analyses, meta-regression of study quality, results from alternative methods of analysis, and temporal trends)	Yes	
Discussion	25.1	Summarise the main findings in terms of the magnitude of effect	Yes	
	25.2	Summarise the main findings in terms of the precision of effects (e.g. size of confidence intervals, statistical significance)	Yes	
	25.3	Summarise the main findings in terms of their heterogeneity	Yes	
	25.4	Summarise the main findings in terms of their biological/practical relevance	Yes	
	25.5	Compare results with previous reviews on the topic, if available	Yes	
	25.6	Consider limitations and their influence on the generality of conclusions, such as gaps in the available evidence (e.g. taxonomic and geographical research biases)	Yes	
Contributions and funding	26.1	Provide names, affiliations, and funding sources of all co-authors	Yes	
	26.2	List the contributions of each co-author	Yes	
	26.3	Provide contact details for the corresponding author	Yes	
	26.4	Disclose any conflicts of interest	NA	There were no conflicts of interest
References	27.1	Provide a reference list of all studies included in the systematic review or meta-analysis	Yes	
	27.2	List included studies as referenced sources (e.g. rather than listing them in a table or supplement)	Yes	

Table A1.2. Studies included in the meta-analysis, with the unique identifier, RecordNo, that can be used in cross-reference with the data provided at http://doi.org/10.5281/zenodo.5111893.

RecordNo	References
5	(Abbey-Lee *et al.*, 2018)
9	(Adriaenssens & Johnsson, 2013)
10	(Akçay, Campbell & Beecher, 2015)
12	(Altschul *et al.*, 2018)
15	(Arcese & Smith, 1985)
17	(Ariyomo & Watt, 2013)
18	(Armitage & Van Vuren, 2003)
21	(Ballew, Mittelbach & Scribner, 2017)
25	(Belda, Barba & Monrós, 2007)
26	(Belgrad & Griffen, 2016)
27	(Belgrad & Griffen, 2018)
28	(Bergeron *et al.*, 2013)
29	(Berning *et al.*, 2012)
30	(Betini & Norris, 2012)
31	(Bijleveld *et al.*, 2014)
33	(Biro & Sampson, 2015)
34	(Blake *et al.*, 2018)
35	(Blake & Gabor, 2014)
36	(Blanckenhorn, 1991b)
37	(Bonnot *et al.*, 2018)
38	(Boon, Réale & Boutin, 2007)
39	(Boon, Réale & Boutin, 2008)
41	(Boulton *et al.*, 2018)
42	(Bouwhuis *et al.*, 2014)
43	(Bremner-Harrison, Prodohl & Elwood, 2004)
47	(Brommer *et al.*, 2014)
49	(Burrow, 2001)
50	(Burtka & Grindstaff, 2015)
54	(Carlson & Langkilde, 2014)
55	(Carlstead, Mellen & Kleiman, 1999)
58	(Class, Kluen & Brommer, 2014)
59	(Colchester & Harrison, 2016)
61	(Contreras-Garduno, Lanz-Mendoza & Cordoba-Aguilar, 2007)
62	(Cooke *et al.*, 2011)
63	(Cooke *et al.*, 2017)
65	(Costanzo *et al.*, 2018)
66	(Cote, Dreiss & Clobert, 2008)
69	(Davidson *et al.*, 2018)
70	(Debecker *et al.*, 2016)
71	(Delnat, Debecker & Stoks, 2017)
72	(DiRienzo *et al.*, 2019)
74	(Duckworth, 2006)
76	(Edenbrow & Croft, 2011)
84	(Foster *et al.*, 2017)
86	(Fu *et al.*, 2017)
87	(Fuiman, Meekan & McCormick, 2010)
89	(Gabriel & Black, 2012b)
90	(Gangloff, Sparkman & Bronikowski, 2018)
91	(Gavojdian *et al.*, 2015)
92	(Germano *et al.*, 2017)
93	(Goulet *et al.*, 2016)
95	(Greenberg & Holekamp, 2017)
98	(Grunst *et al.*, 2019)
99	(Guenther, 2018)
100	(Haage *et al.*, 2017)
103	(Han & Brooks, 2013a)
104	(Han & Brooks, 2014)
105	(Han, Brooks & Jablonski, 2016)
106	(Han & Dingemanse, 2017)
107	(Heynen, Bunnefeld & Borcherding, 2017)
109	(Hoi-leitner, Nechtelberger & Dittami, 1993)
113	(Hulthén *et al.*, 2017)
116	(Jablonszky *et al.*, 2018)
117	(Jennings, Hayden & Gammell, 2013)
122	(Kalb *et al.*, 2016)
123	(Kasimanickam *et al.*, 2014)
125	(Kim & Velando, 2016)
126	(Kontiainen *et al.*, 2009)
127	(Koosa & Tilgar, 2016)
130	(Kralj-Fišer *et al.*, 2016)
132	(Kralj-Fišer *et al.*, 2013a)
134	(Krams *et al.*, 2013b)
135	(Krams *et al.*, 2013a)
136	(Krams *et al.*, 2014)

RecordNo	References
137	(Krippel, Ballentine & Hyman, 2017)
141	(Le Coeur *et al.*, 2015)
142	(Le Galliard *et al.*, 2013)
143	(Le Galliard, Paquet & Mugabo, 2015)
145	(Logue *et al.*, 2009)
146	(Lopes *et al.*, 2017)
147	(Madden *et al.*, 2018)
152	(May, Page & Fleming, 2016)
153	(McCormick & Meekan, 2010)
154	(McCowan, Rollins & Griffith, 2014)
155	(McCowan *et al.*, 2015)
157	(McGhee, Fuller & Travis, 2007)
159	(Meagher, Bechard & Mason, 2012)
160	(Meagher *et al.*, 2011)
162	(Michalko & Rezucha, 2018)
165	(Miyatake *et al.*, 2004)
166	(Monceau *et al.*, 2017)
167	(Monestier *et al.*, 2015)
168	(Montiglio *et al.*, 2014)
170	(Montiglio *et al.*, 2017)
172	(Mullers & Tinbergen, 2009)
173	(Murphy *et al.*, 2008)
174	(Mutzel *et al.*, 2013)
175	(Nakayama & Miyatake, 2010)
177	(Näslund *et al.*, 2018)
178	(Natoli *et al.*, 2005)
179	(Nicolaus *et al.*, 2015)
181	(Nicolaus *et al.*, 2016)
183	(Niemelä, Lattenkamp & Dingemanse, 2015)
184	(Nunes, 2014)
185	(Olsen *et al.*, 2012)
186	(O'Rourke & Mendelson, 2014)
188	(Parent *et al.*, 2013)
189	(Patrick *et al.*, 2012)
190	(Patrick & Weimerskirch, 2014a)
191	(Patrick & Weimerskirch, 2014b)
192	(Patrick & Weimerskirch, 2015)
193	(Patterson & Schulte-Hostedde, 2011)
195	(Penteriani *et al.*, 2002)

RecordNo	References
197	(Piquet *et al.*, 2018)
201	(Pruitt *et al.*, 2017)
204	(Pruitt, Stachowicz & Sih, 2012)
206	(Quinn *et al.*, 2009)
208	(Réale & Festa-Bianchet, 2003)
209	(Réale *et al.*, 2000)
210	(Réale *et al.*, 2009)
211	(Reaney & Backwell, 2007)
212	(Redmond *et al.*, 2009)
215	(Rivera-Gutierrez *et al.*, 2017)
216	(Roche & Brown, 2013)
217	(Rodel *et al.*, 2015)
218	(Rosenbaum *et al.*, 2018)
219	(Santicchia *et al.*, 2018)
220	(Santos *et al.*, 2015)
223	(Scherer, Kuhnhardt & Schuett, 2017)
224	(Scherer, Kuhnhardt & Schuett, 2018)
225	(Schielzeth *et al.*, 2011)
228	(Schuett, Laaksonen & Laaksonen, 2012)
231	(Seltmann *et al.*, 2014)
234	(Sih, Chang & Wey, 2014)
235	(Sinn, Apiolaza & Moltschaniwskyj, 2006)
236	(Sinn *et al.*, 2014)
238	(Smith & Blumstein, 2010)
242	(Stein & Bell, 2012)
243	(St-Hilaire, Réale & Garant, 2017)
245	(Strong *et al.*, 2017)
246	(Stuart-Smith & Boutin, 1995)
247	(Sweeney *et al.*, 2013)
249	(Taylor *et al.*, 2014)
250	(Teyssier *et al.*, 2014)
251	(Toscano, 2017)
252	(Traisnel & Pichegru, 2018)
254	(Turchen, Cosme & Guedes, 2018)
257	(Vainikka, Tammela & Hyvärinen, 2016)
258	(Valente *et al.*, 2017)
260	(van Lier *et al.*, 2017)
261	(van Overveld, Adriaensen & Matthysen, 2015)
262	(Vander Wal *et al.*, 2015)
267	(Ward-Fear *et al.*, 2018)

RecordNo	**References**
269	(West *et al.*, 2019)
271	(Wetzel & Westneat, 2014)
272	(Wey *et al.*, 2015)
274	(White *et al.*, 2013)
275	(White *et al.*, 2016)
278	(Wilson, Godin & Ward, 2010a)
280	(Winney *et al.*, 2018)
284	(Worthington & Swallow, 2010)
287	(Yoshida, Van Meter & Holekamp, 2016)
288	(Zavorka *et al.*, 2015)
289	(Zavorka *et al.*, 2016)
290	(Zou *et al.*, 2019)
291	(Armitage, 1986)
292	(Banks, Norrdahl & Korpimaki, 2002)
293	(Blanckenhorn, 1991a)
294	(Cavigelli & McClintock, 2003)
296	(Dewsbury, 1984)
297	(Dingemanse *et al.*, 2004)
299	(Godin & Davis, 1995)
300	(Hemsworth *et al.*, 1999)
301	(Janczak *et al.*, 2003)
303	(Korhonen & Niemelä, 1996)

RecordNo	**References**
304	(Lenington *et al.*, 1996)
306	(Murphy *et al.*, 1994)
307	(Sarno & Franklin, 1999)
308	(Shackleton, Jennions & Hunt, 2005)
309	(Spritzer, Meikle & Solomon, 2005)
311	(Wielebnowski, 1999)
314	(Snekser, Wynne & Itzkowitz, 2017)
315	(Weiss *et al.*, 2013)
316	(Silk *et al.*, 2010)
317	(Archie *et al.*, 2014)
318	(Thompson & Cords, 2018)
319	(Lapiedra *et al.*, 2018)
320	(Keiser *et al.*, 2018)
321	(Santostefano *et al.*, 2017)
323	(Marshall *et al.*, 2016)
324	(Kain & McCoy, 2016a)
325	(Morales *et al.*, 2013)
326	(Kralj-Fišer, Hebets & Kuntner, 2017)
328	(Niemelä *et al.*, 2019)

Table A1.3. List of excluded studies with reasons for exclusion.

References	Reasons for exclusions
1. (Abrahms *et al.*, 2018)	No correlation between fitness and behaviour reported
2. (Adamo, Kovalko & Mosher, 2013)	No correlation between fitness and behaviour reported
3. (Adriaenssens & Johnsson, 2011)	No correlation between fitness and behaviour reported
4. (Alonso *et al.*, 2012)	No correlation between fitness and behaviour reported
5. (Anderson & Boutin, 2002)	No correlation between fitness and behaviour reported
6. (Andersen, Berg & Bøe, 2005)	Inappropriate fitness measure (crushing piglets)
7. (Ariyomo & Watt, 2012)	More than 2 behavioural categories
8. (Arroyo, Mougeot & Bretagnolle, 2017)	Insufficient information provided to calculate effect size when requested from authors
9. (Auclair, Konig & Lindholm, 2013)	No correlation between fitness and behaviour reported
10. (Barlow, 1986)	No correlation between fitness and behaviour reported
11. (Barnett, Hemsworth & Newman, 1992)	Not measured at individual level
12. (Barrozo *et al.*, 2012)	No correlation between fitness and behaviour reported
13. (Beehner *et al.*, 2006)	Wrong publication type (book)
14. (Biro & Booth, 2009)	No correlation between fitness and behaviour reported
15. (Both *et al.*, 2005)	No direction of estimate
16. (Brent *et al.*, 2014)	Insufficient statistics reported
17. (Bretman *et al.*, 2012)	Behaviour not of interest or unclear (mating duration)
18. (Bridger, Bonner & Briffa, 2015)	Fitness not of interest (spermatophore size)
19. (Burns *et al.*, 2013)	No correlation between fitness and behaviour reported
20. (Cam *et al.*, 2002)	Behaviour not of interest or unclear (squatting)
21. (Cam, Monnat & Royle, 2004)	No correlation between fitness and behaviour reported
22. (Cardona *et al.*, 2017)	No fitness measures reported
23. (Chang & Sih, 2013)	Not measured at individual level
24. (Charmantier *et al.*, 2017)	No correlation between fitness and behaviour reported
25. (Chism & Rogers, 1997)	No correlation between fitness and behaviour reported
26. (Conrad & Sih, 2009)	No correlation between fitness and behaviour reported
27. (Costa *et al.*, 2015)	No correlation between fitness and behaviour reported
28. (Dammhahn, 2012)	No fitness measures reported
29. (Daunt *et al.*, 2014)	No correlation between fitness and behaviour reported
30. (DiRienzo, Pruitt & Hedrick, 2013)	Retraction requested by authors
31. (Duckworth & Kruuk, 2009)	Not measured at individual level
32. (Dugatkin, 1992)	More than 2 behavioural categories
33. (Edwards *et al.*, 2016)	No fitness measures reported
34. (Edwards *et al.*, 2018)	Interaction is significant, cannot extract estimate
35. (Eguchi, Asai & Yamagishi, 2009)	No fitness measures reported
36. (Elliott *et al.*, 2014)	No correlation between fitness and behaviour reported
37. (Fabre, Garcia-Galea & Vinyoles, 2014)	No correlation between fitness and behaviour reported
38. (Fagen & Fagen, 2009)	Not measured at individual level
39. (Fisher *et al.*, 2018)	No correlation between fitness and behaviour reported; although included in Moiron et al. 2019,

References	**Reasons for exclusions**
	fitness metric is not consistent with the definition used in this study.
40. (Fisher *et al.*, 2015)	No fitness measures reported
41. (Fox & Millam, 2014)	Not measured at individual level
42. (Gabriel & Black, 2012a)	Not measured at individual level
43. (Grace & Anderson, 2013)	Wrong publication type (proceedings)
44. (Greggor *et al.*, 2017)	Not measured at individual level
45. (Grist *et al.*, 2017)	Temporal scale of behaviour (annual migration) does not match other estimates
46. (Haigh, O'Riordan & Butler, 2017)	No correlation between fitness and behaviour reported
47. (Han & Brooks, 2013b)	No behaviour reported
48. (Heynen, Rentrop & Borcherding, 2014)	No fitness measures reported
49. (Hojesjo *et al.*, 2011)	Not measured at individual level
50. (Hoye *et al.*, 2012)	Behaviour not of interest or unclear (migration)
51. (Huebner, Fichtel & Kappeler, 2018)	Behaviour not of interest or unclear (cognition)
52. (Ingley *et al.*, 2016)	No direction of estimate
53. (Isden *et al.*, 2013)	Behaviour not of interest or unclear (cognition)
54. (Johnson *et al.*, 2015)	No fitness measures reported
55. (Johnson & Sih, 2005)	No correlation between fitness and behaviour reported
56. (Johnson *et al.*, 2017)	No fitness measures reported
57. (Kazama *et al.*, 2011)	Incorrect response variable
58. (Korhonen, Niemelä & Siirila, 2001)	More than 2 behavioural categories
59. (Korhonen, Jauhiainen & Rekila, 2002)	Insufficient information provided to calculate an effect size
60. (Korpela, Sundell & Ylönen, 2011)	No fitness measures reported
61. (Kralj-Fišer, Schneider & Kuntner, 2013b)	Wrong publication type (opinion piece)
62. (Lacey & Wieczorek, 2001)	No fitness measures reported
63. (Landsman *et al.*, 2017)	No correlation between fitness and behaviour reported
64. (Lapinski *et al.*, 2013)	More than 2 behavioural categories
65. (Larsen *et al.*, 2015)	No correlation between fitness and behaviour reported
66. (Lee & Bereijikian, 2008)	No correlation between fitness and behaviour reported
67. (Madden & Whiteside, 2014)	Interaction is significant, cannot extract estimate
68. (Malia *et al.*, 2016)	No correlation between fitness and behaviour reported
69. (Martin-Wintle *et al.*, 2017)	Not measured at individual level
70. (May *et al.*, 2008)	No correlation between fitness and behaviour reported
71. (McDermott *et al.*, 2014)	No fitness measures reported
72. (McLean & McLaughlin, 2018)	No fitness measures reported
73. (McPhee & Quinn, 1998)	No correlation between fitness and behaviour reported
74. (Meng, Gong & Xiang, 2011)	No fitness measures reported
75. (Miles, 2004)	Behaviour not of interest or unclear (sprint speed)
76. (Mills, Gardner & Oliver, 2005)	No correlation between fitness and behaviour reported
77. (Møller & Garamszegi, 2012)	Not measured at individual level

References	Reasons for exclusions
78. (Montiglio *et al.*, 2015)	No correlation between fitness and behaviour reported
79. (Nakayama, Rapp & Arlinghaus, 2017)	No fitness measures reported
80. (Nicolaus *et al.*, 2012)	No correlation between fitness and behaviour reported
81. (Niedzielski & Bowman, 2014)	No behaviour reported
82. (Pajor *et al.*, 2010)	More than 2 behavioural categories
83. (Pedersen *et al.*, 2006)	Behaviour not of interest or unclear (crushing)
84. (Perez *et al.*, 2016)	Temporal scale of behaviour (annual migration) does not match other estimates
85. (Pitts *et al.*, 2002)	Behaviour not of interest or unclear (getting away)
86. (Price *et al.*, 2012)	No correlation between fitness and behaviour reported
87. (Prokop & Semelbauer, 2017)	No correlation between fitness and behaviour reported
88. (Pruitt & Riechert, 2009)	Insufficient statistics reported
89. (Pruitt & Riechert, 2011)	No direction of estimate
90. (Qu, Chen & Zhang, 2018)	Behaviour not of interest or unclear (dispersal)
91. (Rangassamy *et al.*, 2015)	Not measured at individual level
92. (Riebli *et al.*, 2012)	No fitness measures reported
93. (Ringsby *et al.*, 2009)	Not measured at individual level
94. (Rolandsen *et al.*, 2017)	Temporal scale of behaviour (annual migration) does not match other estimates
95. (Sanderson *et al.*, 2015)	No fitness measures reported
96. (Sawa *et al.*, 2017)	No fitness measures reported
97. (Scales, Hymanb & Hughes, 2013)	Not measured at individual level
98. (Schuett *et al.*, 2015)	More than 2 behavioural categories; Models from raw data did not converge
99. (Schuett, Dall & Royle, 2011)	No fitness measures reported
100. (Schurch & Heg, 2010)	No correlation between fitness and behaviour reported
101. (Schweitzer *et al.*, 2017)	No correlation between fitness and behaviour reported
102. (Serrano-Davies *et al.*, 2017)	Not measured at individual level
103. (Shoji *et al.*, 2015)	No correlation between fitness and behaviour reported
104. (Smiley & Adkins-Regan, 2016)	No correlation between fitness and behaviour reported
105. (Snijders *et al.*, 2014)	No correlation between fitness and behaviour reported
106. (Soroka & Morrison, 2005)	Not measured at individual level
107. (Stapley & Keogh, 2005)	Behavioural measure did not meet definition
108. (Strohm & Linsenmair, 2000)	No behaviour reported
109. (Szasz *et al.*, 2014)	No fitness measures reported
110. (Trnka, Samas & Grim, 2018)	No correlation between fitness and behaviour reported
111. (Twiss *et al.*, 2012)	No correlation between fitness and behaviour reported
112. (Uchida, Kuwada & Tsukamoto, 1993)	Wrong publication language
113. (Vallon *et al.*, 2016)	No correlation between fitness and behaviour reported
114. (Vander Zanden *et al.*, 2014)	More than 2 behavioural categories
115. (Vargas, Mackenzie & Rey, 2018)	Not measured at individual level
116. (Vetter *et al.*, 2016)	No correlation between fitness and behaviour reported
117. (Vitousek, Jenkins & Safran, 2014)	No correlation between fitness and behaviour reported

References	**Reasons for exclusions**
118. (Vrublevska *et al.*, 2015)	Not measured at individual level
119. (Wechsler & Hegglin, 1997)	No fitness measures reported
120. (Wetzel, 2017)	Behaviour not of interest or unclear (cognition)
121. (While, Sinn & Wapstra, 2009)	No direction of estimate
122. (Whitfield *et al.*, 2009)	No behaviour reported
123. (Wilson *et al.*, 1993)	No correlation between fitness and behaviour reported
124. (Wilson *et al.*, 2010b)	No correlation between fitness and behaviour reported
125. (Wilson *et al.*, 2011)	No fitness measures reported
126. (Wischhoff *et al.*, 2018)	No correlation between fitness and behaviour reported
127. (Wiszniewski *et al.*, 2012)	No behaviour reported
128. (Woo *et al.*, 2008)	No behaviour reported
129. (Yli-Renko, Vesakoski & Pettay, 2015)	More than 2 behavioural categories
130. (Yli-Renko, Pettay & Vesakoski, 2018)	More than 2 behavioural categories

Table A1.4. Definitions used for coding behaviour, with direction of coding.

Behavioural category	**Definition**	**Subcategories**	**Examples**	**Coding**	**N estimates**
Activity	Measure of activity in a non-novel, non-risky environment (from Réale et al. 2007)		Home range size; distance travelled; tendency to lead pack; movement in enclosure; time active; distance of diel migration; distance moved	Higher values indicate higher expression of activity	34
Aggression	Agonistic interaction toward conspecifics or heterospecifics in a non-predatory and non-courtship context	Territoriality, sexual cannibalism, nest aggression	Nest competition; nest aggression; response to mirror-simulation test; Sexual cannibalism; dominance rank; aggressive signalling	Higher values indicate higher expression of aggression	129
Boldness	Activity in the presence of a risky situation that is not new, including to predators (including simulations and chemical cues) and humans (from Réale et al. 2007)	Reproductive boldness	Propensity to be caught in traps; alarm calling; vigilance; death-feigning; predator inspection; tonic immobility; escape behaviour; latency to become active following attack	Higher values indicate higher expression of boldness	153
Courtship	Signalling behaviour to attract mates		Singing (songbirds); web deconstruction (spiders); time to attract a mate	Higher values indicate higher expression of courtship	16
Exploration	Response to a novel environment, including activity and neophilia & information gathering (from Réale)		Distance travelled/dispersal in a translocated (new) environment; novel environment test; novel object test; predator inspection; nest prospecting	Higher values indicate higher expression of exploration	244

Foraging	Food searching and consumption behaviour		Time spent in rewarding patch; strikes toward prey; foraging trip range & duration	Higher values indicate higher expression of foraging	23
Parental care	Care provided to offspring, including in a cooperative setting		Provisioning; brood fanning; babysitting; latency to leave nest when approached	Higher values indicate higher expression of parental care	25
Social behaviour	Reaction to the presence or absence of conspecifics, excluding aggressive behaviour (from Réale et al. 2007)		Sociability; extraversion; agreeableness; smelling conspecifics; time spent in presence of conspecifics; time to approach conspecifics; network centrality and connectedness; grooming	Higher values indicate lower expression of social behaviour (according to POLS)	41
Stress	Reaction to handling by humans		Reactivity; breathing rate; flight speed; response to handlers; time struggling	Higher values indicate higher expression of reactivity (low proactivity, according to POLS)	95

Table A1.5. Regression coefficients (Estimate) and 95% confidence intervals (CIs) of the Egger regression test to assess publication bias.

Fixed effect	Estimate	Lower CI	Upper CI
Intercept (Reproduction, Activity, Among)	0.1084	-0.0349	0.2517
Sqrt(VZr)	0.2172	-0.2711	0.7055
Behaviour: Aggression	-0.0275	-0.1574	0.1023
Behaviour: Boldness	-0.0042	-0.1204	0.1119
Behaviour: Courtship	0.2556	0.0061	0.5051
Behaviour: Exploration	-0.0761	-0.1849	0.0326
Behaviour: Foraging	-0.1577	-0.3563	0.0409
Behaviour: Parental care	0.0478	-0.1584	0.2541
Behaviour: Social behaviour	-0.0395	-0.173	0.0941
Behaviour: Stress	-0.1754	-0.3003	-0.0505
Fitness proxy: Survival	-0.0314	-0.0966	0.0337
Level: Phenotypic	-0.023	-0.0726	0.0266
Level: Within-individual	-0.0906	-0.2216	0.0404

Table A1.6 Regression coefficients (Estimate) and 95% confidence intervals (CIs) of the regression test to assess a time lag effect of the publication of non-significant effect sizes.

Fixed effect	Estimate	Lower CI	Upper CI
Intercept (Reproduction, Activity, Among)	4.419	-10.8802	19.7181
Year	-0.0021	-0.0097	0.0055
Behaviour: Aggression	-0.0312	-0.1614	0.0989
Behaviour: Boldness	-0.0057	-0.1217	0.1104
Behaviour: Courtship	0.2563	0.0062	0.5063
Behaviour: Exploration	-0.078	-0.1867	0.0306
Behaviour: Foraging	-0.1578	-0.3564	0.0409
Behaviour: Parental care	0.0489	-0.1574	0.2553
Behaviour: Social behaviour	-0.0424	-0.1758	0.0909
Behaviour: Stress	-0.1791	-0.3037	-0.0545
Fitness proxy: Survival	-0.0339	-0.0987	0.0309
Level: Phenotypic	-0.0222	-0.0717	0.0274
Level: Within-individual	-0.0924	-0.2233	0.0385

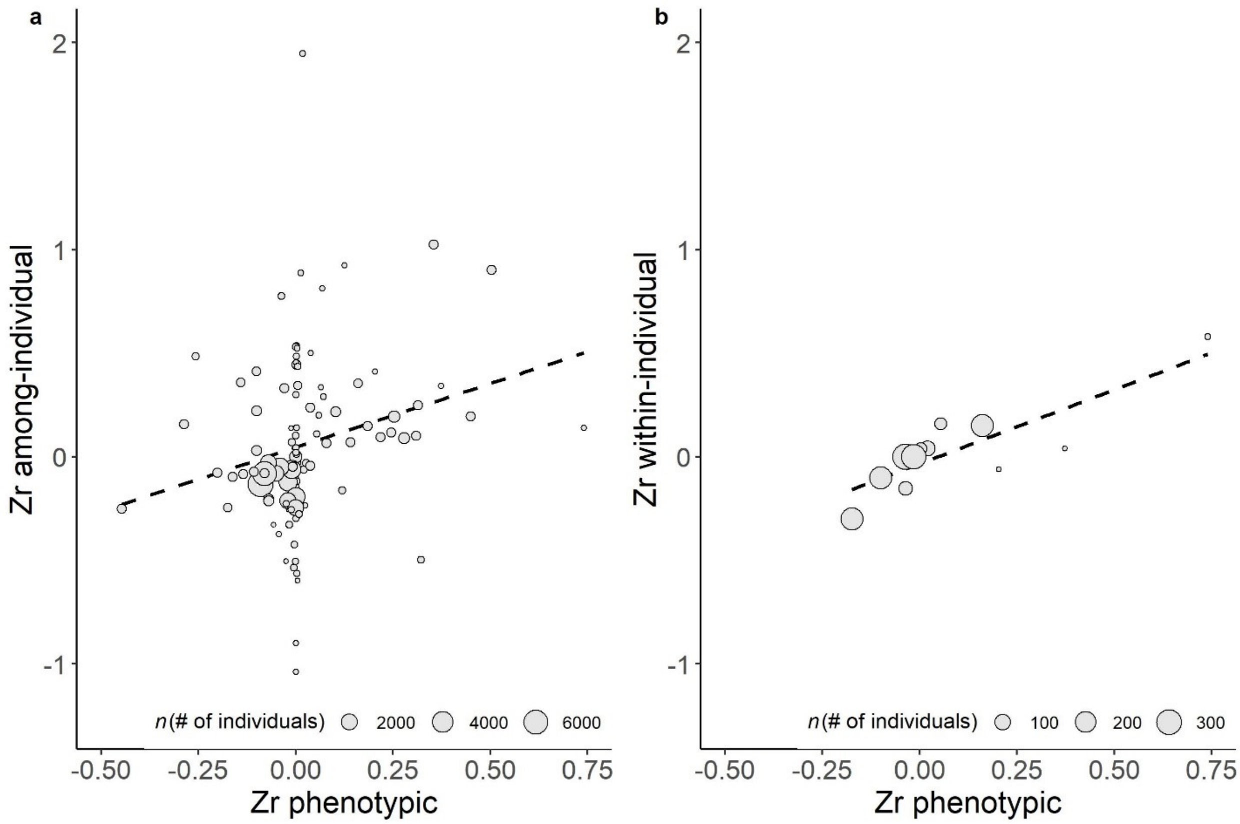

Figure A1.1. Correlation between a) phenotypic estimates and among-individual estimates, and b) between phenotypic and within-individual estimates. In a) r= 0.228 (0.042-0.399 CIs), and in b) r= 0.840 (0.538-0.951 CIs).

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Appendix 2- Supplementary material for: *Sampling to survive: energetic constraints shape sampling decisions in black-capped chickadees (Poecile aticapillus)*

Table A2.1. Experimental schedule for the sampling study. *Full-Full*: both feeders at each feeding station were full. *Full-Empty*: one feeder at each station was randomly emptied, the other remained full. *Empty-Full*: The empty and full feeders at each site switched profitability. *Empty-Empty*: both feeders at each site were empty.

Day	Treatment	Trial #	Sampling Measured	Battery Change
Nov 29, 2019	Full-Full	1	No	X
Nov 30, 2019	Full-Full	1	No	
Dec 1, 2019	Full-Full	1	No	
Dec 2, 2019	Full-Full	1	No	
Dec 3, 2019	Full-Empty	1	Yes	X
Dec 4, 2019	Full-Empty	1	Yes	
Dec 5, 2019	Full-Empty	1	Yes	
Dec 6, 2019	Full-Empty	1	Yes	
Dec 7, 2019	Empty-Full	1	Yes	X
Dec 8, 2019	Empty-Full	1	Yes	
Dec 9, 2019	Empty-Full	1	Yes	
Dec 10, 2019	Empty-Full	1	Yes	
Dec 11, 2019	Empty-Empty	1	Yes	X
Dec 12, 2019	Empty-Empty	1	Yes	
Dec 13, 2019	Empty-Empty	1	Yes	
Dec 14, 2019	Empty-Empty	1	Yes	
Dec 15, 2019	Empty-Empty	1	No	X
Dec 16, 2019	Empty-Empty	1	No	
Dec 17, 2019	Empty-Empty	1	No	
Dec 18, 2019	Empty-Empty	1	No	
Dec 19, 2019	Empty-Empty	1	No	X
Dec 20, 2019	Empty-Empty	1	No	
Dec 21, 2019	Empty-Empty	1	No	
Dec 22, 2019	Empty-Empty	1	No	
Dec 23, 2019	Full-Full	2	No	X
Dec 24, 2019	Full-Full	2	No	
Dec 25, 2019	Full-Full	2	No	
Dec 26, 2019	Full-Full	2	No	
Dec 27, 2019	Full-Empty	2	Yes	X
Dec 28, 2019	Full-Empty	2	Yes	
Dec 29, 2019	Full-Empty	2	Yes	
Dec 30, 2019	Full-Empty	2	Yes	
Dec 31, 2019	Empty-Full	2	Yes	X
Jan 1, 2020	Empty-Full	2	Yes	
Jan 2, 2020	Empty-Full	2	Yes	

Jan 3, 2020	Empty-Full	2	Yes	
Jan 4, 2020	Empty-Empty	2	Yes	X
Jan 5, 2020	Empty-Empty	2	Yes	
Jan 6, 2020	Empty-Empty	2	Yes	
Jan 7, 2020	Empty-Empty	2	Yes	
Jan 8, 2020	Empty-Empty	2	No	X
Jan 9, 2020	Empty-Empty	2	No	
Jan 10, 2020	Empty-Empty	2	No	
Jan 11, 2020	Empty-Empty	2	No	
Jan 12, 2020	Empty-Empty	2	No	X
Jan 13, 2020	Empty-Empty	2	No	
Jan 14, 2020	Empty-Empty	2	No	
Jan 15, 2020	Empty-Empty	2	No	
Jan 16, 2020	Full-Full	3	No	X
Jan 17, 2020	Full-Full	3	No	
Jan 18 2020	Full-Full	3	No	
Jan 19, 2020	Full-Full	3	No	
Jan 20, 2020	Full-Empty	3	Yes	X
Jan 21, 2020	Full-Empty	3	Yes	
Jan 22, 2020	Full-Empty	3	Yes	
Jan 23, 2020	Full-Empty	3	Yes	
Jan 24, 2020	Empty-Full	3	Yes	X
Jan 25, 2020	Empty-Full	3	Yes	
Jan 26, 2020	Empty-Full	3	Yes	
Jan 27, 2020	Empty-Full	3	Yes	
Jan 28, 2020	Empty-Empty	3	Yes	X
Jan 29, 2020	Empty-Empty	3	Yes	
Jan 30, 2020	Empty-Empty	3	Yes	
Jan 31, 2020	Empty-Empty	3	Yes	
Feb 1, 2020	Empty-Empty	3	No	X
Feb 2, 2020	Empty-Empty	3	No	
Feb 3, 2020	Empty-Empty	3	No	
Feb 4, 2020	Empty-Empty	3	No	
Feb 5, 2020	Empty-Empty	3	No	X
Feb 6, 2020	Empty-Empty	3	No	
Feb 7, 2020	Empty-Empty	3	No	
Feb 8 2020	Empty-Empty	3	No	
Feb 9, 2020	Full-Full	4	No	X
Feb 10, 2020	Full-Full	4	No	
Feb 11, 2020	Full-Full	4	No	
Feb 12, 2020	Full-Full	4	No	
Feb 13, 2020	Full-Empty	4	Yes	X
Feb 14, 2020	Full-Empty	4	Yes	
Feb 15, 2020	Full-Empty	4	Yes	
Feb 16, 2020	Full-Empty	4	Yes	
Feb 17, 2020	Empty-Full	4	Yes	X

Feb 18, 2020	Empty-Full	4	Yes	
Feb 19, 2020	Empty-Full	4	Yes	
Feb 20, 2020	Empty-Full	4	Yes	
Feb 21, 2020	Empty-Empty	4	Yes	X
Feb 22, 2020	Empty-Empty	4	Yes	
Feb 23, 2020	Empty-Empty	4	Yes	
Feb 24, 2020	Empty-Empty	4	Yes	
Feb 25, 2020	Empty-Empty	4	No	X
Feb 26, 2020	Empty-Empty	4	No	
Feb 27, 2020	Empty-Empty	4	No	
Feb 28, 2020	Empty-Empty	4	No	
Feb 29, 2020	Empty-Empty	4	No	X
Mar 1, 2020	Empty-Empty	4	No	
Mar 2, 2020	Empty-Empty	4	No	
Mar 3, 2020	Empty-Empty	4	No	

Prior used in Bayesian multivariate mixed effect model (adapted from Houslay and Thomas 2017):

```
prior.houslay<-list(R = list(V = diag(c(1,1,1,0.0001),4,4), nu = 1.002, fix = 4),

             G = list(G1 = list(V = diag(4), nu = 3,

                          alpha.mu = rep(0,4),

                          alpha.V = diag(25^2,4))))
```

Model structure used to assess among-individual effects of sampling behaviour on survival (based on the method presented in Houslay and Thomas 2017):

```
mb7<-MCMCglmm(cbind(Luxury, Necessity, baseline_rate, Survived) ~ trait-1 +

          at.level(trait,1): scale(AvgTemp)+ at.level(trait,2): scale(AvgTemp)+ at.level(trait,3):
         scale(baseline_temp)+

          trait:DNASex,

         random = ~ us(trait):TransponderHexCode ,

         rcov = ~ us(trait):units,

         family = c("categorical", "categorical", "gaussian","categorical"),

         data=as.data.frame(lux_nec2), prior =prior.houslay,

         verbose = TRUE,nitt=4000000,thin=150,burnin=1000000)
```