

1 **The optimal clutch size revisited: separating individual quality from** 2 **the costs of reproduction**

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9

10 **Abstract**

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

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34 Main

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36 Across taxa, we see wide variation in life-history traits, such as the number of offspring
37 produced and time spent raising young¹⁻³. The central idea in life-history theory is that
38 resources are finite, forcing trade-offs, meaning that investment in one aspect of life requires
39 the sacrifice of another⁴⁻⁷. As reproduction is considered to be one of the most energetically
40 demanding life stages, it is expected that within-species variation in offspring production will
41 be driven by the cost of producing and raising young. It is thought that the fitness costs of
42 reproduction are largely incurred as a decrement to survival, which would explain the fast-
43 slow life-history continuum between reproduction and lifespan across species⁶. As
44 reproduction and survival are the two components of life-history most closely related to
45 fitness, this central trade-off has been the subject of much theoretical and empirical
46 research.

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48 Brood size manipulations of birds in natural conditions have provided arguably the best
49 experimental paradigm in which to test the survival costs of reproduction. Experimental
50 increases in brood size result in increased parental effort, suggesting that parents can
51 typically cope with increased reproductive demands⁸⁻¹². However, the expected increased
52 costs of parental investment are not always detected and the current estimate across studies
53 suggests only a small and inconsistent effect¹³⁻¹⁶. The absence of a cost of reproduction on
54 survival means that costs must arise elsewhere or, alternatively, that individuals may differ in
55 quality. Individuals may each be operating at their own maximum reproductive output,
56 determined by their phenotypic condition, local or temporal genetic adaptation, and the
57 surrounding environment^{8-10,16}. The relative importance of the trade-off between
58 reproduction and survival – central to life-history theory and the biology of ageing¹² –
59 therefore remains unclear. In addition, the compelling theoretical explanation for the lack of
60 an apparent trade-off due to the confounding effects of individual quality has not been
61 investigated on a quantitative level^{5,11,16}.

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

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

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80 To predict the evolutionary consequences of the effect sizes that we estimated using meta-
81 analysis, we projected the fitness consequences for a change in brood-size life-history
82 strategy. We found that the effects on parental survival translate into negligible fitness costs,
83 with a relatively flat fitness landscape, suggesting that birds underproduce in terms of brood
84 size, given the absence of fitness costs. This conclusion fits with our comparative finding that
85 suggests that only brood sizes manipulated beyond the natural range incur substantial
86 survival costs. Our results therefore suggest that, in wild populations, parental survival costs
87 are, at most, a small component of the total fitness costs of investing parental effort. Our
88 results do suggest that a cost of reproduction can be detected when an organism is pushed
89 to the extreme of its reproductive capacity. We therefore infer that, though the survival–
90 parental care trade-off does exist within species, it is too minimal to explain why variation in
91 clutch size persists within a population. In addition, our work shows that differences in
92 individual quality counterbalance the trade-off between survival and reproduction, as
93 previously theorised⁵, and as such constrain reproductive effort and maintain clutch size
94 variation in a population.

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97 **Results**

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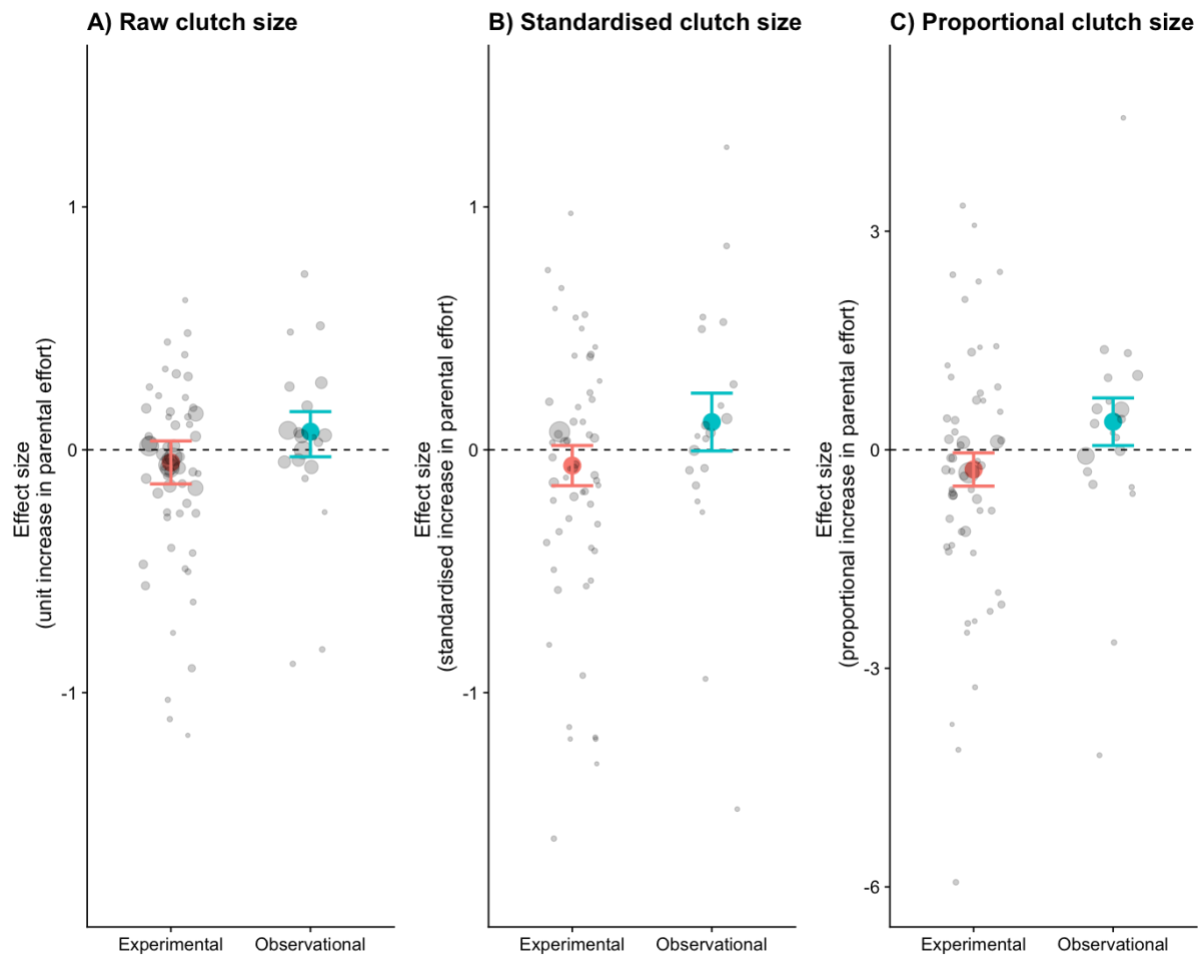
99 The relationship between clutch size and survival was significantly different and opposite
100 between observational and brood manipulation studies, irrespective of how brood size was
101 scaled ($p < 0.01$, Figure 1, Table 1). Within observed natural variation, parents with larger
102 clutches showed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

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

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116 Males and females did not differ in their survival response to changing clutch size
117 (Supplementary Table 2, Supplementary Figure 1, contrary to Santos & Nakagawa 2012¹⁵).
118 The variance assigned to the random effects in the model was largely accounted for by
119 study (Supplementary Table 3). Species accounted for more variation than the phylogeny,
120 indicating that species vary in their survival for their brood size raised, irrespective of their
121 shared evolutionary ancestry. However, our dataset included few closely related species,
122 which reduces our ability to estimate phylogenetic effects (Supplementary Figure 2).

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128 **Figure 1:** The effects size (log odds of survival) for three different measures of clutch size: (A) raw, (B)

129 standardised, and (C) proportional clutch size. Coloured points are the combined effect sizes of the

130 odds ratios with their 95% confidence intervals. Points are coloured by whether they represent

131 brood manipulation experiments (costs of reproduction) or they are observational (quality). Grey

132 points are the odds ratios of each study, with their sizes weighted by the variance.

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

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Parameter			Effect size	95% CI lower bounds	95% CI upper bounds	<i>p</i>	(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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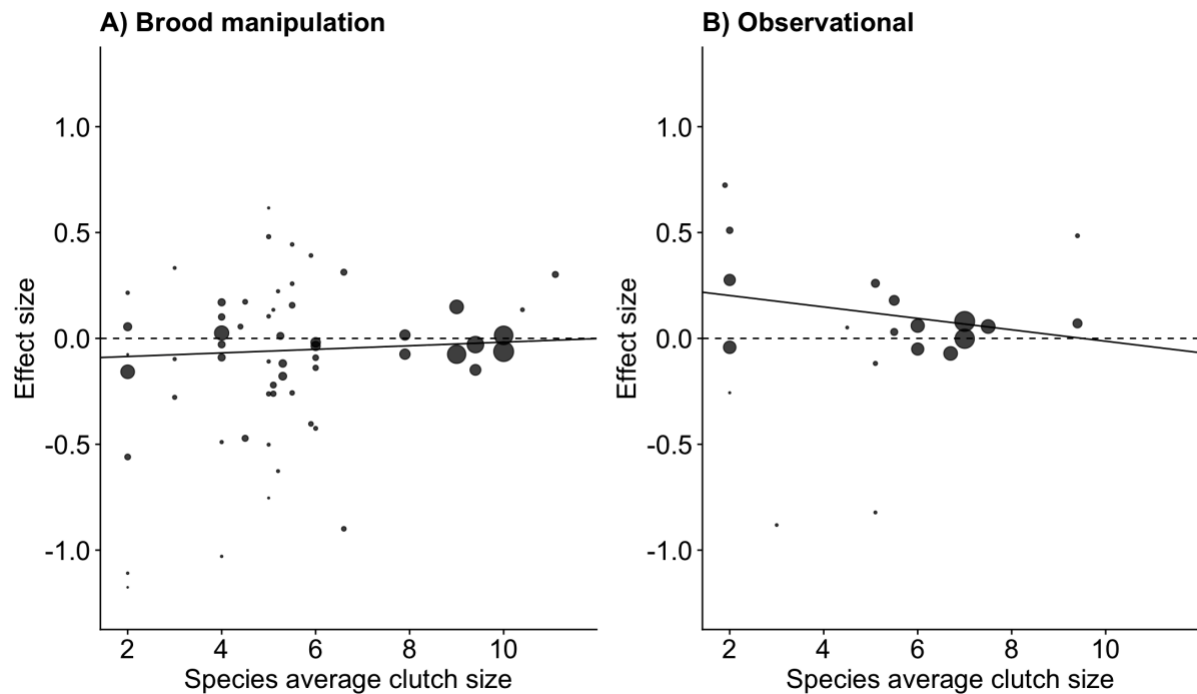
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162 **Figure 2:** The meta-analytic linear regression (Table S1) of the effect of increasing clutch size (per
163 egg) on parental survival, given the average clutch size for the species. Species with small clutch sizes
164 showed stronger costs of reproduction and a stronger relationship with quality ($p = 0.015$). The
165 points are the survival effect sizes (log odds ratio) per egg (as in Figure 1A) on parental survival in
166 each study, with the point size reflecting the meta-analytic weight of that study.

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169 **Projected fitness consequences of the costs of reproduction**

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

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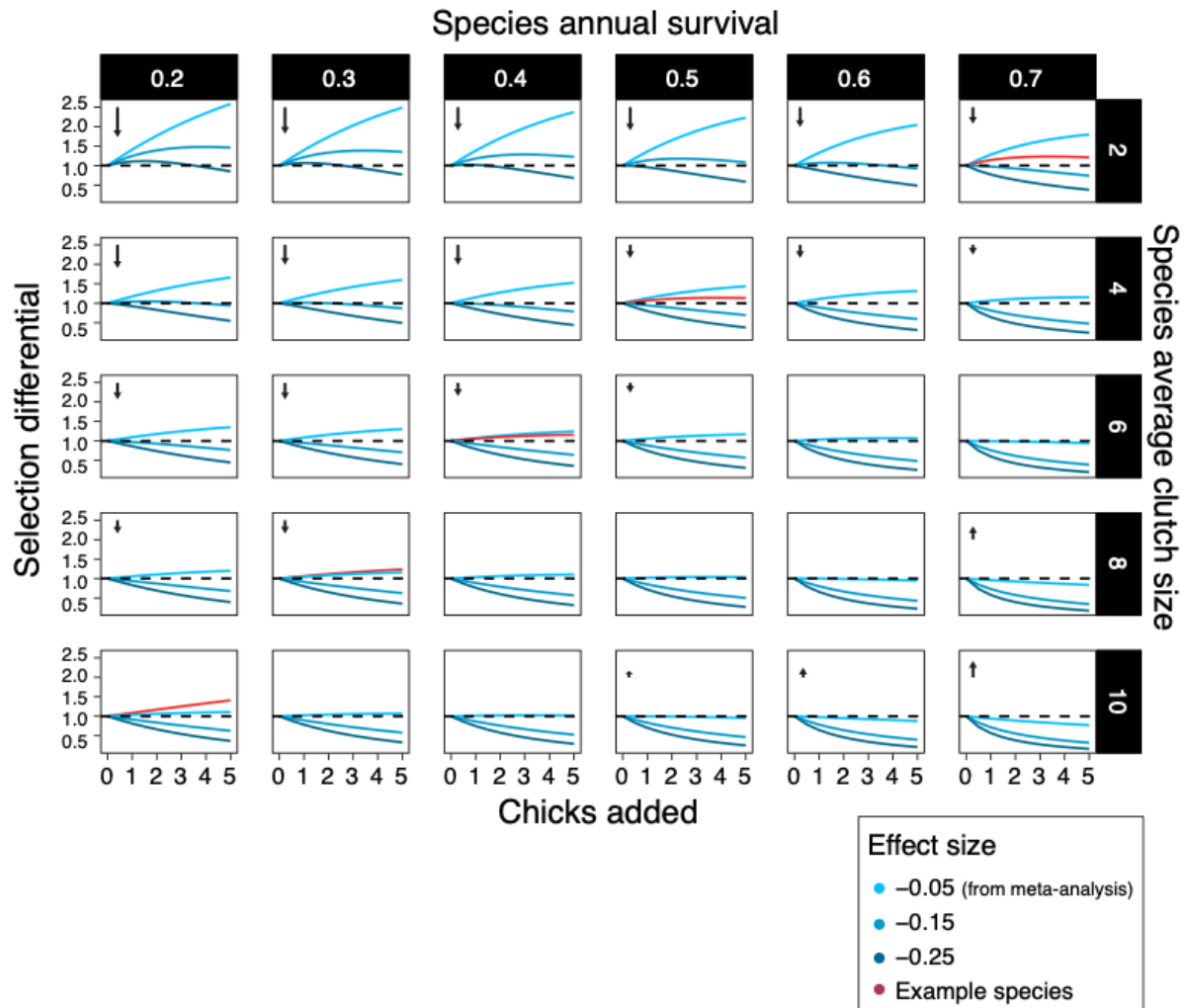
183 Under long-term evolution these selection differentials should lead to individual hypothetical
184 species moving towards the diagonal (bottom left to the right top corner). This diagonal
185 represents the observed fast–slow pace of life continuum observed among species¹⁷.
186 Exemplar species (i.e., with survival and average clutch size combinations observable in wild
187 populations), for which we predicted the fitness consequences of the costs of reproduction,
188 lie on this comparative diagonal in life history. In these exemplar species, the selection
189 differential was observed to lie slightly above one, indicating that individuals having a higher
190 clutch size than the species' average would gain a slight fitness benefit. The fitness costs
191 and benefits did, in general, not diverge substantially with the addition of chicks, but
192 flattened, suggesting that the costs of survival counterbalance the benefits of reproduction
193 across a range of reproductive outputs within a species.

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195 The low costs of reproduction that we estimated could still be responsible for between-
196 species life-history evolution, constraining species reproductive output and survival
197 combination to fall along the diagonal of the fast–slow pace of life continuum. How selection
198 pressures translate into short term and longer term evolutionary trajectories is uncertain.
199 Often directional selection estimated in the wild does not translate to the inter-generational
200 change on the population level¹⁸. Note, however, that only far away from the diagonal did our
201 fitness projections reach a magnitude that would be predicted to lead to rapid evolutionary
202 change ¹⁹ and see SI) . The weak selection effects that lie on the diagonal are probably to be
203 counterbalanced in the wild by factors such as environmental effects and genetic effects
204 (e.g., gene flow from immigration or random mutation) ²⁰. We argue that within-species the
205 minimal costs of reproduction, a flat fitness landscape and quality effects together explain
206 why individuals appear to under-produce. Only when individuals are pushed beyond the
207 observed between-species constraint do costs become apparent (Figures 1,2).

208

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



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

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

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236 **Discussion**

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238 Our results provide the first meta-analytic evidence that differences in individual quality drive
239 variation in clutch size. Here, we use the definition of quality as a combination of traits that
240 give an individual higher fitness⁵. The reason selection is not acting on these individuals is
241 currently unknown but it is likely that environmental variability leads to alternative
242 phenotypes being selected for at different points in space and time (also discussed in¹⁸). It
243 is possible that the quality effect could be representative of a terminal effect, where
244 individuals have lower reproductive output in the year preceding their death, thereby driving
245 the trend for naturally lower laying birds to have lower survival (e.g.,^{21,22}; also see²³ for age-
246 related changes in reproductive output). The effect of birds having naturally-larger clutches
247 was significantly opposite to the result of increasing clutch size through brood manipulation.
248 For both costs of reproduction and quality effects, we found that species that laid the
249 smallest clutches showed the largest effects. Brood manipulations that affect parental
250 survival are thus likely to be the result of pushing parental effort beyond its natural limits. The
251 classic trade-off between adult survival and the clutch size cared for is only apparent when
252 an individual is forced to raise a clutch outside of its individual optimum, and these effects
253 are confounded or even fully counterbalanced by differences in quality (as theorised in⁵).

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

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

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280 **Methods**

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282 *Study sourcing & inclusion criteria*

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

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

304

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

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313

314 *Extracting effect sizes*

315

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

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328

329 *Meta-analysis*

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331 We ran a single model for each clutch size transformation to determine the cost of survival,
332 given an increase in parental effort using the *metafor* package³² in R 3.3.2³³. From these
333 models we were also able to directly compare the effect size of brood manipulation studies
334 and observational studies. We included phylogeny in these meta-analytic models to correct
335 for shared ancestry. The phylogeny was obtained using BEAST to measure a distribution of
336 1,000 possible phylogenetic trees of the focal 30 species extracted from BirdTree³⁴. We also
337 included species and each studies' journal reference as random effects in the model. From

338 these models, we calculated the proportion of variance explained by the phylogenetic effect
339 ³⁵.

340

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

348

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

354

355

356 *Publication bias*

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

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362

363 *Fitness projections*

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365 We calculated various isoclines using the brood-manipulation overall effect size (based on
366 raw clutch size) that we estimated. Here, an isocline is a trendline representing the change
367 in fitness returns, given an increase in individual clutch size. An estimated lifetime
368 reproductive fitness was calculated for hypothetical control populations, where all individuals
369 consistently reproduce at the level of a species mean and have a consistent annual survival
370 rate. We assumed species average clutch sizes to be 2, 4, 6, 8 and 10 and survival rates of
371 0.2, 0.3, 0.4, 0.5, 0.6 and 0.7, which reflected the range of clutch sizes and survival rates
372 seen in the species in our meta-analysis. This lifetime reproductive fitness estimate was then
373 repeated for a hypothetical population that reproduces at an increased level compared to
374 control, i.e., brood size enlargement, throughout their lives. To obtain this, we added a range

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

388

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398 **References**

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- 400 1. Lack, D. The Significance of Clutch-size. *Ibis* **89**, 302–352 (1947).
- 401 2. Harvey, P. H. & Clutton-Brock, T. H. Life history variation in primates. *Evolution* **39**, 559–
402 559 (1985).
- 403 3. Ricklefs, R. E. Density Dependence, Evolutionary Optimization, and the Diversification of
404 Avian Life Histories. *Ornithol. Appl.* **102**, 9–22 (2000).
- 405 4. Stearns, S. C. Life-History Tactics: A Review of the Ideas. *Q. Rev. Biol.* **51**, 3–47 (1976).
- 406 5. van Noordwijk, A. J. & de Jong, G. Acquisition and Allocation of Resources: Their

- 407 Influence on Variation in Life History Tactics. *Am. Nat.* **128**, 137–142 (1986).
- 408 6. Kirkwood, T. B. L. & Rose, M. R. Evolution of senescence: late survival sacrificed for
409 reproduction. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **332**, 15–24 (1991).
- 410 7. Lemaître, J. F. & Gaillard, J. M. Reproductive senescence: new perspectives in the wild.
411 *Biol. Rev.* **92**, 2182–2199 (2017).
- 412 8. Charnov, E. L. & Krebs, J. R. On Clutch-Size and Fitness. *Ibis* **116**, 217–219 (1974).
- 413 9. Pettifor, R. A., Perrins, C. M. & McCleery, R. H. Individual optimization of clutch size in
414 great tits. *Nature* **336**, 160–162 (1988).
- 415 10. Wilson, A. J. & Nussey, D. H. What is individual quality? An evolutionary perspective.
416 *Trends Ecol. Evol.* **25**, 207–214 (2010).
- 417 11. Descamps, S., Gaillard, J.-M., Hamel, S. & Yoccoz, N. G. When relative allocation
418 depends on total resource acquisition: implication for the analysis of trade-offs. *J. Evol.*
419 *Biol.* **29**, 1860–1866 (2016).
- 420 12. Kirkwood, T. B. L. & Austad, S. N. Why do we age? *Nature* **408**, 233–238 (2000).
- 421 13. Reznick, D. Costs of Reproduction : An Evaluation of the Empirical Evidence. *Oikos* **44**,
422 257–267 (1985).
- 423 14. Zera, A. J. & Harshman, L. G. The physiology of life history trade-offs in animals. *Annu.*
424 *Rev. Ecology Syst.* **32**, 95–126 (2001).
- 425 15. Santos, E. S. A. & Nakagawa, S. The costs of parental care: a meta-analysis of the
426 trade-off between parental effort and survival in birds. *J. Evol. Biol.* **25**, 1911–1917
427 (2012).
- 428 16. Cohen, A. A., Coste, C. F. D., Li, X.-Y., Bourg, S. & Pavard, S. Are trade-offs really the
429 key drivers of ageing and life span? *Funct. Ecol.* **34**, 153–166 (2020).
- 430 17. Healy, K., Ezard, T. H. G., Jones, O. R., Salguero-Gómez, R. & Buckley, Y. M. Animal
431 life history is shaped by the pace of life and the distribution of age-specific mortality and
432 reproduction. *Nat. Ecol. Evol.* **3**, 1217–1224 (2019).
- 433 18. Pujol, B. *et al.* The Missing Response to Selection in the Wild. *Trends Ecol. Evol.* **33**,
434 337–346 (2018).

- 435 19. Gingerich, P. D. Rates of Evolution. *Annu. Rev. Ecol. Evol. Syst.* **40**, 657–675 (2009).
- 436 20. Postma, E., Visser, J. & Van Noordwijk, A. J. Strong artificial selection in the wild results
437 in predicted small evolutionary change: Evolution is predictable, also in the wild. *J. Evol.*
438 *Biol.* **20**, 1823–1832 (2007).
- 439 21. Coulson, J. C. & Fairweather, J. A. Reduced reproductive performance prior to death in
440 the Black-legged Kittiwake: senescence or terminal illness? *J. Avian Biol.* **32**, 146–152
441 (2001).
- 442 22. Rattiste, K. Reproductive success in presenescent common gulls (*Larus canus*): the
443 importance of the last year of life. *Proc. R. Soc. Lond. B Biol. Sci.* **271**, 2059–2064
444 (2004).
- 445 23. Hammers, M., Richardson, D. S., Burke, T. & Komdeur, J. Age-Dependent Terminal
446 Declines in Reproductive Output in a Wild Bird. *PLoS ONE* **7**, e40413 (2012).
- 447 24. Smith, H. G., Kallander, H. & Nilsson, J.-A. The Trade-Off Between Offspring Number
448 and Quality in the Great Tit *Parus major*. *J. Anim. Ecol.* **58**, 383–401 (1989).
- 449 25. Conrad, K. F. & Robertson, R. J. Intra-seasonal effects of clutch manipulation on parental
450 provisioning and residual reproductive value of eastern phoebes (*Sayornis phoebe*).
451 *Oecologia* **89**, 356–364 (1992).
- 452 26. Reid, W. V. The cost of reproduction in the glaucous-winged gull. *Oecologia* **74**, 458–
453 467 (1987).
- 454 27. Kalmbach, E., Griffiths, R., Crane, J. E. & Furness, R. W. Effects of experimentally
455 increased egg production on female body condition and laying dates in the great skua
456 *Stercorarius skua*. *J. Avian Biol.* **35**, 501–514 (2004).
- 457 28. Järvistö, P. E., Calhim, S., Schuett, W., Velmala, W. & Laaksonen, T. Sex-dependent
458 responses to increased parental effort in the pied flycatcher. *Behav. Ecol. Sociobiol.* **70**,
459 157–169 (2016).
- 460 29. Daan, S., Dijkstra, C. & Tinbergen, J. M. Family planning in the kestrel (*Falco*
461 *Tinnunculus*): The ultimate control of covariation of laying date and clutch size.
462 *Behaviour* **114**, 1–4 (1990).

- 463 30. Verhulst, S. & Tinbergen, J. M. Experimental Evidence for a Causal Relationship
464 between Timing and Success of Reproduction in the Great Tit *Parus M. major*. *J. Anim.*
465 *Ecol.* **60**, 269–282 (1991).
- 466 31. Lemaître, J.-F. *et al.* Early-late life trade-offs and the evolution of ageing in the wild.
467 *Proc. Biol. Sci.* **282**, 20150209–20150209 (2015).
- 468 32. Viechtbauer, W. Conducting meta-analyses in R with the metafor package. *J. Stat.*
469 *Softw.* **36**, 1–48 (2010).
- 470 33. R Development Core Team. *R: A Language and Environment for Statistical Computing*.
471 (R Foundation for Statistical Computing, 2009).
- 472 34. Rubolini, D., Liker, A., Garamszegi, L. Z., Møller, A. P. & Saino, N. Using the birdtree.org
473 website to obtain robust phylogenies for avian comparative studies: A primer. *Curr. Zool.*
474 **61**, 959–965 (2015).
- 475 35. Nakagawa, S. & Santos, E. S. A. Methodological issues and advances in biological
476 meta-analysis. *Evol. Ecol.* **26**, 1253–1274 (2012).
- 477