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1 **A review and perspective on context-dependent genetic effects of extra-pair mating in**
2 **birds**

3

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15

16 **Abstract**

17 The evolutionary origin and the maintenance of extra-pair mating in birds has been a major
18 field of study in the last decades, but no consensus has been reached on the adaptive
19 significance of this behaviour for female birds. The genetic benefit hypothesis proposes that
20 extra-pair sires provide alleles of superior quality and/or better compatibility compared to the
21 social mate, resulting in offspring of higher reproductive value. One frequently adopted
22 approach to test this idea compares the performance of maternal half-siblings in broods with
23 multiple paternity. However, results from such comparisons are inconsistent. Here I discuss the
24 idea that the magnitude of genetic fitness benefits from extra-pair mating depends on the
25 environmental context. Context-dependent genetic effects in maternal half-sibling comparisons
26 have been demonstrated for only five passerine bird species up to date. In none of the studies
27 were the crucial environmental conditions experimentally manipulated and the potentially
28 confounding effects of differential maternal investment in relation to paternity were mostly not
29 accounted for either. A number of high-quality data sets on fitness consequences of extra-pair
30 mating behaviour are available that could be (re-) analysed for context-dependence given
31 relevant gradients of the environment have been recorded and their use is well justified *a priori*.
32 Such relevant variation may include, for example, the time of breeding in temperate regions,
33 hatching order, but also offspring sex. Primarily, however, experimental approaches are
34 required that systematically and gradually vary fitness-relevant environmental gradients like
35 food availability or parasite abundance and analyse the resulting differential fitness effects
36 while controlling for differential investment. Context-dependence of genetic effects of extra-
37 pair mating behaviour may offer an opportunity for reconciling conflicting results from
38 different extra-pair paternity studies within and across species. More generally, it could allow
39 better understanding under which environmental conditions selection may act to maintain a
40 female mating bias towards extra-pair males with potentially far-reaching implications for the
41 ecology and evolution of mating preferences and the maintenance of genetic variation in
42 (sexually) selected traits.

43

44 **Keywords**

45 compatible genes; context-dependence; differential investment; extra-pair paternity; genotype-
46 by-environment interaction; good genes; fitness consequences; half-sibling comparison;
47 multiple mating.

48

49 **Introduction**

50 Extra-pair paternity (EPP) arises when female birds engage in extra-pair copulations (EPC)
51 with males other than their social mates, frequently resulting in broods with multiple paternity
52 which contain offspring sired by the social male (within-pair offspring, WPO) and offspring
53 sired by extra-pair males (extra-pair offspring, EPO). A large and solid body of evidence has
54 impressively demonstrated that EPP is the rule rather than the exception in birds (especially in
55 passerines), and a number of synthetic contributions have reviewed this field with its various
56 ramifications over the last two decades (e.g. Westneat et al. 1990; Birkhead and Møller 1992;
57 Petrie and Kempenaers 1998; Griffith et al. 2002; Westneat and Stewart 2003; Akçay and
58 Roughgarden 2007).

59 As EPP is so widespread and so common and because it must be considered a powerful
60 source of pre- as well as postcopulatory sexual selection, no comprehensive understanding of
61 avian mating systems and sexual selection in birds seems possible without understanding the
62 evolutionary causes and consequences of this phenomenon. However, despite the very
63 substantial research effort in the field, there is still no consensus on a number of fundamental
64 questions related to this topic. For example, there is sustained debate about which sex is
65 actually in control of EPC behaviour and, particularly, about the adaptive significance of extra-
66 pair mating behaviour for female birds (e.g. Griffith et al. 2002; Westneat and Stewart 2003;
67 Arnqvist and Kirkpatrick 2005; Griffith 2007; Akçay and Roughgarden 2007; Griffith and
68 Immler 2009). A number of different hypotheses have been put forward to explain why female
69 birds mate extra-pair, which are discussed in more detail in the reviews mentioned above. In
70 this contribution I will focus on the idea that has gained most attention and stimulated the most
71 intense and most controversial debate in the past, i.e. that genetic benefits from a mating bias
72 towards extra-pair sires select for extra-pair mating behaviour in females (for a more general
73 review and discussion of genetic benefit models of mate choice see e.g. Jennions and Petrie
74 2000; Mays and Hill 2004; Neff and Pitcher 2005).

75 After briefly introducing the genetic benefit hypothesis of extra-pair mating and the
76 advantages and potential problems of using maternal half-sibling comparisons to test it, I will
77 outline the idea that the magnitude of genetic benefits of extra-pair matings may depend on

78 environmental context and illustrate potential consequences for the evolution of female mating
79 preferences and the maintenance of genetic variation for traits under selection. Then I will
80 briefly summarise and review the main results of the few empirical studies that have
81 demonstrated context-dependent genetic effects of extra-pair matings and suggest potential
82 directions for future research in this field. In line with other recent conceptual contributions
83 (e.g. Greenfield and Rodriguez 2004; Bussière et al. 2008; Ingleby et al. 2010), this paper aims
84 at promoting an approach that puts work on sexual selection more explicitly into the ecological
85 context within which it operates.

86

87 **Genetic benefit hypothesis of extra-pair mating – good and/or compatible alleles**

88 The principal idea behind the genetic benefits hypothesis is that, by engaging in extra-pair
89 matings, females express a mating preference that is otherwise constrained, for example
90 because social monogamy precludes many females from mating with the few top genetic
91 quality males in a population or because the best social and the best genetic mate for any
92 individual female are not identical. This hypothesis therefore assumes that female birds have a
93 substantial degree of control over extra-pair fertilizations through either pre-copulatory extra-
94 pair mate choice and/or cryptic postcopulatory mechanisms that bias paternity in favour of
95 (particular) extra-pair sires. In the following, I will subsume both these possibilities under the
96 term "mating preference" (for extra-pair males), which does therefore not necessarily imply
97 classic precopulatory mate choice. A further assumption of the genetic benefit hypothesis is that
98 extra-pair mating behaviour is costly for females and needs to be balanced by some sort of
99 fitness benefit. This benefit may lie in the higher viability or fecundity and/or sexual
100 attractiveness of offspring sired through EPCs with males that are of higher genetic quality or
101 of better genetic compatibility compared to the respective social mate. The proposed genetic
102 benefits may therefore be assumed to be additive genetic (acquisition of "good alleles") or
103 represent non-additive effects presupposing an interaction of maternal and paternal genotype
104 (acquisition of "compatible alleles" sensu Kempenaers 2007, i.e. broadly defined as alleles that
105 increase fitness contingent on the genetic make-up of the choosing individual). Thus, a mating
106 preference for mates with compatible alleles may, for example, include biasing paternity to
107 maximise offspring heterozygosity, minimise the risk of close inbreeding, or optimise
108 immunogenetic complementarity. Both types of benefits are not mutually exclusive but could
109 also operate in concert.

110

111

112 **Revealing paternal genetic effects on offspring traits by maternal half-sibling comparisons**

113 The most straightforward test of the genetic benefit hypothesis of extra-pair mating is a
114 comparison of the performance of maternal half-siblings from multiply sired broods (Sheldon et
115 al. 1997). Here, potentially confounding, non-genetic effects of a common environment of sire
116 and offspring as well as maternal effects on offspring fitness-related traits are controlled for
117 (but see paragraph on differential maternal investment below). Maternal half-siblings share, by
118 definition, on average half of their maternally inherited nuclear genes and experience the same
119 early environment, including, for example, the same parenting skills of the respective social
120 parents or exposure to the same parasite load in the shared nest. Therefore, any systematic
121 differences in phenotypic traits between the two maternal half-siblings can only be attributed to
122 the differential paternal genetic contribution (differential paternity hereafter) of the respective
123 genetic sires. A consistently superior performance of EPO compared to their WPO maternal
124 half-siblings is thus considered strong evidence in favour of the genetic benefit hypothesis
125 (Sheldon et al. 1997; Griffith et al. 2002). In principal, this statement is true regardless of
126 whether the proposed genetic benefits are assumed to represent additive or non-additive effects
127 (but see Griffith and Immler 2009).

128

129 **Extra-pair paternity and genetic benefits – inconsistent results**

130 Evidence for a genetic type of benefit based on maternal half-sibling comparisons is rather
131 mixed across studies. Some highly cited landmark studies spectacularly support the genetic
132 benefit hypothesis. For example, in Collared Flycatchers *Ficedula albicollis*, EPO were in
133 better body condition near fledging compared to their maternal half-siblings (Sheldon et al.
134 1997), and nestling condition has been shown to positively affect recruitment in this species
135 (Lindén et al. 1992). Furthermore, the difference in mean body condition between half-siblings
136 was predicted by the difference in size of an at least partly intersexually selected male ornament
137 of the respective sires (the white forehead patch, Sheldon et al. 1997). In Bluethroats *Luscinia*
138 *svecica*, EPO nestlings showed better cellular immunocompetence than their maternal and,
139 notably, also their paternal half-siblings, suggesting not only a genetic benefit from an extra-
140 pair mating preference, but also an interaction effect of maternal and paternal genotype on
141 offspring immunocompetence (Johnsen et al. 2000; see also Fossøy et al. 2008). Strong support
142 in favour of the genetic benefit hypothesis of extra-pair mating also comes from a study in the
143 Blue Tit *Cyanistes caeruleus*. Here, EPO sired by non-local extra-pair males showed higher
144 average heterozygosity compared to their maternal half-siblings and individual heterozygosity
145 was positively correlated with a number of fitness-related traits in both sexes (Foerster et al.

146 2003). In contrast to these findings, other studies failed to reveal any systematic differences in
147 maternal half-sibling performance, sometimes in the same or in closely related species (e.g.
148 Strohbach et al. 1998; Lubjuhn et al. 1999; Whittingham and Dunn 2001; Schmoll et al. 2003;
149 Edly-Wright et al. 2007; Rosivall et al. 2009; Dunn et al. 2009). Furthermore, application of
150 identical experimental protocols (e.g. the phytohemagglutinin test of cellular
151 immunocompetence) in different species with similar extra-pair mating systems produced
152 mixed results (Johnsen et al. 2000; Kleven and Lifjeld 2004; Kleven et al. 2006; Fossøy et al.
153 2008; Wilk et al. 2008; Forsman et al. 2008; Butler et al. 2009). The inconsistencies of results
154 across EPP studies may be caused by methodological challenges and/or reflect true and
155 meaningful differences in the respective study systems. In either case, it is important to address
156 this heterogeneity in order to evaluate how reproducible and how generalisable these results
157 may or may not be.

158

159 **Effect sizes of genetic benefits likely to be small**

160 The inconsistency of results across EPP studies may be related to the fact that additive genetic
161 fitness benefits from mate choice are likely to be small in general (e.g. Kirkpatrick and Barton
162 1997; Møller and Alatalo 1999; Arnqvist and Kirkpatrick 2005). Thus, even studies with
163 comparatively large sample sizes may fail to detect any effects of differential paternity on
164 offspring fitness due to a type II statistical error (accepting the null hypothesis when it is
165 wrong), which may contribute to the observed heterogeneity in results across EPP studies.
166 Given small expected effect sizes, the other side of the same coin is that studies actually
167 demonstrating differences in maternal half-sibling performance based on comparatively small
168 samples sizes may be prone to a type I statistical error (rejecting the null hypothesis when it is
169 true), potentially seconded by differential maternal investment in relation to paternity (see
170 below).

171 Recent conceptual contributions emphasize the potential of non-additive genetic
172 benefits from extra-pair mating (e.g. Kempenaers 2007; Griffith and Immler 2009). For
173 example, a number of studies have reported that EPO were more heterozygous than their WPO
174 maternal half-siblings (e.g. Foerster et al. 2003; Stapleton et al. 2007; Suter et al. 2007; Fossøy
175 et al. 2008; but see Wetzel and Westneat 2009) or that EPO not only outperformed their
176 maternal, but also their paternal half-siblings (Johnsen et al. 2000; Garvin et al. 2006),
177 suggesting non-additive rather than additive genetic benefits of extra-pair matings. However, a
178 recent meta-analytical approach revealed that effect sizes of heterozygosity-fitness correlations
179 are generally positive in sign, but not large either (Chapman et al. 2009). Accordingly, the

180 magnitude of non-additive fitness benefits to be potentially obtained through extra-pair mating
181 may be expected to be rather small, too. This may not be the case for all types of non-additive
182 genetic effects, however, for example if extra-pair mating helps preventing fertilisations which
183 would lead to a substantial fitness loss due to pronounced inbreeding (e.g. Keller 1998; Kruuk
184 et al. 2002) or outbreeding (Veen et al. 2001) depression.

185

186 **Differential maternal investment may confound paternal genetic effects**

187 Selection may favour females with the ability to bias resource allocation in favour of offspring
188 descending from preferred sires (Burley 1986; Møller and Thornhill 1998). If females
189 selectively favour their extra-pair offspring because their sires were of superior genetic quality,
190 superior EPO performance may at least partly be due to maternal rather than paternal genetic
191 effects. Thus, differential maternal investment with respect to paternity may have the potential
192 to confound paternal genetic effects on offspring fitness (Mousseau and Fox 1998; Møller and
193 Thornhill 1998). On the other hand, it can be argued that a biased investment in favour of EPO
194 may make a case for rather than against the genetic benefit hypothesis, since differential
195 investment solely depends on differential paternity (Sheldon 2000). This argumentation seems
196 less straightforward in light of recent studies suggesting that EPO occur earlier in the laying
197 order and, accordingly, in the hatching sequence than their WPO maternal half-siblings, giving
198 them a head start in sibling competition (e.g. Magrath et al. 2009; Ferree et al. 2010). For
199 example, Magrath et al. (2009) not only demonstrated that EPO hatch slightly earlier than
200 WPO, but also that statistically significant differences between maternal half-siblings in
201 morphology and survival until fledging tend to diminish once hatching sequence is statistically
202 controlled for. At present, it is unclear whether females time EPCs to occur early in their laying
203 phase, whether these sequence effects reflect mating effort patterns of social or extra-pair sires,
204 or whether they simply represent a by-product of social or ecological constraints on EPC
205 behaviour (discussed in Magrath et al. 2009). In any case, such effects have the potential to
206 confound paternal genetic effects on offspring fitness for both, additive as well as non-additive
207 genetic benefits, possibly leading to an overestimation of the effects of differential paternity.

208

209 **Context-dependent genetic benefits of mating preferences and their implications**

210 Another explanation for inconsistent results from maternal half-sibling comparisons may be
211 that the genetic benefits of extra-pair matings vary in magnitude in relation to the prevailing
212 environmental conditions (please note that, while in the compatible alleles model the genetic
213 background of a female may well be seen as an "environment" or a "context" within which

214 paternal alleles are expressed and with which they may interact, I reserve the use of these terms
215 for extra-genomic components of the environment). Benefits may be large enough to be
216 detectable in some ecological circumstances, but too small or non-existent in others. Such
217 context-dependent genetic effects presuppose temporal and/or spatial variation in the
218 environment - a ubiquitous feature in most natural bird populations. They also presuppose
219 genotypes to differ in how their fitness is affected by variation in the environment, i.e.
220 genotype-by-environment interactions for fitness must be present. If this is *not* the case, the
221 relative genetic benefit a female may obtain from choosing among different sires is identical
222 across environments (Fig. 1 a, b). However, whenever such genotype-by-environment
223 interactions exist, there is a potential for context-dependent genetic effects to occur (Fig. 1 c,
224 d). This refers to sire as well as offspring genotypes in the case of additive genetic effects, but
225 only to offspring genotypes in the case of non-additive genetic effects for which offspring
226 fitness is not normally a function of sire genotype but determined by the interaction of maternal
227 and sire genotype.

228 Two principal cases of genotype-by-environment interactions can be distinguished.
229 First, if fitness reaction norms do not cross and the fitness rank order of genotypes is preserved
230 across the environments that are experienced, context-dependent genetic effects will affect the
231 magnitude of the genetic benefit a female can potentially obtain, although not its sign (Fig. 1 c).
232 Single best male genotypes on the level of the population (in case of additive genetic effects) or
233 most compatible male genotypes on the level of the individual female (in case of non-additive
234 genetic effects) may exist and they are transient across these environments. Second, if fitness
235 reaction norms cross and the fitness rank order of genotypes is not preserved across the
236 environments that are experienced, context-dependent genetic effects will not only affect the
237 magnitude of the genetic benefit a female may obtain, but also its sign, rendering preferences
238 for particular sire genotypes adaptive in some of these environments, but not in others (Fig. 1 d,
239 also termed ecological cross-over). Here, no single best male genotypes on either the level of
240 the population or the level of the individual female do exist. Indeed, the terms "good alleles" or
241 "compatible alleles" in reference to any particular male genotype do not make sense under this
242 scenario. In both cases, however, context-dependent genetic effects suggest selection on female
243 mating preferences to vary across environments, which has interesting implications for the
244 evolution of mating preferences and the maintenance of genetic variation in traits that are under
245 sexual selection.

246 If relevant gradients of the environment that offspring will experience are fairly well
247 predictable, we may expect females to show phenotypically plastic instead of static mating

248 preferences (discussed in Qvarnström 2001). In the case of non-crossing fitness reaction norms,
249 they may be selected to balancing direct costs of choice against expected genetic rewards and
250 hence express any given preference more or less strongly depending on environmental
251 variation. In the case of additive genetic effects, the strength of sexual selection on preferred
252 male traits (secondary sexual characters and genetically correlated traits) will then vary
253 accordingly and episodes of relaxed selection could slow down the depletion of genetic
254 variance in these traits or even contribute to its maintenance by allowing more time for
255 deleterious mutations to occur. In the case of ecological cross-over, plastic preferences would
256 need to be reversed to be adaptive and would hence directly support maintenance of genetic
257 variation in male traits. If the environmental conditions that offspring will experience are
258 largely unpredictable, however, females may not benefit at all from expressing mating
259 preferences for any particular sire genotype. For example, in the case of ecological cross-over
260 in fitness, females have no means to evaluate the relative genetic quality of potential mates and
261 they may rather opt for genetic bet-hedging, mate multiply and thereby sample a number of
262 different sires in order to increase the within-cohort genetic diversity of their offspring (see
263 Yasui 1998 for more background on this argument and Schmolle et al. 2007 for an application to
264 extra-pair mating behaviour in birds).

265 Context-dependent genetic benefits from mate choice in general have been shown in a
266 range of taxa including insects (Jia and Greenfield 1997), anurans (Welch 2003; Sheldon et al.
267 2003), and mammals (Mills et al. 2007). Furthermore, context-dependent genetic benefits from
268 mate choice may be inferred from studies demonstrating genotype-by-environment interactions
269 on the expression of male sexual signal traits under directional intersexual selection (e.g.
270 Qvarnström 1999; Jia et al. 2000; David et al. 2000; Danielson-François et al. 2006; see also
271 Greenfield and Rodriguez 2004). In the following paragraph, I will apply the idea of context-
272 dependent genetic effects to extra-pair mating behaviour in birds and briefly review the few
273 studies that have suggested such effects up to date.

274

275 **Context-dependent genetic effects of extra-pair mating**

276 In order to demonstrate context-dependent additive genetic effects of extra-pair matings, it is
277 necessary to test for a two-way interaction effect of differential paternity and the focal
278 environmental variable on offspring traits, i.e. EPO and WPO "genotypes" are predicted to
279 react in a different manner to different environmental conditions. In a purely operational view,
280 the same is true for non-additive genetic effects, although conceptually, a three-way interaction
281 effect of maternal genotype, paternal genotype and the environment is predicted. Here, the

282 magnitude of the fitness effects of the interaction between maternal and paternal genotypes
283 depends on the environmental context.

284 As far as I am aware, only five studies – relating to five different species – have
285 demonstrated context-dependent genetic effects when testing for maternal half-sibling
286 performance. In the socially monogamous Coal Tit *Parus ater* EPO had a higher
287 probability of local recruitment into the breeding population compared to their WPO maternal
288 half-siblings only when they originated from late (i.e. second) broods, but not when they
289 originated from early (i.e. first) broods (Schmoll et al. 2005). Recruitment probability in
290 general was significantly reduced in late broods, such that the superior performance of EPO
291 coincides with environmental conditions that are stressful compared to those in early broods
292 (Schmoll et al. 2005). First-year reproductive performance was affected in a similar way,
293 reflecting the differential recruitment patterns (Schmoll et al. 2005). No context-dependent
294 effects were apparent in the same study population in an analysis of fitness-related traits that
295 are expressed beyond recruitment (Schmoll et al. 2009).

296 In the socially monogamous Common Yellowthroat *Geothlypis trichas*, EPO mounted a
297 stronger cellular immune response than their WPO maternal half-siblings only in the colder of
298 two study years, but not in the warmer one (Garvin et al. 2006). Low ambient temperatures
299 negatively affect offspring immunocompetence (directly and/or indirectly e.g. via food
300 abundance) such that superior performance of EPO coincides with environmental conditions
301 that are relatively stressful (Garvin et al. 2006).

302 In the socially polygynous Red Bishop *Euplectes orix*, WPO were found to be more
303 immunocompetent than their EPO maternal half-siblings only in the hotter of two study years,
304 but not in the cooler one (Edler and Friedl 2008). Compared to the yellowthroat study (Garvin
305 et al. 2006), the pattern thus appears reversed with respect to both, the relative genetic quality
306 of maternal half-siblings and the effect of ambient temperature as a key environmental variable.
307 Hotter seasons, however, are likely to provide *less* favourable breeding conditions in this
308 African species due to a lack of nestling food and increased heat stress (Edler and Friedl 2008).
309 The fact that WPO instead of EPO perform better under such stressful conditions may be
310 explained by the polygynous mating system of this species. Females paired to highly attractive
311 and therefore more strongly polygynous males face an increased risk that their social mate runs
312 out of sperm and seem to use EPC as a means to insure themselves against their high-quality
313 social mates being temporarily infertile. Consequently, mainly less attractive males of
314 presumably lower genetic quality may be successful in siring EPO (Friedl and Klump 2005;
315 Edler and Friedl 2008). In this mating system, it thus seem to be WPO, not EPO, which are of

316 higher genetic quality, so that the superior performance of offspring of relatively better genetic
317 quality coincides with relatively stressful environmental conditions (Edler and Friedl 2008).

318 In the socially monogamous Tree Swallow *Tachycineta bicolor*, EPO had longer ninth
319 primary feathers at nestling day 16 than their maternal half-siblings only when natural parasite
320 abundance was low *and* when they had hatched early relative to their WPO maternal half-
321 siblings (O'Brien and Dawson 2007). The difference in ninth primary length at a particular
322 developmental stage (i.e. near fledging) is seen as reflecting a genetic benefit of extra-pair
323 mating, because nestling wing length predicts time of fledging and wing length at fledging is
324 positively related to recruitment probability in the study species (discussed in O'Brien and
325 Dawson 2007). This study differs from the previous ones not only in that it considers,
326 conceptually, a three-way interaction (the effects of differential paternity were dependent on the
327 interaction of *two* environmental dimensions, parasite abundance and relative hatch order). In
328 contrast to the former studies, it was also in relatively favourable, not stressful, conditions that
329 EPO have differed from their WPO half-siblings (O'Brien and Dawson 2007).

330 Finally, in the predominantly socially monogamous House Wren *Troglodytes aedon*
331 WPO were more immunocompetent than their EPO maternal-half-siblings in two out of three
332 study years, but the publication did not give reference as to whether these differences were
333 related to relevant variation in (the quality of) the environment (Forsman et al. 2008).

334

335 **Poor environmental quality – revealing or concealing paternal genetic effects?**

336 The studies summarised above differ in how they see the role of environmental quality in
337 determining the extent of genetic variation that is expressed in offspring phenotypes. Three out
338 of the five studies that have demonstrated context-dependent genetic effects show a pattern
339 where only comparatively poor environments seem to reveal genetic variation. An explanation
340 for this could be that under beneficial environmental conditions all offspring may perform
341 relatively well irrespective, to some degree, of their genetic quality (i.e. of being sired within-
342 pair or extra-pair). Beneficial environments may thus have the potential to mask genetic
343 variation in fitness-related traits, and, as a consequence, it would be difficult to demonstrate the
344 differences in maternal half-sibling performance predicted by the genetic benefit hypothesis.
345 This is particularly relevant when taking into account that the magnitude of genetic benefits of
346 mate choice must be expected to be small in general (see above). In contrast, comparatively
347 stressful conditions where essential resources are limited may reveal this genetic variation and
348 it is only then that the small genetic differences between maternal half-siblings are reflected in
349 their phenotypic performance and become detectable with limited sample sizes. Along similar

350 lines, inbreeding depression is generally (although not universally) more pronounced under
351 stressful conditions across a wide range of taxa according to a recent meta-analysis (Fox and
352 Reed 2011). As an example in birds, Keller et al. (2002) report a case of inbreeding-by-
353 environment interaction in the Cactus Finch *Geospiza scandens*. For example, inbreeding
354 depression for adult survival was most severe under unfavourable conditions (i.e. dry climate
355 and high population densities), but substantially less pronounced under a range of other
356 conditions (Keller et al. 2002). Similarly, nestling survival in great tits *Parus major* was
357 negatively affected by parental genetic similarity only late in the season when food resources
358 are likely to be more restricted (Van de Castele et al. 2003). Thus in both examples inbred
359 versus outbred genotypes differed in their response to varying conditions with only stressful
360 environments reflecting the existing genetic variation in the phenotype (see also Marr et al.
361 2006; Szulkin and Sheldon 2007).

362 In contrast to the former work, the Tree Swallow study by O'Brien et al. (2007) found
363 that it is in relatively favourable conditions when half-siblings differ in performance. The
364 difference between this study and the previous ones may be the type of focal trait considered or
365 the type of genetic effect supposed to create the observed differential half-sibling performance.
366 In the case of a morphological character such as feather length, the underlying type of effect is
367 likely to be additive genetic and the full range of existing genetic variation may only be
368 expressed in the phenotype under favourable conditions, when individual genotypes can max
369 out their genetic potential (Hoffmann and Merilä 1999; see also Qvarnström 1999 reporting
370 higher heritability of a sexually selected feather ornament under beneficial conditions). The
371 other studies did not address differences in morphological characters but traits that seem more
372 closely related to fitness. In contrast to morphometric traits, the phenotypic expression of
373 genetic variation for such traits does not seem to be promoted by favourable conditions
374 (Charmantier and Garant 2005). Neither do differences in these traits necessarily reflect
375 *additive* genetic benefits of extra-pair matings. For example, a significantly better performance
376 of EPO not only in maternal, but also in paternal half-sibling comparisons reported in Garvin et
377 al. (2006) indicates a non-additive type of benefit in this case.

378

379 **Conclusions**

380 In conclusion, only five empirical studies have suggested context-dependent genetic effects of
381 extra-pair mating in birds up to date. None of these studies, however, has experimentally
382 manipulated the focal environmental dimensions and hence results are open for alternative
383 explanations. Furthermore, four of the studies have not controlled for maternal effects in

384 general and hatching sequence in particular. This is problematic because differential maternal
385 investment in favour of EPO may not only confound effects of differential paternity in general,
386 but lead to effects similar to those predicted from the context-dependence hypothesis. Finally, it
387 is also mostly not clear, how variation in offspring quality traits relates to variation in fitness
388 and how variation in the environmental variables highlighted in these studies affects offspring
389 quality traits (with year effects being a case in point). Thus evidence for context-dependent
390 genetic benefits from extra-pair matings in birds is suggestive rather than conclusive at present
391 and it is unclear how important and how widespread context-dependent genetic effects of extra-
392 pair mating may actually be and how consistently specific (e. g. high-stress versus low-stress)
393 environments may affect the context-dependent expression of genetic variation.

394

395 **Perspectives**

396 Studies addressing the genetic benefits of extra-pair matings by comparing maternal half-
397 siblings have generally used a range of different offspring quality traits and the few studies that
398 have demonstrated context-dependent effects have likewise picked a number of different
399 environmental variables to test for interactions with differential paternity (see above). The
400 availability of many such potential response variables and, in particular, the availability of
401 many potentially important predictor variables (i.e. environmental dimensions) harbours the
402 risk of revealing spurious associations when testing for two-way (or even higher-order)
403 interactions with differential paternity. Obviously, focal offspring quality traits must exhibit a
404 verifiably close relationship with fitness, preferably as demonstrated in the very study
405 population, to allow meaningful inference regarding the fitness consequences of extra-pair
406 mating behaviour (frequently this relationship is assumed rather than established). Furthermore,
407 to qualify as a "relevant" dimension of environmental quality, any candidate variable should
408 predictably affect the focal offspring quality trait, preferably in a manner that is also understood
409 mechanistically in some detail. Which offspring quality traits may be regarded and which
410 particular dimension of the environment may be considered "relevant" will ultimately depend
411 on the particular study system, but response and predictor variable(s) should be carefully
412 chosen and well defined *a priori* for both, the observational as well as the experimental
413 approaches outlined below.

414 A number of high-quality data sets on maternal half-sibling performance is meanwhile
415 available (or being collected) and may frequently have been sampled across different
416 environmental contexts. These data could be (re-) analysed while explicitly considering
417 relevant environmental variation. Studies that have failed to establish the predicted differences

418 in maternal half-sibling performance may then find that under some circumstances these effects
419 are detectable (note that there was no support for an "overall" (i.e. main) effect of differential
420 paternity in some of the studies that demonstrated context-dependence, cf. Fig.1 in Schmolle et
421 al. 2005). However, also studies that *have* shown differences in maternal half-sibling
422 performance may benefit by allowing a deeper understanding when taking ecology into
423 account, for example if an overall effect of differential paternity largely relates to particular
424 sub-samples in the data sets (but see discussion on the risk of spurious findings above). At this
425 stage, reporting a lack of evidence for context-dependence is also of considerable interest
426 (given sample sizes are reasonably large), to avoid publication bias and obtain a balanced view
427 on how common such effects may or may not be in natural populations.

428 As an example, in many bird populations in temperate regions, environmental
429 conditions deteriorate predictably and substantially over the breeding season while laying
430 and/or hatching date are recorded routinely in many studies. They could thus serve
431 retrospectively as a proxy for ecological contexts of varying quality to compare the relative
432 performance of maternal half-siblings against, even if more meaningful data like quantitative
433 estimates of food abundance are not available. Similarly, available weather data combined with
434 longterm data sets could identify key meteorological variables affecting fitness-related traits
435 and these gradients of environmental variation could be used to test for interactions with
436 differential paternity.

437 Instead of considering laying or hatching order primarily a potentially confounding
438 factor when analysing maternal half-sibling performance (see above), it could also be seen as
439 reflecting yet another relevant dimension of the natural environment. There is evidence that
440 hatching order directly affects early survival prospects in many altricial bird species through
441 asymmetrical sibling competition, particularly when hatching asynchrony is pronounced
442 (Magrath 1990; see also Magrath et al. 2009). Thus, once hatching sequence has been recorded
443 in order to control its effects, testing for differential paternity-by-hatching sequence interactions
444 may also represent a valuable option for testing the context-dependence hypothesis.

445 Different from the truly ecological variables discussed above, offspring sex may also be
446 regarded a relevant dimension of environmental context. Fitness effects of particular alleles
447 may be sex-dependent, for example due to sexually antagonistic selection resulting from
448 intralocus sexual conflict (Bonduriansky and Chenoweth 2009). Such sexually antagonistic
449 fitness variation could render effects of paternal genetic contribution sex-dependent, too. Thus
450 it may be worthwhile considering offspring sex as an (intra-genomic) dimension of the
451 environment within which paternal alleles are expressed, and test for differential paternity-by-

452 offspring sex effects on fitness traits in both, observational and experimental approaches (see
453 below). Of course, the magnitude of such effects may again depend on external dimensions of
454 the environment, which may require testing for three-way interactions of differential paternity,
455 offspring sex and quality of the environment. If the effects of differential paternity were indeed
456 sex-dependent or even sexually antagonistic, it would be adaptive for females to adjust sex
457 allocation in relation to paternity, because only then would they be able to obtain a (maximum)
458 net genetic benefit from extra-pair mating. For example, male extra-pair offspring may inherit
459 alleles from their attractive (i.e. extra-pair) fathers that will make themselves more attractive as
460 extra-pair sires while the same alleles may negatively affect the fitness prospects and thus the
461 reproductive value of female offspring. In general, there is good evidence for the ability of
462 female birds to facultatively bias offspring sex ratio, for example in relation to the sexual
463 attractiveness (e.g. Ellegren et al. 1996) or the genetic compatibility (e.g. Pryke and Griffith
464 2009) of their social mates. However, in the context of extra-pair mating behaviour, evidence
465 for facultative sex allocation in relation to paternity is rather weak. Only a single study has
466 unequivocally demonstrated the predicted sex ratio bias towards males in extra-pair offspring
467 (Johnson et al. 2009), while many others tried, but failed (e.g. Sheldon and Ellegren 1996;
468 Leech et al. 2001; Dietrich-Bischoff et al. 2006). Thus, if differential paternity was indeed
469 sexually antagonistic in its effects, fitness gains realised via the advantaged sex would possibly
470 have to exceed the fitness costs incurred by the disadvantaged sex to render extra-pair matings
471 adaptive.

472 Most importantly, however, experimental approaches are needed that systematically
473 manipulate relevant environmental contexts and subsequently test for differential paternity-by-
474 treatment effects. If genetic benefits are assumed to be apparent more clearly under relatively
475 poor conditions, the goal is provoking genetic effects by deteriorating environmental contexts
476 to a degree that provides stressful conditions that could be encountered by the study population
477 (at least from time to time), but that is still acceptable from an ethical point of view (and does
478 also not lead to an overwhelmingly detrimental environmental effect which would also blur
479 differences between genotypes). We may then predict a significant interaction between
480 paternity and experimental treatment with differences between half-siblings being more
481 pronounced under relatively poor conditions. Ideally, any treatment would create more than just
482 two experimental environments to better understand the predicted differential reaction norm
483 trajectories of offspring quality traits (which may not necessarily be linear as assumed in Fig. 1
484 for the sake of clarity). As expected effect sizes are small, such experiments need to be carried
485 out on a larger scale that maximises the number replicates (i.e. broods with multiple paternity).

486 Given that differential maternal investment with respect to paternity may lead to the same type
487 of context-dependent effects as predicted by the genetic benefit hypothesis, future studies need
488 to control such effects in general and hatching order in particular.

489 In the field, brood size manipulation experiments are one straightforward option to
490 manipulate the degree of sibling competition and thus resource availability. Cross-fostering
491 designs may then easily be tailored to create a range of experimental environments of different
492 quality. Furthermore, by separating offspring from their natural parents at an early stage
493 through cross-fostering of entire (half-) sibships, potential post-hatching effects of maternal or
494 paternal differential allocation in relation to paternity could be controlled. Manipulation of
495 parasite prevalence and/or abundance or nest temperature regimes or enforcing replacement
496 clutches while taking advantage of naturally deteriorating conditions in seasonal environments
497 offer further opportunities depending on the biology of the focal species.

498 In order to unequivocally demonstrate genetic benefits of female mating preferences, it
499 is necessary to allocate paternity randomly to a focal female's offspring, raise her progeny
500 under identical environmental conditions and then test for differences in fitness between
501 maternal half-sibships descending from preferred versus less preferred sires. This is
502 comparatively easily achieved in laboratory studies of externally fertilising species by means of
503 split-clutch in-vitro fertilisations (e.g. Barber et al. 2001; Welch 2003) and feasible to some
504 degree within captive (semi-natural) populations of certain internally fertilising species (e.g.
505 Petrie 1994). However, the use of artificial insemination techniques in laboratory populations
506 would offer interesting perspectives here, too. Such systems would not only exclude differential
507 maternal investment, but also allow for a much better control and resolution of the experimental
508 environments. One drawback here is that in the few established model species such as the zebra
509 finch, EPP may play only a minor role in natural populations (Griffith et al. 2010).

510 As the magnitude of the genetic benefits a female may obtain from extra-pair mating is
511 expected to be small (see above), comparatively large sample sizes will normally be required to
512 demonstrate them. When analysing the fitness consequences of extra-pair mating, a replicate
513 typically consists of a brood with multiple paternity and it may thus be challenging to achieve
514 substantial samples, especially in species with relatively low frequencies of EPP. Properly
515 controlling potentially confounding effects of differential maternal investment (see above)
516 makes this an even more difficult enterprise. However, in species where EPO have been
517 unequivocally shown to be more heterozygous than their WPO maternal half-siblings (see
518 above), a shortcut may be testing for the context-dependence of the predicted heterozygosity-
519 fitness correlations in the study population/study species instead of testing the context-

520 dependence of the fitness effects of differential paternity directly. Similar to context-dependent
521 effects of (close) inbreeding discussed above, heterozygosity-fitness correlations may vary in
522 their strength across environments of different quality, giving rise to heterozygosity-by-
523 environment interactions (for an interesting example in anurans see Lesbarrères et al. 2005).
524 This approach would not only allow making use of (much) larger samples by also including
525 offspring from broods without multiple paternity (in observational as well as experimental
526 studies). As we can expect substantial random variation in the degree of individual
527 heterozygosity also within each of the two groups of maternal half-siblings (i.e. WPO and
528 EPO), it might also provide a means to efficiently control differential maternal investment,
529 because significant heterozygosity-fitness correlations as well as heterozygosity-by-
530 environment interactions *within* these groups cannot be confounded by differential maternal
531 investment in relation to paternity.

532 Context-dependent genetic benefits imply that it would be adaptive to express costly
533 mating preferences in a phenotypically plastic manner, depending on the expected net benefit
534 within a given environment (Qvarnström 2001; Welch 2003) and there are remarkable
535 examples of adaptive phenotypic plasticity in female mate choice in birds (e.g. Qvarnström et
536 al. 2000; Chaine and Lyon 2008). This flexibility presupposes the ability of females to evaluate
537 the specific quality of the environment that their offspring are likely to experience, which
538 should not pose a major problem in seasonal environments that may vary predictably in quality
539 (see above). Assuming extra-pair matings to be costly, we may thus predict adaptive
540 phenotypic plasticity in female propensity to engage in extra-pair matings. For example, in the
541 Coal Tit population referred to above, the frequency of EPP was substantially higher in second
542 broods (relatively stressful environment) compared to first broods (relatively beneficial
543 environment, Dietrich et al. 2004). This pattern is compatible with a plastic female response in
544 relation to differential environmental conditions, although other explanations may seem more
545 likely (for example a better availability of extra-pair mating opportunities with preferred sires,
546 Dietrich et al. 2004). Nevertheless, comparing the frequency of EPP against the magnitude of
547 genetic benefits (i.e. the difference in half-sibling performance) across different environments
548 (within as well as across populations) may represent a first step to elucidate this idea further.

549 If context-dependent genetic effects could be demonstrated in a robust and repeatable
550 manner, it may be of interest to determine how frequently environmental contexts arise that
551 allow females to realise a net genetic fitness benefit by mating extra-pair and thus maintain
552 selection for this behaviour in the long run. Analysis of long-term data sets – where available –

553 may help to evaluate this and could possibly be used to parameterise models that address the
554 maintenance of mating preferences for extra-pair sires in heterogeneous environments.

555 This article has focused on how variation in environmental quality may affect the
556 phenotypic expression of the predicted, genetically based differences between EPO and WPO
557 maternal half-siblings, assuming that genotype fitness ranks are maintained across
558 environments (i.e. non-crossing reaction norms as illustrated in Fig. 1c). However, different
559 environments as opposed to environments of different quality (for example in terms of the
560 prevalence of different *types* of parasites) may also reflect relevant environmental heterogeneity
561 and ecological cross-over of reaction norms in fitness-related traits has been demonstrated in
562 other taxa (e.g. Jia and Greenfield 1997; Welch 2003; Mills et al. 2007) and may also be
563 considered.

564 The idea of a context-dependence of genetic benefits of extra-pair matings may offer
565 one possible approach for reconciling mixed results from different EPP studies and may thus
566 contribute to resolving the longstanding puzzle why female birds mate extra-pair so frequently.
567 More generally, it may allow understanding under which environmental conditions selection
568 will act to maintain a female mating bias towards extra-pair males. This has potentially far-
569 reaching implications for the ecology and evolution of female mating preferences, the
570 maintenance of genetic variation in (sexually) selected traits and possibly the co-evolution of
571 male sexual signals and female mating preferences. Taking into consideration that evidence
572 from other taxa also suggests that context-dependence of genetic benefits of mate choice may
573 be of considerable importance, I conclude that context-dependent genetic effects of mate choice
574 in birds deserve more attention in general and in the context of extra-pair mating in particular.

575

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580

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784

785 **Figure captions**

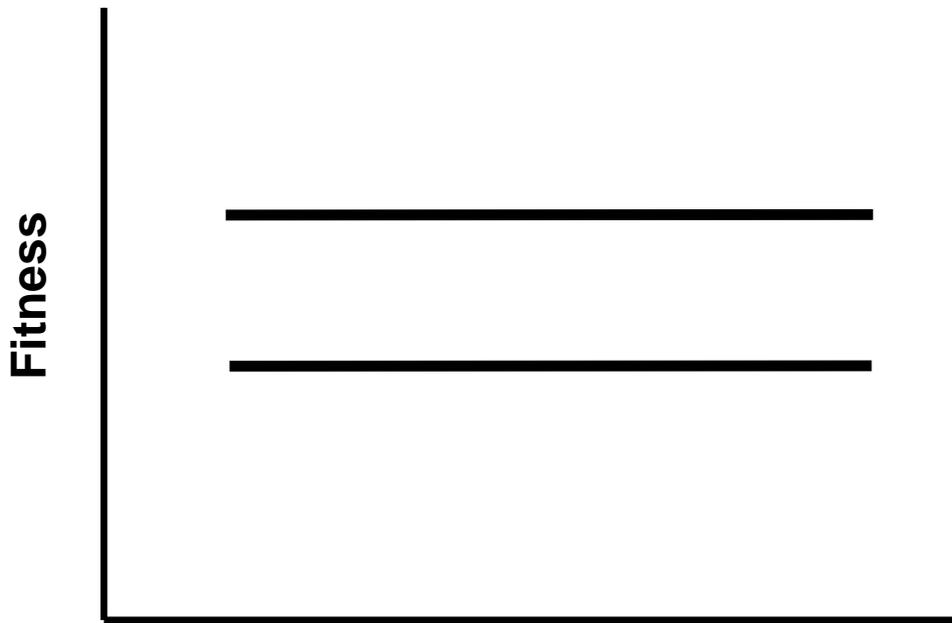
786 **Fig. 1** Schematic representation of linear fitness reaction norms of two offspring genotypes
787 (represented by lines) to illustrate potential effects of genotype-by-environment interactions on
788 the genetic benefits of mate choice. **a** Genotypes show no phenotypically plastic response, the
789 slopes of their reaction norms are identical and equal zero (parallel reaction norms, no
790 genotype-by-environment interaction). **b** Genotypes show a phenotypically plastic response, the
791 slopes of their reaction norms are identical, but different from zero (parallel reaction norms, no
792 genotype-by-environment interaction). **c** Genotypes show a phenotypically plastic response, the
793 slopes of their reaction norms are different, but reaction norms do not cross within the range of
794 environmental conditions experienced (genotype-by-environment interaction with non-crossing
795 reaction norms). **d** Genotypes show a phenotypically plastic response, the slopes of their
796 reaction norms are different, and reaction norms cross within the range of environmental
797 conditions experienced (genotype-by-environment interaction with crossing reaction norms,
798 ecological cross-over). Relative genetic fitness benefits from preferring a male siring either one
799 or the other offspring genotype are identical (a), (b), differ in magnitude (c), or may even be
800 reversed (d) across environments.

801

802 **Figures**

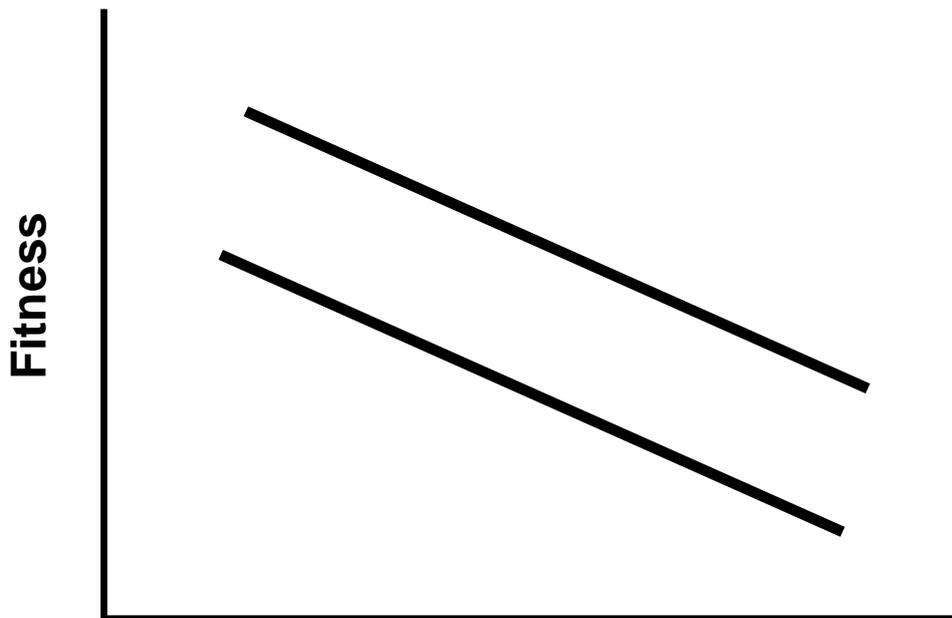
803 Figure 1

804 (a)



805

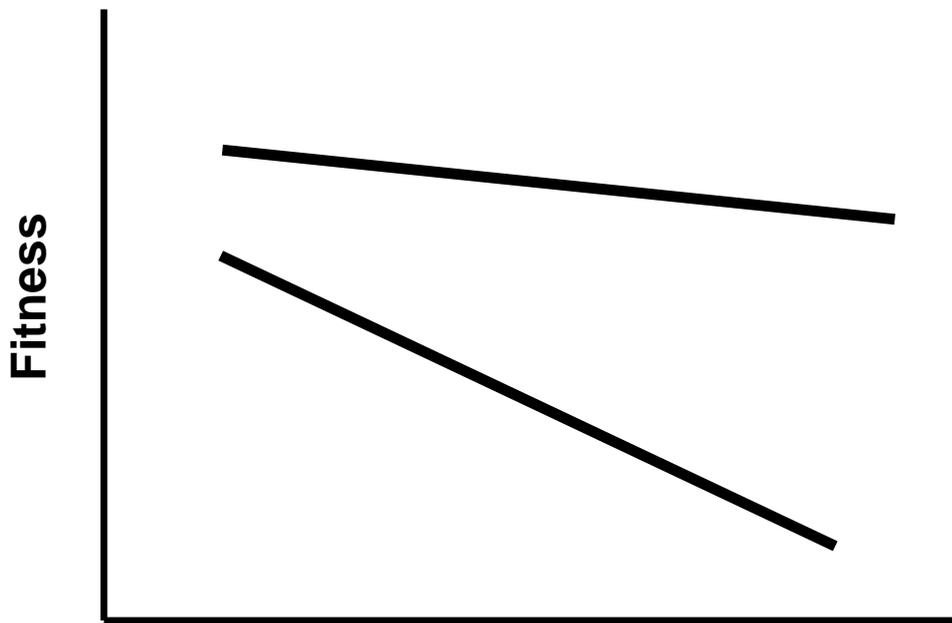
806 (b)



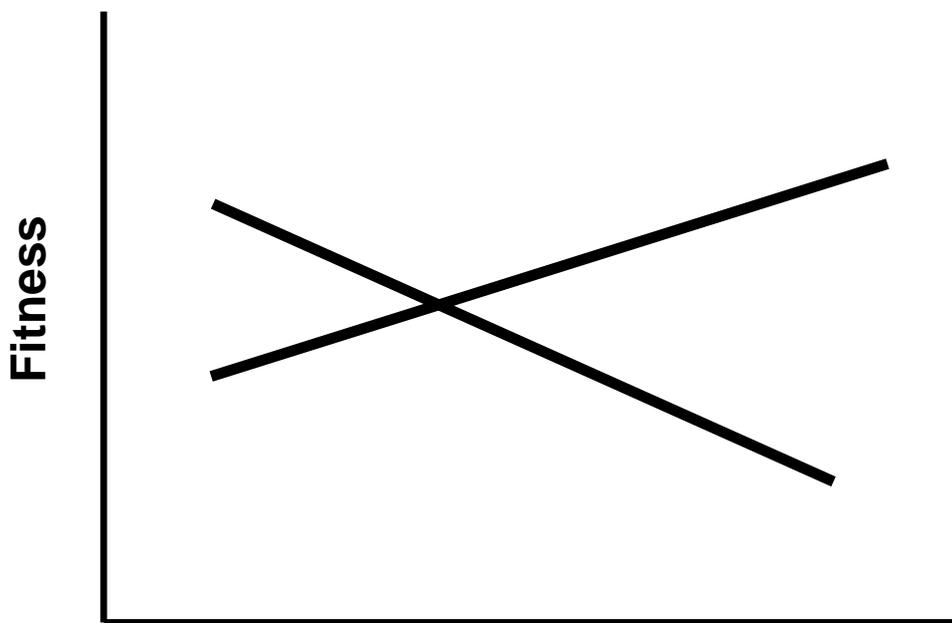
807

808

809 (c)



810
811 (d)



Experienced environmental variation

812
813
814
815

German abstract for article 10336-683: A review and perspective on context-dependent genetic effects of extra-pair mating in birds

816 **Kontextabhängige genetische Effekte von Fremdkopulationen bei Vögeln: Review und**
817 **Perspektive**

818

819 Der evolutionäre Ursprung und die Aufrechterhaltung von außerpaarlichem
820 Kopulationsverhalten bei Vögeln sind in den letzten Jahrzehnten intensiv untersucht worden.
821 Allerdings konnte bisher kein Konsens bezüglich des adaptiven Nutzens dieses Verhaltens für
822 Vogelweibchen erzielt werden. Die genetische Vorteile-Hypothese postuliert, dass
823 Fremdkopulationspartner Genvarianten von höherer Qualität oder besserer Kompatibilität im
824 Vergleich zum sozialen Paarpartner aufweisen, was zu Nachkommen von höherem
825 Reproduktionswert führen würde. Ein häufig genutzter Ansatz zur Überprüfung dieser
826 Hypothese besteht darin, mütterliche Halbgeschwister in Brutten mit multiplen Vaterschaften
827 bezüglich fitness-relevanter Merkmale zu vergleichen. Die Ergebnisse solcher Vergleiche sind
828 allerdings nicht konsistent. In diesem Beitrag diskutiere ich die Idee, dass das Ausmaß
829 genetischer Fitnessvorteile aus Fremdkopulationen vom Umweltkontext abhängt. Kontext-
830 abhängige genetische Effekte wurden bisher nur bei fünf Singvogelarten nachgewiesen. In
831 keiner der betreffenden Studien wurden jedoch die entscheidenden Umweltvariablen
832 experimentell manipuliert. Auch wurden die potentiell konfundierenden Effekte von
833 differentiellem mütterlichen Investment in Abhängigkeit der Vaterschaft zumeist nicht
834 kontrolliert. Eine Reihe von hochqualitativen Datensätzen zu den Fitnesskonsequenzen von
835 Fremdkopulationsverhalten ist verfügbar, die bezüglich ihrer Umweltabhängigkeit (re-)
836 analysiert werden könnten. Dies gilt, sofern relevante Umweltgradienten erfasst wurden und
837 ihre Berücksichtigung *a priori* plausibel gemacht werden kann. Relevante Variation könnte
838 zum Beispiel den Zeitpunkt des Brütens in gemäßigten Breiten, die Reihenfolge des Schlupfes,
839 aber auch das Geschlecht der Nachkommen umfassen. In erster Linie sind jedoch
840 experimentelle Ansätze nötig, die fitnessrelevante Gradienten der Umwelt wie
841 Futtermittelfürbarkeit oder Parasitenbelastung systematisch und graduell variieren. Die
842 Kontextabhängigkeit genetischer Effekte von Fremdkopulationen könnte möglicherweise
843 erlauben, widersprüchliche Resultate verschiedener Studien innerhalb und zwischen Arten zu
844 integrieren. Eine solche Kontextabhängigkeit könnte aber auch ganz allgemein helfen zu
845 verstehen, unter welchen Umweltbedingungen Selektion eine weibliche Paarungspräferenz für
846 Fremdkopulationspartner aufrechterhält. Dies hätte potenziell weit reichende Folgen für die
847 Ökologie und Evolution von Paarungspräferenzen und die Aufrechterhaltung genetischer
848 Variation von (sexuell) selektierten Merkmalen.
849