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► **To cite this version:**

Josefa Bleu, Marlène Gamelon, Bernt-Erik Saether. Reproductive costs in terrestrial male vertebrates: insights from bird studies. *Proceedings of the Royal Society B: Biological Sciences*, 2016, 283 (1823), 10.1098/rspb.2015.2600 . hal-02635503

HAL Id: hal-02635503

<https://hal.inrae.fr/hal-02635503>

Submitted on 7 Dec 2023

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1 **Reproductive costs in terrestrial male vertebrates: what can we**
2 **learn from birds?**

3
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16
17 **Running title:** Reproductive costs in males

18

19

20 Abstract

21 Reproduction requires resources that cannot be allocated to other functions resulting in direct
22 reproductive costs, i.e. trade-offs between current reproduction and subsequent
23 survival/reproduction. In wild vertebrates, direct reproductive costs have been widely
24 described in females, but their occurrence in males remains to be explored. To fill this gap, we
25 gathered 53 studies on 48 species testing direct reproductive costs in male vertebrates. We
26 found a trade-off between current reproduction and subsequent performances in 29% of the
27 species and in every taxa. As 73% of the studied species are birds, we focused on that class to
28 investigate whether such trade-offs are associated with i) levels of paternal care, ii) polygyny
29 or iii) pace of life. More precisely for this third question, it is expected that fast species (i.e.
30 short lifespan, early maturity, high fecundity) pay a cost in terms of survival whereas slow
31 species (with opposite characteristics) in terms of fecundity. Our findings tend to support this
32 hypothesis. Finally, we pointed out the potential confounding effects that should be accounted
33 for when investigating reproductive costs in males and strongly encourage the investigation of
34 such costs in more taxa to understand to what extent our results are relevant for other
35 vertebrates.

36

37 **Keywords:** Costs of reproduction, Generation time, Life history, Paternal care, Polygyny,
38 Trade-off, Vertebrates

39

40 1. Introduction

41 Trade-offs, resulting from constraints on the evolution of linked traits, play a central
42 role in life history theory [1]. According to the principle of allocation [2], individuals allocate
43 their limited amount of resources to a function at the cost of other ones. Therefore, the
44 maximum fitness an individual can reach is limited by trade-offs among fitness components.
45 The theory about reproductive trade-offs, first formalized by Williams [3], suggested that, as
46 reproduction is energy-demanding, individuals should trade current reproduction versus future
47 reproduction via reduced future fecundity (i.e., fecundity costs of reproduction) and/or
48 reduced future survival (i.e., survival costs of reproduction) [1,4]. However, as formulated by
49 the van Noordwijk and de Jong's model [5], even if two traits compete for the same resource
50 at the individual level, such a negative trade-off can remain undetected at the population level,
51 because individuals can differ in both resource acquisition and resource allocation to each trait
52 depending on the quality of their habitat or on their own quality.

53 Nearly 50 years after Williams's publication [3], studies investigating costs of
54 reproduction have flourished. Stearns reviewed studies investigating the effects of
55 reproduction on growth, parental survival, late fecundity and longevity in a wide range of taxa
56 and with different methods, including laboratory experiments, unmanipulated and
57 manipulated field populations [1]. More recently, studies investigating specifically direct
58 reproductive costs in wild mammals, i.e. the co-variations between current reproduction (at
59 time t) and subsequent reproduction and/or survival (at time $t+1$), have been reviewed [6].
60 Interestingly, most of the studies gathered in this review focused on females [6]. There have
61 in fact been considerably fewer attempts to assess trade-offs among fitness components in
62 wild males. This bias may be in part explained by methodological problems, i.e. it is often
63 more difficult to assess reproductive effort in wild males than females [7]. Also, while it has

64 become an accepted notion that reproduction is costly for males as well [8–10], studies
65 dealing with costs of reproduction in males are often rooted in the theory of sexual selection
66 and therefore refer to the cost of producing or maintaining sexual traits on future survival [8]
67 (see [11] for a recent review on the relationship between strength of sexual selection and age-
68 specific survival patterns across vertebrates). Investigating reproductive costs in males,
69 specifically through the co-variations between life history traits (also called direct fitness
70 traits *sensu* Roff [4], i.e. fecundity and survival) can be important because such costs that are
71 expressed at the individual level may also have implications at the population level [12].
72 Thus, in the perspective of the development of more realistic population models that include
73 both females and males, a better understanding of constraints shaping fitness traits in males
74 appears important.

75 In a broad evolutionary context, theory predicts that i) the intensity of mating
76 competition in polygynous species should translate into higher costs of reproduction for males
77 compared to socially monogamous species [13]. At the same time, ii) species characterized
78 with high level of paternal care are expected to be the ones with the highest reproductive
79 costs, as parental care is energy-demanding [3,14,15]. While a high level of polygyny or
80 paternal care is expected to be costly for males, such costs of reproduction can also strongly
81 depend upon the position of the species on the fast-slow continuum of life history variation
82 [16,17]. Indeed, the recent extension of the van Noordwijk and de Jong’s model [5] predicts
83 that reproductive costs are closely linked to the position of a given species on the fast-slow
84 continuum [6], that contrasts fast species with early maturity, high fecundity, and short
85 lifespan, to slow species with opposite characteristics (see [18] for a recent review). Briefly,
86 iii) fast species characterized with high variance in survival and low variance in reproduction
87 should exhibit survival costs of reproduction, whereas slow species should rather suffer from

88 fecundity costs. While this evolutionary model has been first supported in female mammals
89 [6], its validity for male vertebrates remains to be investigated.

90 In this review, we summarize the empirical tests of reproductive trade-off between two
91 breeding seasons in males in unmanipulated wild terrestrial and seasonally reproducing birds,
92 mammals, squamates and amphibians (figure S1 and ESM1). We choose to focus on these
93 taxa because most of the long-term individual based field studies, essential in this context, are
94 done on these species [19]. Experimental approaches have been useful tools to study trade-
95 offs and to show relationship of causality [20]. Thus, numerous studies have investigated
96 costs of reproduction in males from experimental field populations, by assessing for instance
97 the effect of brood size manipulation in birds (i.e., reduced or enlarged) on subsequent
98 survival and/or reproduction (e.g. [21,22] for reviews of experimental studies). However, as
99 we aim here to report tests of direct reproductive costs with potential demographic
100 consequences, we focus our literature survey on males of unmanipulated wild populations.
101 Then, we compare the occurrence of direct costs of reproduction between taxa and species. As
102 most of the gathered studies in our review use birds as case studies, we focus on that taxon to
103 question the link between direct costs of reproduction and i) level of polygyny, ii) level of
104 paternal care, and iii) pace of life (i.e. the position on the fast-slow continuum). Moreover, we
105 discuss possible biases of correlative studies in the wild with regard to identifying
106 reproductive costs in males. Finally, we discuss the implication of our results for the other
107 taxa of terrestrial vertebrates and suggest some future lines of research. In particular, we
108 encourage the inclusion of trade-offs between fitness-related traits in males into demographic
109 models of population growth to better predict the fate of wild vertebrate populations.

110

111 2. Tests of direct costs of reproduction in males

112 We gathered 53 studies on 48 vertebrate species investigating the co-variations
113 between current (t) reproduction and subsequent ($t+1$) reproduction/survival (search protocol
114 in ESM2, results of the literature search in table S1). It is noteworthy that the most
115 represented class is the bird one with 35 species for which such co-variations have been
116 investigated. We found only 7 mammalian species, 4 squamate species and 2 amphibian
117 species. In total, we reported 116 co-variations (including one non-informative co-variation)
118 between reproductive trait at t and reproduction/survival at $t+1$ (tables S1 and S2, figure 1).

119 Because of high variability of traits considered at t in the reviewed studies (table S1),
120 we summarized them into 6 types of traits namely “number of young” (e.g. when clutch size
121 has been considered as a reproductive trait at t), “breeding status” (e.g. comparison of
122 subsequent performances of breeders vs. non breeders), “mating” (e.g. number of matings),
123 “paternal care” (e.g. a measure of feeding rate), “timing” (e.g. comparison of early vs. late
124 breeders) and “number of breeding” (e.g. number of broods produced). In 74% of the co-
125 variations (i.e. 85/115), the number of young produced or breeding status was used to assess
126 reproductive effort at time t (table S2). The use of breeding status as a trait at t means that
127 direct costs of reproduction are investigated through the comparison of subsequent
128 performances of breeders (or successful breeders) with subsequent performances of non-
129 breeders (or failed breeders) (table S1). Thus, negative co-variations between current
130 reproduction and subsequent performances, i.e. when non-breeders at t (or failed breeders at t)
131 outperformed breeders at t (or successful breeders at t) the subsequent breeding season ($t+1$),
132 suggest the existence of direct costs of reproduction. Reproductive traits linked to the level of
133 paternal care, the timing of breeding, the number of matings or the number of breeding may
134 be difficult to measure in the field and are specific of the ecology/reproductive cycle of each
135 species. That can explain why these traits are less often used in the reviewed studies (table
136 S2). For example, in the black grouse (*Tetrao tetrix*), a lekking species for which the amount

137 of paternal care is absent, the authors used the number of matings as a reproductive trait at
138 time t [23].

139 Negative co-variations between reproduction at t and survival or reproduction at time
140 $t+1$ were detected in 29% of the reported species (table S1). Despite the low number of
141 studies on some taxa, it seems that males of all the taxa have equal probability to exhibit
142 direct costs of reproduction (figure 1, table S3). More precisely, these costs correspond to 16
143 negative co-variations between life history traits among the 115 co-variations reported (tables
144 S1 and S2). Interestingly, even if the traits “breeding status” and “matings” have a tendency to
145 be more frequently involved in such negative co-variations, there is no significant effect of the
146 types of trait considered at t on the probability to detect reproductive costs (tables S2 and S4).
147 Therefore, breeding (or successfully breeding) in a given breeding season may negatively
148 affect male survival to the next breeding season (this is the case for 3 species out of 21) and
149 may also affect reproduction (for 4 out of 15 species) (table S2). Similarly, for some species, a
150 high number of young, of paternal care, of matings or of breeding reduces male survival or
151 reproduction the next breeding season (table 1). Moreover, the probability to find a negative
152 co-variation in a study does not depend on the number of co-variations tested (table S5) or the
153 number of types of traits tested neither (table S6), suggesting that the differences in sample
154 sizes between studies do not bias our results.

155 Regarding traits considered at $t+1$, 57% of the studies investigated only survival costs,
156 34% both survival and fecundity costs, and only 9% investigated fecundity costs alone (table
157 S1). Interestingly, no study investigating both types of costs provided support for both. For
158 instance, in Laysan albatross (*Phoebastria immutabilis*) or Nazca booby (*Sula granti*), male
159 breeders (or successful breeders) can pay a cost in terms of survival to the next breeding
160 season but not in terms of fecundity (i.e. probability to reproduce given survival) [24,25]. In
161 king penguin (*Aptenodytes patagonicus*), Southern giant petrel (*Macronectes giganteus*) and

162 spotted owl (*Strix occidentalis*), the effect was opposite: breeding affected future breeding
163 probability but not survival [26–28]. Similarly, in great reed warbler (*Acrocephalus*
164 *arundinaceus*), there is a cost of paternal care on future reproduction (timing of settlement)
165 but no detectable cost on survival [29]. This stresses the importance to study both fecundity
166 costs of reproduction and survival costs of reproduction.

167

168 3. Reproductive costs in male birds and their link with paternal care, 169 polygyny and pace of life

170 For some species, negative co-variation between reproduction at time t and subsequent
171 reproductive performance occurred, whereas for others species, the co-variation was null or
172 positive (figure 1). These differences among species may be explained by differences in
173 mating systems, levels of paternal care or pace of life resulting in different life history
174 strategies. Indeed, we expect higher costs for males in polygynous mating systems, or when
175 males invest more in paternal care. Moreover, as highlighted for female mammals, a close
176 relationship between pace of life and the type of direct reproductive costs detected may be
177 expected, i.e. fast species should be affected by survival costs of reproduction whereas slow
178 species by fecundity costs of reproduction [6]. Generation time provides a relevant measure to
179 rank the species on the fast-slow continuum [17]. Therefore, we expect an increase of the
180 probability to find a fecundity cost of reproduction compared to the probability to find a
181 survival cost of reproduction with longer generation times.

182 We chose to test these predictions only for male birds because 73% of the species in
183 the reviewed studies are birds. Moreover, the different bird species gathered in this review
184 exhibit a wide range of avian life histories along the fast-slow continuum, diverse mating
185 systems and levels of paternal care which is essential to test these three hypotheses. More

186 precisely, 11 studies revealed direct costs of reproduction in males (7 found survival costs and
187 4 fecundity costs of reproduction) among the 35 different bird species we gathered (table S1).
188 For most species, a score of paternal care and polygyny was available from the literature [30]
189 (see table 1 for details on score calculation) and, for each species, the generation time (in
190 years) was retrieved from species specific demographic studies (table 1). We found that the
191 probability to observe a cost of reproduction in one species did not depend on the level of
192 polygyny (table S7.A) or the level of paternal care (table S7.B). Thus, with the current
193 dataset, there is no evidence that species suffering from direct reproductive costs are the ones
194 with the highest levels of paternal care or polygyny. However, as expected, species suffering
195 from fecundity costs of reproduction have longer generation times than species suffering from
196 survival costs of reproduction, except for one outlier, the Laysan albatross [25] (figure 2).
197 This result tends to support a relationship between the pace of life and reproductive costs [6].
198 It remains to see from studies in other taxa whether this is a general pattern in vertebrates.

199 The results of these statistical comparisons should be considered with some caution.
200 First, the power of our tests may be low due to the number of studies that include data on
201 costs of reproduction. Second, the levels of polygyny, of paternal care and the generation
202 times were calculated at the species level. However, it is true that some variation in these
203 variables can exist among populations of the same species [31–33] and even among
204 individuals within a population [e.g. for paternal care 34]. As a consequence, investigating the
205 relationship between reproductive trade-offs and levels of paternal care, polygyny or pace of
206 life measured at different levels of biological organization (such as at the population level)
207 may be really interesting. It is noteworthy that in this review, we reported opposite results in
208 terms of reproductive costs in two populations of the same species, the willow tit (*Parus*
209 *montanus*). In one of them, survival costs of reproduction have been detected [35] but not in
210 the other one [36]. Whether these two populations differ in their level of paternal care,

211 polygyny or pace of life and whether these differences are translated into different costs of
212 reproduction remain to be explored.

213

214 4. Negative, positive or null co-variations between current 215 reproduction and subsequent performances and the detection of 216 reproductive costs

217 We reported 14% of negative co-variations between current reproduction and
218 subsequent performances and also 58% of null and 28% of positive co-variations (figure 1).
219 The high proportions of null and positive co-variations may partly explain why studies
220 dealing with reproductive costs are often oriented towards females in the literature.

221 A negative co-variation between current reproduction and subsequent performances
222 may indicate that males trade their current reproduction versus their subsequent performances
223 and thus that males suffer from direct reproductive costs [3]. However, this pattern may be
224 more complex. In mating systems where males and females interact, the investment of one
225 sex in a current reproductive event may depend on the characteristics of the other sex. For
226 instance, the theory of differential allocation predicts that a mate may invest more or less in
227 reproduction when paired with their preferred mate (or with high quality mate) [positive or
228 negative differential allocation: 37]. This pattern can create positive or negative correlations
229 between life history traits for males that are driven by females' investment in reproduction
230 and that are not linked to male reproductive costs. However, because positive differential
231 allocation seems more frequent than negative differential allocation (at least in birds [38]), it
232 should be rare to find a negative co-variation between male life history traits in absence of
233 real reproductive costs for males.

234 A null or a positive co-variation between current reproduction and subsequent
235 performances may indicate the absence of direct reproductive costs in males. Again,
236 interaction between the sexes may drive this pattern, for example if the absence of
237 reproductive costs in males is correlated to the presence of such costs in females. Such
238 correlations may depend on how strong the sexual conflict over parental investment is and
239 how it is resolved in each species [30,39]. Therefore, it would be particularly interesting to
240 compare both males and females in the same study. Moreover, it is noteworthy that males that
241 do not exhibit direct reproductive costs may pay a cost later in life [40], or may suffer from
242 other types of costs, such as inter-generational or cumulative costs of reproduction (see
243 ESM1).

244 Remarkably, null or positive co-variations between current reproduction and
245 subsequent performances may be found even if direct reproductive costs are present. First, in
246 certain cases, individuals that try to reproduce but do not succeed to sire offspring may pay
247 quite similar fitness costs than successful breeders. This could be more important in males
248 than females because typically males can invest large amount of energy prior to mating (e.g.
249 actively searching for mates, trying to defend a territory, injuries during combat) without
250 managing to successfully sire offspring [7]. Also, brood loss may happen late in the season or,
251 at least, after that most of the energy allocated for reproduction has already been invested in
252 the current reproductive event. Therefore, in these cases, one will fail to detect any difference
253 in terms of future survival and/or reproduction between breeders (or successful breeders) and
254 non-breeders (or failed breeders) even if direct costs of reproduction occur. Second, the
255 detection of reproductive costs may be masked by phenotypic differences in individual
256 quality. Indeed, in case of high variance in resources acquisition, individuals able to acquire
257 more resources (i.e. high quality individuals) are also able to allocate more resources than
258 other individuals to both current reproduction and future survival and/or reproduction, which

259 can prevent the detection of costs of reproduction at the population level [5]. These limitations
260 due to individual heterogeneity explain in part why experimental studies have been widely
261 used to study trade-offs [e.g. 22]. However, studies of unmanipulated wild populations are
262 still essential to understand the ecological consequences of life history variations and to obtain
263 realistic estimates of demographic parameters [19]. Thanks to the development of appropriate
264 statistical tools, accounting for individual heterogeneity is possible, making the correlative
265 studies more powerful [6,41]. Yet, it is likely that among the high proportion of studies that
266 reported no negative co-variation between current reproduction and subsequent performances,
267 some of them actually concluded to the absence of direct costs of reproduction even if they
268 occurred in the considered species.

269 More generally, it is also possible that some studies may fail to detect negative co-
270 variation between reproduction at time t and survival/fecundity at time $t+1$, even if there are
271 some real costs of reproduction, because appropriate co-factors are not taken into account. For
272 example, differences in individual quality may be more pronounced in years with harsher
273 environmental conditions when resources are more limited, resulting in annual variations in
274 trade-off detection [e.g. 24,42]. Accounting for age-effects may also be recommended while
275 investigating direct reproductive costs. Indeed, reproductive performances may be age-
276 specific, with for example lower reproductive output at old ages compared to younger ages
277 due to senescence [43,44], or at the opposite lower reproductive output at young ages due to
278 inexperience [45], possibly preventing the detection of reproductive costs. Carefully
279 disentangling the age effects from the costs of previous reproduction appears crucial.
280 Moreover, it is also important to keep in mind that the age of the individuals can mediate the
281 trade-offs between current reproduction and subsequent reproduction and/or survival. In other
282 words, reproductive costs themselves can be dependent on the age. For example, reproduction
283 can be more costly in young individuals [46] or on the contrary more costly in old individuals

284 [47], or appear more costly due to terminal investment [48]. Therefore, studies combining the
285 information of age effects and life history trade-offs should be developed to strengthen
286 comparative studies and to improve our general understanding of such patterns.

287 Finally, in many of the studies included in the present review, it is assumed that the
288 social and genetic father is the same. In birds for instance, the number of eggs/chicks present
289 in the nests is used as an estimator of male reproductive success. However, thanks to
290 molecular genetic tools, it is now accepted that, even in socially monogamous species,
291 individuals can engage in extra-pair copulations [14,49]. In particular, males involved in such
292 extra-pair copulations can increase their reproductive success without increasing their amount
293 of paternal care. This means that some traits measured at time t may be more or less
294 correlated to the reproductive success and the paternal investment of the males. For example,
295 certainty of paternity has been shown to covary with paternal care in birds [50]. Thus, even if
296 a male has a large clutch, its investment may be low if some chicks are sired by a different
297 male. This is why the quantification of extra-pair paternity can allow more precise
298 measurement of reproductive effort, which may allow highlighting different relationships
299 between reproduction at time t and fitness-related trait at $t+1$.

300

301 5. Conclusion and perspectives

302 In this review, we gathered studies exploring the co-variations between current
303 reproduction and subsequent reproduction and/or survival of wild unmanipulated terrestrial
304 male birds, mammals, squamates and amphibians. It is noteworthy that our review reports
305 some studies highlighting positive co-variations between life history traits, suggesting that the
306 individual quality hypothesis is often supported in male vertebrates. But we also found
307 empirical evidence of direct reproductive costs in several species, belonging to all taxa, even

308 with the inherent difficulties of correlative studies. It is thus obvious that direct reproductive
309 costs concern both males and females in wild populations.

310 We showed that the occurrence of reproductive costs in males is not correlated to
311 polygyny and levels of paternal care but is associated with pace of life, in birds at least.
312 Unfortunately, the small number of studies in the other taxa did not allow us testing our
313 evolutionary hypotheses in other terrestrial vertebrates. However, we are confident that our
314 results, drawn from birds, may also be relevant to other taxa. Indeed, after some evidence of a
315 link between pace of life and costs of reproduction in female mammals [6], our review
316 provides support for that life-history model in male birds. Yet, exploring to what extent such a
317 model can be generalized to all terrestrial vertebrates, and, in particular, unravelling the
318 factors that may explain variations among taxa remain an exciting challenge. For example, in
319 line with a comparative study that has shown that birds have a slower life-history than
320 mammals for the same body mass [51], one could expect different relationships between pace
321 of life and costs of reproduction in males in these two taxa. Another important difference
322 within vertebrates is the mode of temperature regulation. Indeed, ectotherms can store energy
323 more efficiently than endotherms like birds, and thus rely more often on stored resources to
324 fuel reproduction (capital vs. income breeders) [52]. Such different reproductive strategies
325 may induce different reproductive costs. Thus, we strongly encourage further studies in more
326 taxa with diverse mating systems and life history strategies to be able to broaden these results.

327 Correlations between life history traits and in particular, reproductive trade-offs, can
328 have demographic consequences and can influence population dynamics [53]. It is true that
329 most models in population dynamics are female-based and neglect males [54] but there is now
330 growing evidence that males may markedly influence population dynamics as well (e.g.
331 [55,56]). While methodological developments now provide the tools to integrate costs of
332 reproduction into population models [53,57], a promising avenue of research could be to take

333 into account reproductive costs in males as well as females into population dynamic models.
334 Even if all models are approximations, capturing the fluctuation of demographic parameters
335 and accounting for it into population models is the best way to provide sustainable and
336 relevant management and conservation scenarios.

337

338 **Data accessibility**

339 The datasets supporting this article are in tables 1 and S1.

340 **Competing interests**

341 We have no competing interests.

342 **Authors' contributions**

343 JB and MG proposed the study and performed the literature search; JB, MG and BES wrote
344 the paper.

345 **Acknowledgments**

346 We thank Andras Liker and Tamas Szekely for sharing data on paternal care in birds. We
347 warmly thank Jean-François Lemaître, Irja Ida Ratikainen, Per Lundberg and three
348 anonymous referees for their helpful comments on a previous draft.

349 **Funding**

350 This work was supported by the European Research Council (grant STOCHPOP to BES) and
351 by the Research Council of Norway through its Centres of Excellence funding scheme,
352 project number 223257.

353

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- 566

567 **Table 1. Scores of paternal care, polygyny and pace of life.** Details on the bird species for which direct reproductive costs have been tested in
568 males. We present their order and family, and their associated scores of paternal care and polygyny. These scores were calculated by Olson et al.
569 [30]. Briefly, the method to calculate the score of paternal care consists in scoring paternal investment in 5 different activities: nest building,
570 incubation, brooding, chick feeding, and chick defence. For each activity, the participation of males was scored on a 5-points scale: 0 (no male
571 care), 1 (1–33% male care), 2 (34–66% male care), 3 (67–99% male care) or 4 (100% male care). Thus the maximum score for each species is 20.
572 The score of polygyny represents the percentage of males exhibiting polygyny, with: 0 (no polygyny or less than 0.1% of individuals), 1 (rare
573 polygyny: 0.1–1%), 2 (uncommon polygyny: 1–5%), 3 (moderate polygyny: 5–20%) and 4 (common polygyny, greater than 20%). Generation
574 time (in years), a measure ranking the species on the fast-slow continuum, was extracted from Birdlife International database
575 (<http://www.birdlife.org/datazone/home>). The column “*Negative co-variation?*” indicates whether at least one negative co-variation between
576 reproduction at t and fecundity (“ F ”) and/or survival (“ S ”) at $t+1$ was found for the considered species or not (“ N ”).

Species	Order	Family	Paternal care	Polygyny	Generation time	Negative co-variation?	Ref.
Barn swallow (<i>Hirundo rustica</i>)	Passeriformes	Hirundinidae	7	1	3.9	N	[58]
Barnacle goose (<i>Branta leucopsis</i>)	Anseriformes	Anatidae	6	0	10.5	N	[59]
Black grouse (<i>Tetrao tetrix</i>)	Galliformes	Phasianidae	0	4	6.4	N	[23]
Blue tit (<i>Cyanistes caeruleus</i>)	Passeriformes	Paridae	4	3	4.4	N	[60]
Brown Thornbill (<i>Acanthiza pusilla</i>)	Passeriformes	Acanthizidae	4**	NA	5.7	N	[61]
Cliff swallow (<i>Petrochelidon pyrrhonota</i>)	Passeriformes	Hirundinidae	10	0	4.3	S	[62]

Collared Flycatcher (<i>Ficedula albicollis</i>)	Passeriformes	Muscicapidae	4	3	3.9	N	[63]
Crested tit (<i>Parus cristatus</i>)	Passeriformes	Paridae	2	0	4	N	[35]
Great reed warbler (<i>Acrocephalus arundinaceus</i>)	Passeriformes	Sylviidae	6	2	4.2	F	[29]
Great tit (<i>Parus major</i>)	Passeriformes	Paridae	4	1	4.3	N	[64,65]
Greater prairie-chicken (<i>Tympanuchus cupido</i>)	Galliformes	Phasianidae	0	4	5.5	N	[66]
Green-rumped Parrotlet (<i>Forpus passerinus</i>)	Psittaciformes	Psittacidae	2	0	4.1	N	[67]
Hawai'i 'Elepaio (<i>Chasiempis sandwichensis sandwichensis</i>)	Passeriformes	Monarchidae	NA	NA	5.9	N	[68]
House martin (<i>Delichon urbica</i>)	Passeriformes	Hirundinidae	10	0	4.3	N	[69]
Indigo bunting (<i>Passerina cyanea</i>)	Passeriformes	Cardinalidae	3	3	4.1	N	[70]
Jackdaw (<i>Corvus monedula</i>)	Passeriformes	Corvidae	NA	NA	7.4	N	[71]
King penguin (<i>Aptenodytes patagonicus</i>)	Ciconiiformes	Spheniscidae	6	0	12.7	F	[26]
Kittiwake gull (<i>Rissa tridactyla</i>)	Ciconiiformes	Laridae	10	0	12.9	N	[72,73]
Laysan albatross (<i>Phoebastria immutabilis</i>)	Procellariiformes	Diomedidae	NA	NA	28.5	S	[25]
Long-tailed tit (<i>Aegithalos caudatus</i>)	Passeriformes	Aegithalidae	NA	NA	4.2	N	[74,75]
Marsh tit (<i>Parus palustris</i>)	Passeriformes	Paridae	NA	NA	4.2	N	[76,77]
Monteiro's storm-Petrel (<i>Oceanodroma monteiroi</i>)	Procellariiformes	Hydrobatidae	NA	NA	16.5	N	[78]
Mountain white-crowned sparrow (<i>Zonotrichia leucophrys oriantha</i>)	Passeriformes	Fringillidae	2	2	4.3	S	[79]
Nazca booby (<i>Sula granti</i>)	Suliformes	Sulidae	NA	NA	10	S	[24]
Northern giant petrel (<i>Macronectes halli</i>)	Procellariiformes	Procellariidae	NA	NA	17	N	[27]

Oystercatcher (<i>Haematopus ostralegus</i>)	Charadriiformes	Haematopodidae	9	1	13.7	N	[80]
Savannah sparrow (<i>Passerculus sandwichensis</i>)	Passeriformes	Fringillidae	4	4	3.4	S	[81]
						N	[82]
Snowy Plover (<i>Charadrius nivosus</i>)	Ciconiiformes	Charadriidae	NA	NA	5	N	[83]
Southern giant petrel (<i>Macronectes giganteus</i>)	Procellariiformes	Procellariidae	NA	NA	21.3	F	[27]
Spotted owl (<i>Strix occidentalis</i>)	Strigiformes	Strigidae	4	0	10.1	F	[28]
Tengmalm's owl (<i>Aegolius funereus</i>)	Strigiformes	Strigidae	3	4	5.8	N	[84]
Tree swallow (<i>Tachycineta bicolor</i>)	Passeriformes	Hirundinidae	3	2	4	S	[42]
Wheatear (<i>Oenanthe oenanthe</i>)	Passeriformes	Muscicapidae	4**	NA	4.1	N	[85,86]
Willow ptarmigan (<i>Lagopus lagopus</i>)	Galliformes	Phasianidae	3	3	4.2	N	[87]
Willow tit (<i>Parus montanus</i>)	Passeriformes	Paridae	3	0	4.6	S	[36]
						N	[35]

577 ** Personal communication from Andras Liker and Tamas Szekely

578

579 **Figure captions**

580

581 **Figure 1. Distribution of the number of tested co-variations between current**

582 **reproduction and subsequent performances in male terrestrial vertebrates.** Number of

583 co-variations between reproduction at time t and survival/reproduction at time $t+1$ collected

584 in the literature in amphibians, birds, mammals and squamates.

585

586 **Figure 2. Types of direct costs of reproduction in male birds and pace of life.**

587 Differences in generation times (in years) between the bird species for which fecundity costs

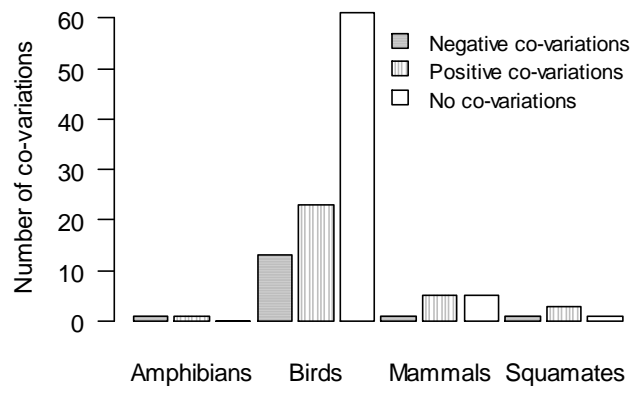
588 of reproduction (in blue) and survival costs of reproduction (in red) have been reported for at

589 least one reproductive trait. Dots represent the data points (see table 1).

590

591 **Figure 1**

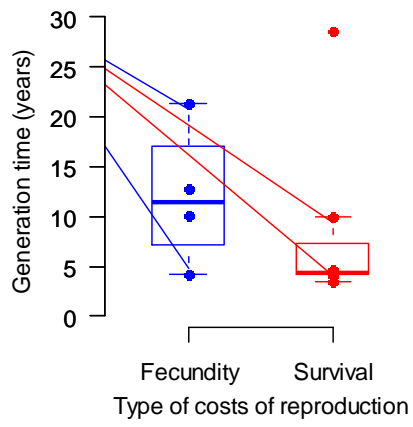
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593

594 **Figure 2**

595



596