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The optimal clutch size revisited: separating individual quality from the costs of reproduction

Lucy A. Winder[1*], Mirre J.P. Simons[1], Terry Burke[1]

[1]Ecology & Evolutionary Biology, School of Biosciences, The University of Sheffield, Sheffield S10 2TN, UK

*Corresponding author: lwinder1@sheffield.ac.uk

Abstract

Life-history theory, central to our understanding of diversity in morphology, behaviour and senescence, describes how traits evolve through the optimisation of trade-offs in investment. Despite considerable study, there is only minimal support for trade-offs within species between the two traits most closely linked to fitness – reproduction and survival – questioning the theory's general validity. We used a meta-analysis to separate quality effects from the costs of reproduction using studies of parental investment and survival in birds. Experimental enlargement of broods caused reduced parental survival. However, the effect of experimental enlargements was small and opposite to the effect of phenotypic quality, where individuals that naturally produced larger clutches also survived better. The opposite effects on survival in experimental and observational studies of parental care provides the first meta-analytic evidence for theory suggesting that quality differences mask trade-offs. Fitness projections using the overall effect size revealed that reproduction presented negligible costs, except when reproductive effort was forced beyond the level observed within species, to that seen between species. We conclude that there is little support for the most fundamental life-history trade-off, between reproduction and longevity, operating within a population. We suggest that within species, the fitness landscape of the reproduction–survival trade-off is flat until it reaches the boundaries of the between-species fast–slow life-history continuum. Our interpretation explains why the costs of reproduction are not apparent and why variation in reproductive output persists within species.

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Main

Across taxa, we see wide variation in life-history traits, such as the number of offspring produced and time spent raising young [1–3]. The central idea in life-history theory is that resources are finite, forcing trade-offs, meaning that investment in one aspect of life requires the sacrifice of another [4–7]. As reproduction is considered to be one of the most energetically demanding life stages, it is expected that within-species variation in offspring production will be driven by the cost of producing and raising young. It is thought that the fitness costs of reproduction are largely incurred as a decrement to survival, which would explain the fast–slow life-history continuum between reproduction and lifespan across species [6]. As reproduction and survival are the two components of life-history most closely related to fitness, this central trade-off has been the subject of much theoretical and empirical research.

Brood size manipulations of birds in natural conditions have provided arguably the best experimental paradigm in which to test the survival costs of reproduction. Experimental increases in brood size result in increased parental effort, suggesting that parents can typically cope with increased reproductive demands [8–12]. However, the expected increased costs of parental investment are not always detected and the current estimate across studies suggests only a small and inconsistent effect [13–16]. The absence of a cost of reproduction on survival means that costs must arise elsewhere or, alternatively, that individuals may differ in quality. Individuals may each be operating at their own maximum reproductive output, determined by their phenotypic condition, local or temporal genetic adaptation, and the surrounding environment [8–10,16]. The relative importance of the trade-off between reproduction and survival – central to life-history theory and the biology of ageing[12] – therefore remains unclear. In addition, the compelling theoretical explanation for the lack of an apparent trade-off due to the confounding effects of individual quality has not been investigated on a quantitative level [5,11,16].

Here, we present a meta-analysis that distinguishes between quality effects and the costs of reproduction. To do this, we tested how parental annual survival in birds is affected by the brood size they cared for in two different contexts: first in brood manipulation studies and, second, in observational studies of natural variation in clutch size. We expressed changes in survival on a per-egg basis, which, for the first time, allows for a quantitative comparison across studies. We find that quality is associated with higher survival chances, and that this effect is opposite but equal in magnitude to the costs of reproduction. The survival trade-off

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for offspring production within a population is therefore offset by differences in quality, potentially constraining the evolution of higher reproductive effort. Our analysis also uniquely allowed a quantitative comparison across species, as survival risk was expressed on a per-egg basis. We transformed the response variable, scaling for variance and mean, given that a per-egg increase in clutch size does not equate to the same proportional increase in parental effort for all species equally. Our findings suggest that species that generally lay smaller clutches are affected more severely by brood-size manipulations. This provides evidence that trade-offs are only detected when an individual is forced to perform far outside its optimum level.

To predict the evolutionary consequences of the effect sizes that we estimated using meta-analysis, we projected the fitness consequences for a change in brood-size life-history strategy. We found that the effects on parental survival translate into negligible fitness costs, with a relatively flat fitness landscape, suggesting that birds underproduce in terms of brood size, given the absence of fitness costs. This conclusion fits with our comparative finding that suggests that only brood sizes manipulated beyond the natural range incur substantial survival costs. Our results therefore suggest that, in wild populations, parental survival costs are, at most, a small component of the total fitness costs of investing parental effort. Our results do suggest that a cost of reproduction can be detected when an organism is pushed to the extreme of its reproductive capacity. We therefore infer that, though the survival–parental care trade-off does exist within species, it is too minimal to explain why variation in clutch size persists within a population. In addition, our work shows that differences in individual quality counterbalance the trade-off between survival and reproduction, as previously theorised [5], and as such constrain reproductive effort and maintain clutch size variation in a population.

Results

The relationship between clutch size and survival was significantly different and opposite between observational and brood manipulation studies, irrespective of how brood size was scaled ($p < 0.01$, Figure 1, Table 1). Within observed natural variation, parents with larger clutches showed increased survival. In contrast, when broods were experimentally manipulated, the opposite relationship was found: increasing brood sizes decreased survival. Although the difference in overall effect size between experimental and natural variation in brood size was strongly significant in each comparison made, the individual

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overall effect sizes only became significant (from zero) when brood size was expressed as a proportional increase. Expressing brood size as a proportional increase corrects for the variation in average clutch size observed across the species included in this analysis, which ranged from 2 to 11. The parental effort required to raise two instead of one chick is potentially doubled, whereas one additional chick in a brood of 11 is likely to require only a marginal increase in effort. Indeed, also when using a between-species comparison, the effects of brood size manipulation and quality were strongest in the species that laid the smallest clutches, suggesting that costs to survival were only observed when a species was pushed beyond its natural limits (Figure 2, Supplementary Table 1).

Males and females did not differ in their survival response to changing clutch size (Supplementary Table 2, Supplementary Figure 1, contrary to Santos & Nakagawa 2012 [15]). The variance assigned to the random effects in the model was largely accounted for by study (Supplementary Table 3). Species accounted for more variation than the phylogeny, indicating that species vary in their survival for their brood size raised, irrespective of their shared evolutionary ancestry. However, our dataset included few closely related species, which reduces our ability to estimate phylogenetic effects (Supplementary Figure 2).

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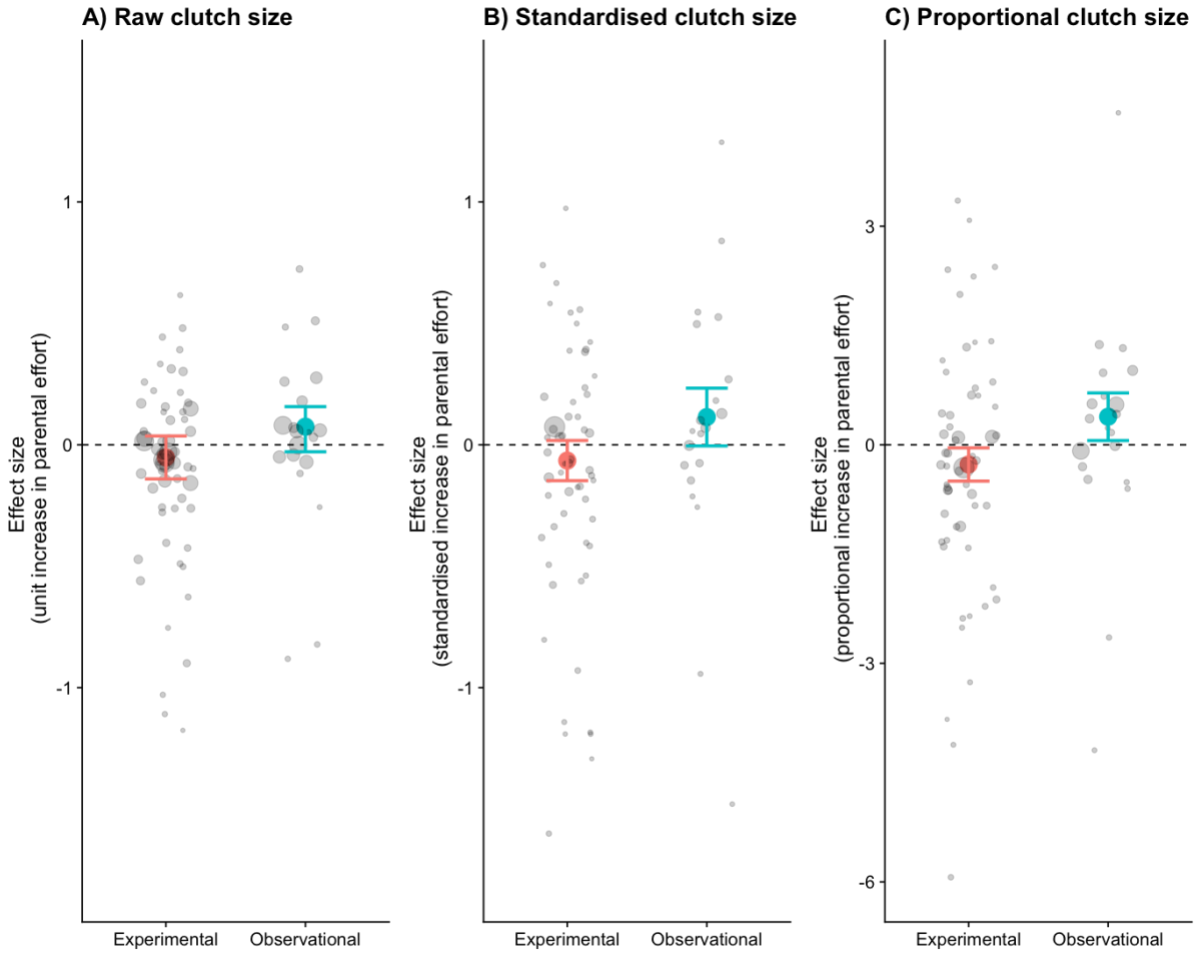

Figure 1: The effects size (log odds of survival) for three different measures of clutch size: (A) raw, (B) standardised, and (C) proportional clutch size. Coloured points are the combined effect sizes of the odds ratios with their 95% confidence intervals. Points are coloured by whether they represent brood manipulation experiments (costs of reproduction) or they are observational (quality). Grey points are the odds ratios of each study, with their sizes weighted by the variance.

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Table 1: Effect size estimates for the odds of survival with increasing clutch size (raw, standardised and proportional clutch size). The p-values indicate the difference between brood manipulations and observational data, with the individual effect *p*-values (from zero) in parentheses.

	Parameter		Effect size	95% CI lower bounds	95% CI upper bounds	*p*	(individual)
Raw	Clutch size	Brood manipulation	-0.0522	-0.1406	0.0363	**0.0007**	(0.2477)
		Observational	0.0747	0.1571	-0.0288		(0.1571)
Standardised	Clutch size	Brood manipulation	-0.0651	-0.1478	0.0177	**0.0065**	(0.1232)
		Observational	0.1143	-0.0046	0.2333		(0.0595)
Proportional	Clutch size	Brood manipulation	-0.2703	-0.4984	-0.0423	**0.0005**	**(0.0202)**
		Observational	0.3850	0.0583	0.7116		**(0.0209)**

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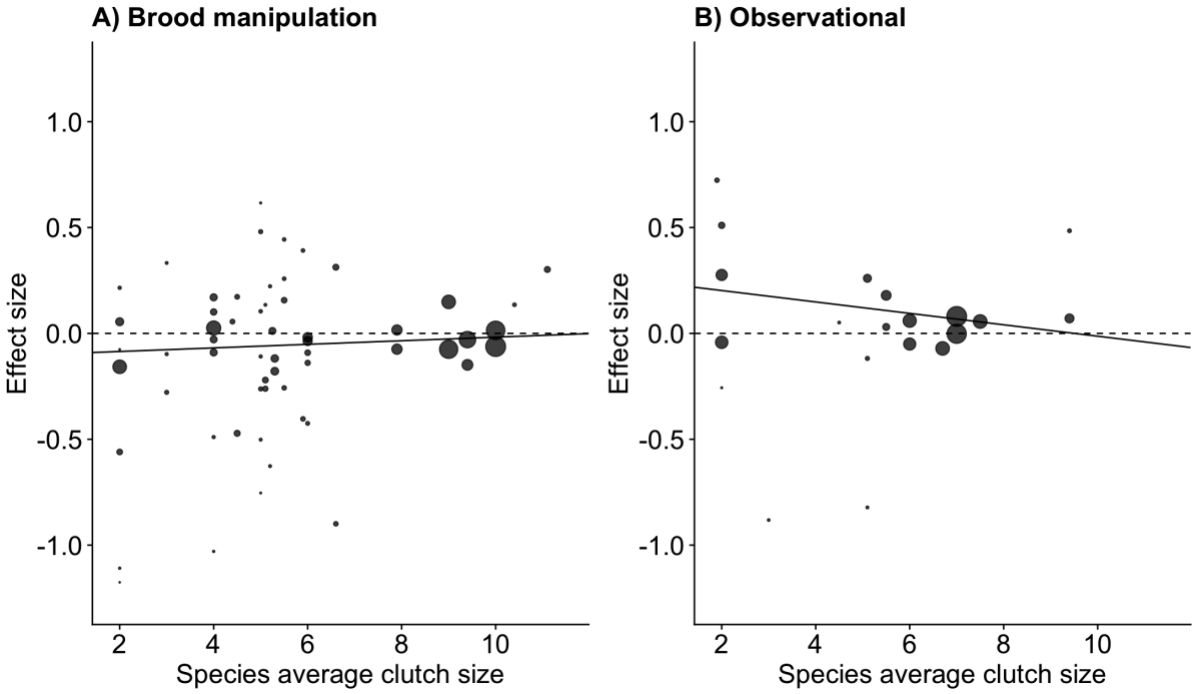

Figure 2: The meta-analytic linear regression (Table S1) of the effect of increasing clutch size (per egg) on parental survival, given the average clutch size for the species. Species with small clutch sizes showed stronger costs of reproduction and a stronger relationship with quality (p = 0.015). The points are the survival effect sizes (log odds ratio) per egg (as in Figure 1A) on parental survival in each study, with the point size reflecting the meta-analytic weight of that study.

Projected fitness consequences of the costs of reproduction

From our meta-analysis we now have a quantifiable and comparable effect size for the survival costs of reproduction that we can use to predict its evolutionary consequences across a range of life histories. To this end, we projected the fitness consequences of increased reproductive effort, starting with the average effect size estimate per egg (Table 1) across a range of life histories, for a range of annual survival rates and clutch sizes (Figure 3). Overall, the effect size estimated in the meta-analysis (-0.05) resulted in a gain of fitness when reproductive output increased, especially in hypothetical species with low survival and small clutches. Conversely, the benefit of higher reproductive output was largely offset by the cost of survival when a species' survival rate and clutch size were high. When we increased the effect size upto five-fold, fitness costs of reproduction became more pronounced, but were still not present in species with small clutches and short lifespans.

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Under long-term evolution these selection differentials should lead to individual hypothetical species moving towards the diagonal (bottom left to the right top corner). This diagonal represents the observed fast–slow pace of life continuum observed among species[17]. Exemplar species (i.e., with survival and average clutch size combinations observable in wild populations), for which we predicted the fitness consequences of the costs of reproduction, lie on this comparative diagonal in life history. In these exemplar species, the selection differential was observed to lie slightly above one, indicating that individuals having a higher clutch size than the species' average would gain a slight fitness benefit. The fitness costs and benefits did, in general, not diverge substantially with the addition of chicks, but flattened, suggesting that the costs of survival counterbalance the benefits of reproduction across a range of reproductive outputs within a species.

The low costs of reproduction that we estimated could still be responsible for between-species life-history evolution, constraining species reproductive output and survival combination to fall along the diagonal of the fast–slow pace of life continuum. How selection pressures translate into short term and longer term evolutionary trajectories is uncertain. Often directional selection estimated in the wild does not translate to the inter-generational change on the population level[18]. Note, however, that only far away from the diagonal did our fitness projections reach a magnitude that would be predicted to lead to rapid evolutionary change [19] and see SI) . The weak selection effects that lie on the diagonal are probably to be counterbalanced in the wild by factors such as environmental effects and genetic effects (e.g., gene flow from immigration or random mutation) [20]. We argue that within-species the minimal costs of reproduction, a flat fitness landscape and quality effects together explain why individuals appear to under-produce. Only when individuals are pushed beyond the observed between-species constraint do costs become apparent (Figures 1,2).

Our interpretation of the reproduction/lifespan life-history trade-off, based on our quantitative meta-analysis and subsequent fitness projections, explains several key observations and contradictions in the field. A strong trade-off is observed between species, but within species this trade-off is not apparent and variation in reproductive output is maintained within fitness boundaries similar to those that determine the between-species life history trade-off. The implication of this conclusion is that the costs of reproduction are likely to operate on a physiological level, but that the fitness consequences will remain largely flat over a species' observed variation in reproductive output. These effects are further obscured by the effects of quality, which are opposite in sign and magnitude to the cost of reproduction (Figure 1) and are likely to further flatten the fitness landscape.

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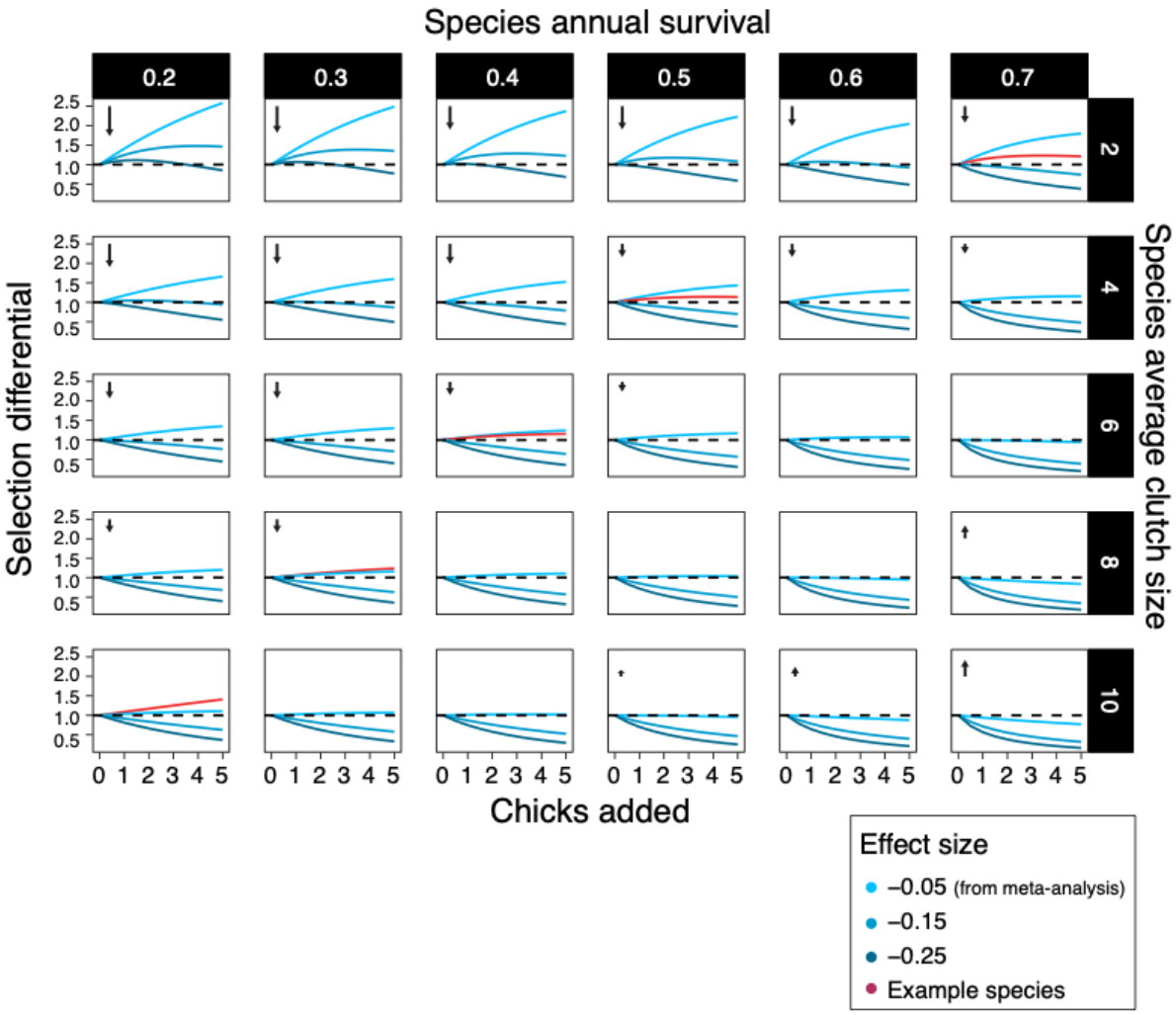

Figure 3: Isoclines of selection differentials among hypothetical control populations (in which individuals reproduce at the species' mean ratee) and hypothetical brood-manipulated populations (where individuals reproduce at an increased rate compared to control) for their whole lives. Selection differentials above 1 represents high lifetime fitness. Survival rates, clutch sizes, the magnitude of the manipulation (chicks added) and effect sizes represent the range of these variables present in the studies used in our meta-analysis. For each clutch size, we used a predicted survival rate and effect size to give isoclines that are biologically meaningful (exemplar birds shown in red). Arrows indicate the relative size and direction of selection in life-history space (on the reproduction axis). The costs of reproduction we estimated within species are predicted to result in a fast–slow life-history continuum across species, and the exemplar species we used as examples fit on this diagonal of survival rate/ clutch size combinations. We suggest that individual species show limited

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costs of reproduction, as they operate within relatively wide constraints imposed by the cost of reproduction that is responsible for the strong life-history trade-off observed across species.

Discussion

Our results provide the first meta-analytic evidence that differences in individual quality drive variation in clutch size. Here, we use the definition of quality as a combination of traits that give an individual higher fitness [5]. The reason selection is not acting on these individuals is currently unknown but it is likely that environmental variability leads to alternative phenotypes being selected for at different points in space and time (also discussed in [18]). It is possible that the quality effect could be representative of a terminal effect, where individuals have lower reproductive output in the year preceding their death, thereby driving the trend for naturally lower laying birds to have lower survival (e.g.,[21,22]; also see [23] for age-related changes in reproductive output). The effect of birds having naturally-larger clutches was significantly opposite to the result of increasing clutch size through brood manipulation. For both costs of reproduction and quality effects, we found that species that laid the smallest clutches showed the largest effects. Brood manipulations that affect parental survival are thus likely to be the result of pushing parental effort beyond its natural limits. The classic trade-off between adult survival and the clutch size cared for is only apparent when an individual is forced to raise a clutch outside of its individual optimum, and these effects are confounded or even fully counterbalanced by differences in quality (as theorised in [5]).

Our fitness projections of the consequences of the costs of reproduction using the overall effect size we estimated suggest that, for current extant species, the within-species fitness landscape of the reproduction survival trade-off is flat. Species' life history decisions are constrained within a broader fast–slow life-history continuum, explaining why variation within species in reproductive effort, such as in clutch size, is large and near universal. Our interpretation assumes that other fitness costs of reproduction are smaller or at least less relevant than survival costs. However, it is possible that such costs are important, such as effects on offspring quality (e.g.,[24,25]), parental condition other than survival (e.g., [26,27]) or future reproductive effort (e.g., [28]). Interestingly, the studies that have measured these different domains that contribute to fitness in brood-size manipulation studies concluded that only in combination do these costs result in balancing selection for the current most common brood size in the population [29,30]. Such classic trade-off explanations do, however, fail to

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explain why variation in reproductive effort is prevalent within species and why between-species life-history trade-offs appear so much stronger and conclusive. Our analysis and interpretation provide a novel explanation suggesting that, at its optimum, the within-species trade-off between survival and reproduction is relatively flat, and thus neutral to selection (supporting the theory presented in [16]). We suggest that the lack of evidence supporting trade-offs driving within-species variation does not necessarily mean that physiological costs of reproduction are non-existent (e.g., [24,31]), but rather that, within the wild and within the natural range of reproductive activities, such costs are not relevant to fitness. One key explanation for this effect supported by our meta-analysis and prior theory [5] is that individuals differ in quality.

Methods

Study sourcing & inclusion criteria

We used the following inclusion criteria (similar to [15]): the study must be on a wild population; must detail variation in the number of raised young (hereafter referred to as clutch size for simplicity) in relation to parental survival to the following year (including both experimental and observational studies) and must provide sample sizes. We did include studies where parental survival was reported for both parents combined. Excluded studies and the grounds for their removal are given in the supplementary information (Supplementary Table 4). We started by, first, extracting data from the included brood-manipulation studies and then searched the literature to include more recently-published studies (Supplementary Methods). In addition, we extracted data from studies that correlated variation in parental survival with natural variation in clutch size (observational studies). We aimed to pair each species in the brood manipulation studies with an observational study to ensure that the effects of quality were estimated across a similar range of species and so facilitate a more direct comparison. Where there was no equivalent study in the same species, we attempted to find a study of a congener. In most cases, observational data were obtained from either the same paper as the one describing brood manipulations, or via searching for other papers by the same authors. If this failed to produce observational data, a search was conducted following the same protocol as for the brood-manipulation experiments, but also specifying species, genus and/or common name in the search. Any additional brood manipulation studies or

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observational studies of different species found using this search were also included in the meta-analysis.

From the literature search, 78 individual effect sizes from 46 papers were used (20 observational and 58 experimental studies). While extracting these studies we also made note of the average clutch size of the species, the within-species standard deviation in clutch size and the longevity of the species. We extracted this information from the paper containing the study but if the information was missing, we searched other published literature with the aim to find the information from a similar population (i.e., at a similar latitude).

Extracting effect sizes

We used raw data to estimate an effect size by performing a logistic regression to obtain the log odds ratio for parental survival, given the clutch size (i.e., positive values indicate an increased chance of survival). Clutch size was averaged (mean) if a single estimate of survival was reported for multiple clutch sizes. 'Year' was included as an explanatory variable to correct for between-year variation in adult survival, where data were presented for multiple years. We standardised the clutch size by the mean of the species and by the within-species standard deviation in clutch size. For species that have no within-species variance in clutch size, we used a value of 0.01 for the standard deviation in clutch size to prevent issues in calculations when using zero. We, therefore, expressed variation in clutch size in three ways: a raw increase in clutch size, a standardised clutch size and a proportional clutch size.

Meta-analysis

We ran a single model for each clutch size transformation to determine the cost of survival, given an increase in parental effort using the *metafor* package [32] in R 3.3.2 [33]. From these models we were also able to directly compare the effect size of brood manipulation studies and observational studies. We included phylogeny in these meta-analytic models to correct for shared ancestry. The phylogeny was obtained using BEAST to measure a distribution of 1,000 possible phylogenetic trees of the focal 30 species extracted from BirdTree [34]. We also included species and each studies' journal reference as random effects in the model. From

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these models, we calculated the proportion of variance explained by the phylogenetic effect [35].

We then tested the effect of the species' mean clutch size on the relationship between parental survival and clutch size. We ran a single model with the species' average clutch size in interaction with treatment (brood manipulation or observational). The clutch size was adjusted by the combined average clutch size of all the species used in the meta-analysis, subtracted from the species mean clutch size for each study. Species, phylogeny and reference were also included as random effects to correct for the similarity of effect sizes within species and studies.

The difference in survival for the different sexes was modelled for each clutch size measure. Brood manipulation studies and observational studies were analysed in separate models. Sex was modelled as a categorical moderator (41 female studies, 27 male studies and 10 mixed studies). Species, phylogeny and reference were included as random effects (Supplementary Table 2 and Supplementary Figure 1).

Publication bias

Much of the data used in this analysis were taken from studies where these data were not the main focus of the study. This reduces the risk that our results are heavily influenced by a publication bias for positive results. A funnel plot for the survival against raw clutch size model is presented in Supplementary Information (Supplementary Figure 3).

Fitness projections

We calculated various isoclines using the brood-manipulation overall effect size (based on raw clutch size) that we estimated. Here, an isocline is a trendline representing the change in fitness returns, given an increase in individual clutch size. An estimated lifetime reproductive fitness was calculated for hypothetical control populations, where all individuals consistently reproduce at the level of a species mean and have a consistent annual survival rate. We assumed species average clutch sizes to be 2, 4, 6, 8 and 10 and survival rates of 0.2, 0.3, 0.4, 0.5, 0.6 and 0.7, which reflected the range of clutch sizes and survival rates seen in the species in our meta-analysis. This lifetime reproductive fitness estimate was then repeated for a hypothetical population that reproduces at an increased level compared to control, i.e., brood size enlargement, throughout their lives. To obtain this, we added a range

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of 1–5 offspring to the clutch sizes of the control populations. Using a range of increased clutch sizes allowed us to investigate how increased reproductive effort would affect lifetime fitness. The survival costs were determined by the overall effect size found for brood manipulation studies (per egg). We modelled effect sizes of -0.05, -0.15 and -0.25, which represent, respectively, the meta-analytic overall effect size, its upper confidence interval and a further severe effect within the observed effect sizes (rounded to the closest 0.05 for simplicity). We then calculated the selection differential ($LRS_{brood\ manipulation}$ / $LRS_{control}$) between the hypothetical control and "brood manipulation" populations for each combination of survival rate, clutch size and effect size, and plotted this as an isocline. We further plotted the fitness consequences for five exemplar species, where survival rate and clutch size combinations are observable in the wild. We used effect sizes from model predictions at these survival rate and clutch size combinations rather than the meta-analytic mean, thereby providing a biological context.

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