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

3  
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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.

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353

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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]

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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

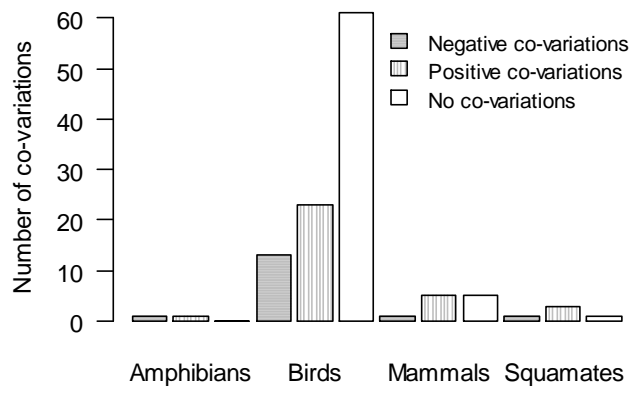
586 **Figure 2. Types of direct costs of reproduction in male birds and pace of life.**

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**

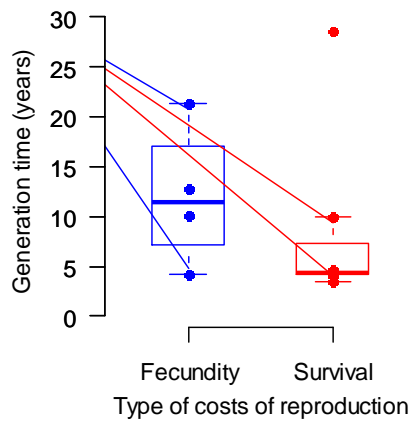
592



593

594 **Figure 2**

595



596