Endless forms of sexual selection

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In recent years, the field of sexual selection has exploded, with advances in theoretical and empirical research complementing each other in exciting ways. This perspective piece is the product of a "stock-taking" workshop on sexual selection and conflict. Our aim is to identify and deliberate on outstanding questions and to stimulate discussion rather than provide a comprehensive overview of the entire field. These questions are organized into four thematic sections we deem essential to the field. First we focus on the evolution of mate choice and mating systems. Variation in mate quality can generate both competition and choice in the opposite sex, with implications for the evolution of mating systems. Limitations on mate choice may dictate the importance of direct vs. indirect benefits in mating decisions and consequently, mating systems, especially with regard to polyandry. Second, we focus on how sender and receiver mechanisms shape signal design. Mediation of honest signal content likely depends on integration of temporally variable social and physiological costs that are challenging to measure. We view the neuroethology of sensory and cognitive receiver biases as the main key to signal form and the 'aesthetic sense' proposed by Darwin. Since a receiver bias is sufficient to both initiate and drive ornament or armament exaggeration, without a genetically correlated or even coevolving receiver, this may be the appropriate 'null model' of sexual selection. Thirdly, we focus on the genetic architecture of sexually selected traits. Despite advances in modern molecular techniques, the number and identity of genes underlying performance, display and

secondary sexual traits remains largely unknown. In-depth investigations into the genetic basis of sexual dimorphism in the context of long-term field studies will reveal constraints and trajectories of sexually selected trait evolution. Finally, we focus on sexual selection and conflict as drivers of speciation. Population divergence and speciation are often influenced by an interplay between sexual and natural selection. The extent to which sexual selection promotes or counteracts population divergence may vary depending on the genetic architecture of traits as well as the covariance between mating competition and local adaptation. Additionally, post-copulatory processes, such as selection against heterospecific sperm, may influence the importance of sexual selection in speciation. We propose that efforts to resolve these four themes can catalyze conceptual progress in the field of sexual selection, and we offer potential avenues of research to advance this progress.

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Abstract

In recent years, the field of sexual selection has exploded, with advances in theoretical and
empirical research complementing each other in exciting ways. This perspective piece is the
product of a "stock-taking" workshop on sexual selection and conflict. Our aim is to identify and
deliberate on outstanding questions and to stimulate discussion rather than provide a
comprehensive overview of the entire field. These questions are organized into four thematic
sections we deem essential to the field. First we focus on the evolution of mate choice and
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opposite sex, with implications for the evolution of mating systems. Limitations on mate choice
may dictate the importance of direct vs. indirect benefits in mating decisions and consequently,
mating systems, especially with regard to polyandry. Second, we focus on how sender and
receiver mechanisms shape signal design. Mediation of honest signal content likely depends on
integration of temporally variable social and physiological costs that are challenging to measure.
We view the neuroethology of sensory and cognitive receiver biases as the main key to signal
form and the 'aesthetic sense' proposed by Darwin. Since a receiver bias is sufficient to both
initiate and drive ornament or armament exaggeration, without a genetically correlated or even
coevolving receiver, this may be the appropriate 'null model' of sexual selection. Thirdly, we
focus on the genetic architecture of sexually selected traits. Despite advances in modern
molecular techniques, the number and identity of genes underlying performance, display and
secondary sexual traits remains largely unknown. In-depth investigations into the genetic basis of
sexual dimorphism in the context of long-term field studies will reveal constraints and
trajectories of sexually selected trait evolution. Finally, we focus on sexual selection and conflict
as drivers of speciation. Population divergence and speciation are often influenced by an
interplay between sexual and natural selection. The extent to which sexual selection promotes or
counteracts population divergence may vary depending on the genetic architecture of traits as
well as the covariance between mating competition and local adaptation. Additionally, post-
copulatory processes, such as selection against heterospecific sperm, may influence the
importance of sexual selection in speciation. We propose that efforts to resolve these four themes
can catalyze conceptual progress in the field of sexual selection, and we offer potential avenues
of research to advance this progress.

Keywords

INTRODUCTION

A great deal of the biodiversity on this planet, especially the spectacular traits at which humans marvel, are direct or indirect results of sexual selection. Darwin (1871) defined sexual selection as *"the advantage which certain individuals have over other individuals of the same sex and species solely in respect of reproduction"* (reproduction, in this context, meaning mating success). The flowers of an alpine meadow, antelope horns, a dawn chorus of songbirds: all are snapshots of long histories of sexually selected diversification and exaggeration of signals and displays that have or once had effects on mating or fertilization success. For sexually reproducing organisms, intrasexual competition for reproductive opportunities is a powerful selective pressure, not only shaping the extravagant 'secondary sexual characters' that Darwin originally set out to explain, but also with obvious potential to reinforce or even trigger speciation and dramatically affect macroevolution and biogeography. To explore biodiversity without an understanding of sexual selection is a bit like laying a jigsaw puzzle upside down.

With our current insight that reproduction is the hard currency of natural selection, it may seem strange that the notion of sexual selection required such a massive volume of reasoning and countless examples (Darwin 1871), and that despite this effort, it remained controversial for so long. Darwin identified two components of sexual selection: contest competition between rivals of the same sex (typically males) and mate choice (typically by females). Female choice in particular attracted criticism, first from Wallace (1895) and later by others (although, ironically, with arguments similar to the often useful 'good genes' models of today; Cronin 1991; Hoquet & Levandowsky 2015; Prum 2012). Even when Fisher (1930) outlined the intuitively plausible runaway process involving a preferred male trait and a preference gene acting in females in his classic monograph, it was rather skeptically reviewed by Huxley (1938a; Huxley 1938b).

90   However, with the exception of Bateman (1948), the subject was largely ignored until the

91   explosion of evolutionary and behavioural ecology in the 1970s, further sparked by the first

92   demonstration of female choice in the wild (Andersson 1982). Conceptions of ornamental traits

93   as quality advertisements (Williams 1966; Zahavi 1975) and how variation in such viability

94   messages can be maintained (notably Hamilton & Zuk 1982), together with edited volumes like

95   Bateson (1983) and Bradbury and Andersson (1987), generated questions and research programs

96   for decades to come.

97   The theoretical genetic modelling of Fisher's trait-preference coevolution was pioneered

98   by O'Donald (1962), Fisher's last Ph.D. student, but runaway dynamics were not fully explored

99   and demonstrated until the landmark models of Lande (1981) and Kirkpatrick (1982). These

100 were advocated as the 'Lande-Kirkpatrick null model' of sexual selection by mate choice by

101 Prum (2010), partly as a reaction to decades of focus on indicator models and direct or indirect

102 benefits of mate choice (reviewed by Kempenaers 2007; Kokko et al. 2003; Mead & Arnold

103 2004). This and the neglect of the social competition that is the essence of sexual selection

104 (Darwin 1871; West-Eberhard 1979), have been called 'sexual selection amnesia' by West-

105 Eberhard (2014).

106   Darwin emphasized adaptations arising from what is now termed pre-copulatory sexual

107 selection, i.e. competition for matings. Since 1970 it has become accepted that sexual selection

108 can continue after mating (post-copulatory sexual selection; see Birkhead 2010), and much work

109 has been completed on its two components analogous to Darwin's male-male competition (i.e.

110 sperm competition, Parker 1970; Parker & Pizzari 2010) and female choice (i.e. sperm selection

111 or cryptic female choice, Eberhard 1996; Firman et al. 2017; Thornhill 1983). Further, it is

112 increasingly appreciated that the process of sexual selection is associated with, and frequently

113   exacerbates, sexual conflict (Table 1), i.e. cases where male and female fitness interests cannot

114   be simultaneously satisfied (Parker 1979; Trivers 1972). Thus, after a long period of quiescence

115   since its inception in 1871, the past 40 years have seen an upsurge of interest in sexual selection

116   with the rise of new theory, modern computer technology, molecular biology and techniques in

117   comparative analysis having fueled extensive developments.

118

119   **SURVEY METHODOLOGY**

120   The enthusiastic resurgence of sexual selection theory in the 1970s and '80s stimulated a

121   Dahlem Conference which sought to identify emerging directions (Bradbury & Andersson 1987)

122   and the intensity of interest in the field has continued unabated. The recent workshop on sexual

123   selection and sexual conflict held at Chalmers University/University of Gothenburg ("Origins of

124   Biodiversity Workshop: Sexual selection and Sexual Conflict", April 2017) aimed a renewed

125   'stock-taking' on diverse aspects of the subject. Our goal is not to review the entire field, or even

126   subfields, of sexual selection and sexual conflict (e.g. Andersson 1994; Arnqvist & Rowe 2005;

127   Birkhead & Møller 1998; Cummings & Endler 2018; Eberhard 1996; Hare & Simmons ; Jones

128   & Ratterman 2009; Kuijper et al. 2012; Rosenthal 2017), but rather to pose a series of open

129   questions emerging from the workshop, naturally colored by our various interests, expertise and

130   empirical systems. The questions we pose delimit broad themes within sexual selection and

131   conflict, answers to which we consider of critical importance to the advancement of the field as

132   a whole. The subsections were either written independently or co-written before being compiled

133   into four research themes within sexual selection (as per Andersson 1994) : 1) the evolution of

134   mate choice and mating systems, 2) sender and receiver mechanisms shaping signal design and

135   evolution, 3) the genetic architecture of sexual selection, and 4) sexual selection and sexual

136   conflict as drivers, or obstacles, of speciation. We hope that these lines of questioning will

137   encourage discussion and offer non-specialists an insight into this ever-expanding area of

138   evolutionary biology.

139

140   **(1) Evolution of mate choice and mating systems**

141   Anisogamy, the size difference between male and female gametes that results from the

142   formation of two sexes, is generally accepted as a primary force behind broad patterns of male-

143   male competition over mating opportunities and female-driven mate choice (e.g. Janicke et al.

144   2016; Schärer et al. 2012). Over the last decade, there has been a revived focus on anisogamy

145   (Table 1) and its evolutionary consequences (e.g. Janicke et al. 2016; Lehtonen & Kokko 2011;

146   Lehtonen et al. 2016; Parker 2014; Schärer et al. 2012). The 'sexual cascade' (Table 1), a

147   successive sequence of events that has occurred during the long-term evolution of sexual strategy

148   (Parker 2014; Parker & Pizzari 2015), provides a null expectation for competitiveness and

149   choosiness in many taxa. Socio-ecological conditions can, however, arise that favor deviations

150   from ancestral behavioural adaptations. Thus, despite the evolutionary irreversibility of

151   anisogamy (Parker 1982), patterns such as male-mate choice and female-female competition

152   over mates do arise and overwrite the ancestral influence of anisogamy. Much of this is well

153   captured by operational sex ratio theory (Emlen & Oring 1977; Clutton-Brock & Parker 1992;

154   reviewed in Kvarnemo & Simmons 2013), explaining often seen variation in competitiveness

155   and choosiness, also on short time scales (e.g. Forsgren et al. 2004). Indeed, sex-specific

156   investment in competition, mate choice, parental care, and sexual dimorphism vary dramatically

157   across the animal kingdom (Ahnesjö & Bussière 2016; Janicke et al. 2016), and this variation

158   deserves our attention and interest.

159   This shift in research interest is reflected by a number of reviews within the last decade

160   demonstrating the prevalence of female competition and male choice (Edward & Chapman 2011;

161   Hare & Simmons 2018; Rosvall 2011; Schlupp 2018; Stockley & Bro-Jørgensen 2011).

162   Importantly, these behaviors are not restricted to species where there is an *a priori* expectation of

163   sex-role 'reversal', because male-mate choice can co-occur with female mate choice, and

164   similarly, both sexes can show intra-sexual competition for mating opportunities. When both

165   sexes vary in their quality as mates, selection can generate mating competition and selective

166   mate choice in either sex (Owens et al. 1994; Owens & Thompson 1994; Parker 1983). It is

167   therefore critical to our understanding of sexual selection that we do not let preconceived ideas

168   about sex roles limit our predictions and study designs.

169   Below we examine a few general topics related to mate choice and mating systems (Table

170   1). How and why organisms choose their partners may hinge on direct contributions to the

171   quality of a reproductive bout or indirect genetic benefits. We discuss how details of pre- and

172   post-copulatory processes can affect sexual selection, and how genetic benefits that derive from

173   mating with a particular individual might be important in the context of both pathogens and

174   inbreeding. Finally, we point out benefits of studying broadcast spawning, as this form of

175   reproduction excludes pre-copulatory sexual selection. Future research into the relative

176   contributions of direct vs. indirect benefits should take into account mating systems, temporal

177   limitations placed on mate choice, and other selection pressures.

178

179   *1a. Direct and indirect benefits of mate choice – implications for mating systems and sexual*

180   *selection*

181   Mate choice can be time consuming, risky and might even result in individuals that are

182   too choosy not succeeding in finding a mate. We therefore expect individuals to gain important

183   benefits from mate choice to cover these costs. Mate choice can evolve through the pursuit of

184   both direct and indirect benefits ('benefits of mate choice', Table 1) and can take the form of

185   either pre- or post-copulatory selection (Edward & Chapman 2011; Jennions & Petrie 2000).

186   Whereas mate choice for direct benefits primarily occurs before mating, mate choice driven by

187   indirect benefits can continue after mating, and may be particularly important if the genetic

188   quality of potential mates cannot be determined prior to mating. Post-copulatory mate choice

189   therefore requires mating with multiple mates.

190   In some taxa, such as migrating passerine birds, pair formation and therefore pre-mating

191   mate choice occurs under severe time stress (e.g. Alatalo et al. 1988; Bensch & Hasselquist

192   1992; Dale & Slagsvold 1996). This likely puts a premium on mate choice for direct benefits

193   such as territory quality and social partner condition. A hasty assessment of indirect attributes

194   such as 'good', 'sexy' or compatible genes (explained under 'benefits of mate choice', Table 1),

195   can then be corrected afterwards by mating with additional (extra-pair) partners. This

196   'correction' can either take the form of trading-up, that is, mating with an extra partner only if

197   the additional partner's genetic quality is better than that of the current social partner(s), or it can

198   be achieved after mating with multiple partners via post-copulatory processes such as sperm

199   competition and cryptic mate choice (Jennions & Petrie 1997; Jennions & Petrie 2000).

200   Genetic compatibility within mated pairs is a key aspect of mate choice that is attributed

201   to selection for indirect benefits. Post-copulatory mate choice for complementary genes involved

202   in immune function has been shown in fish, mammals and lizards (Olsson et al. 2003; Penn

203   2002; Penn & Potts 1999) (sections *1c* and *1e*). In procellariform birds, high olfactory bulb-to-

204   brain ratios co-occur with long-term genetic monogamy (Bried et al. 2003; Zelano & Edwards

205   2002; Zelenitsky et al. 2011), and genetic compatibility based mate choice (Strandh et al. 2012).

206   Might olfaction be causally linked to the evolution of mating systems? If there is such a link,

207   taxa with relatively larger olfactory bulbs would be expected to be better at accurate mate choice

208   for genetic compatibility prior to mating, possibly promoting long term genetic monogamy in

209   such taxa (Colegrave et al. 2002). For example, a recent study shows low levels of extra-pair

210   paternity and male-mediated mate choice based on Major Histocompatibility Complex (MHC)

211   loci in a largely monogamous seabird (Hoover et al. 2018). On the other hand, mating systems

212   other than monogamy (e.g. polygyny in lek-breeding species) may also promote olfaction based

213   mate choice.

214   More research is needed to identify sexually selected traits contributing to direct benefits.

215   When an individual can increase its mating success by offering direct benefits, then the traits that

216   contribute to such benefits (e.g. being fecund, in good condition, able to secure and defend a fine

217   territory, having good parenting skills) may be subject to mate selection. Given a genetic basis of

218   a trait it can also respond to selection. Importantly, this means that many traits that are

219   traditionally seen as products of natural selection are likely to also be affected by sexual

220   selection, and hence pushed away from their naturally selected optima. That parental care can be

221   under sexual selection is already well established (Kvarnemo 2010; Lindström & St. Mary

222   2008), but a broader appreciation of other dually selected traits is likely to improve our

223   understanding of trait evolution.

224

225   *1b. The influence of polyandry on sexual selection and sexual conflict*

226   The level of polyandry of a population will likely reflect the outcome of interactions

227   between male- and female-driven strategies. Whereas male strategies are often assumed to drive

228   and females to resist polyandry, some degree of polyandry can be adaptive and actively

229   promoted by females. Importantly, polyandry is likely to have drastic effects on the operation of

230   sexual selection on males. The key implication is that polyandry creates a new source of

231   variation in male reproductive success in the form of variation in paternity share arising from

232   multiple matings by females and male-male competition over access to fertilization.

233   The resulting two episodes of postcopulatory sexual selection (sperm competition and

234   cryptic female choice; see above) add considerable complexity to the architecture of variation in

235   male fertilization success (Webster et al. 1995), and consequently to the operation of sexual

236   selection. Recent work has demonstrated that – contrary to previous expectations (e.g. Møller

237   1998), polyandry can severely limit variation in fertilization success among males, which

238   weakens precopulatory sexual selection on male mating success. This process can often

239   drastically reduce the total opportunity for sexual selection on males, relegating it primarily to

240   postcopulatory episodes (Collet et al. 2012; Jones et al. 2001; Shuster & Wade 2003). One

241   important consequence of this effect is that polyandry acts to reduce the difference between male

242   and female Bateman gradients (Parker & Birkhead 2013; 'Bateman gradient', Table 1).

243   Theory on the interaction between female strategies of sperm selection and male

244   strategies of sperm allocation needs expansion and further development. For instance, early

245   observations of increased proportional paternity in less as compared to more closely related

246   males (Olsson et al. 1996) were found robust when controlling for effects such as unfertilized

247   eggs and parental inbreeding-induced early offspring mortality (Olsson et al. 1999; Olsson et al.

248   1997). However, male ejaculation economics could also be influenced by detection (e.g. based

249   on olfactory cues) of relatedness with the female and competing rivals (Olsson et al. 2004) as

250   could female sperm choice *per se*, a supposition supported by male-female relatedness

251   interactions on a male's probability of paternity (Olsson et al. 1996). Female strategies may

252   range from mechanical manipulation of ejaculates to biochemical selection for sperm in the

253   female tract and at the ovum surface (Firman et al. 2017). Patterns of cryptic female choice may

254   thus influence male sperm allocation to matings (Ball & Parker 2003). Male strategies involve

255   numerous trade-offs, e.g. between pre-mating expenditures such as mate searching, and post-

256   mating expenditures on sperm allocation, paternity guarding and paternal investment. The nature

257   of precopulatory male-male competition (e.g. contest *vs.* scramble) also affects expenditure on

258   pre- and post-mating male adaptations (Parker et al. 2013). So far, while some evidence exists

259   for a trade-off between pre- and post-mating expenditures (Kvarnemo & Simmons 2013), it

260   appears that the nature of precopulatory male-male competition is complex, and may be

261   influenced by covariation between the scramble-contest axis and the level of polyandry (sperm

262   competition) (reviewed in Parker 2016).

263   When there is negative covariance between male (precopulatory) mating success and

264   (postcopulatory) paternity share, such trade-offs may play a considerable role in the evolution

265   and maintenance of alternative mating tactics (Fig. 1). As more fine-grained data on mating

266   behaviour become available, detailed studies of the distribution of polyandry within populations

267   and its ramifications on sexual selection can be developed, investigating for example how mating

268   success of individual males correlate with the polyandry of their sexual partners (McDonald &

269   Pizzari 2014; McDonald et al. 2013; McDonald & Pizzari 2016; Sih et al. 2009). This parameter

270   represents the extent to which precopulatory sexual selection on male mating success (male

271   'Bateman gradient') can be strengthened or weakened by the distribution of polyandry in a

272   population (McDonald & Pizzari 2016).

273   Finally, while polyandry was originally assumed to exacerbate sexual conflict, there is

274   increasing appreciation that polyandry may have a more nuanced effect, by relaxing conflict over

275   some precopulatory decisions (e.g. mating rates, Parker & Birkhead 2013), while creating

276   conflict over postcopulatory reproductive decisions, such as female selection of sperm or

277   paternal care.

278

279   *1c. Is extrapair mating a "Promiscuous Red Queen"?*

280   Birds provide a particularly interesting study system for genetic polyandry because they

281   often copulate with partners outside the socially monogamous pair bond. Since the advent of

282   molecular parentage testing tools in the 1980s, hundreds of paternity studies in birds have

283   revealed that extrapair paternity is common, though the proportion of offspring sired by extrapair

284   males is quite variable across and even within species (Griffith et al. 2002; Westneat & Sherman

285   1997). Nevertheless, the question of why and how this variation in extrapair mating is

286   maintained, especially among closely related species with similar phenotypes, ecology and life

287   history, is still unresolved.

288   The first generation of hypotheses attempting to explain patterns of paternity share in

289   birds focused on how the opportunity for extrapair copulations may vary with breeding density

290   (Birkhead et al. 1987; Westneat et al. 1990) and breeding synchrony (Stutchbury & Morton

291   1995; Westneat et al. 1990). Although these factors might explain some of the variation within

292   species, they do not explain the broader picture of variation in extrapair paternity rates across

293   species (Bennett & Owens 2002; Westneat & Sherman 1997). Consequently, over the last two

294   decades, several attempts have been made to correlate extrapair paternity rates with various other

295   variables linked to ecology and life history variation. Some evidence suggests that high extrapair

296   paternity rates are associated with fast life histories, reduced paternal care, sexual dichromatism,

297   social monogamy (as opposed to polygyny; 'mating systems', Table 1), seasonal migration and

298   temperate breeding (reviewed in Arnold & Owens 2002; Bennett & Owens 2002; Hasselquist &

299   Sherman 2001; Spottiswoode & Moller 2004). However, there are two major problems with

300   these 'second generation' explanations; they explain rather small proportions of the total

301   variance among species, and causal mechanisms for how they influence extrapair paternity are

302   difficult to infer.

303   Similar conclusions were reached in a recent study restricted to Passerides (songbirds,

304   Lifjeld et al. 2019) where species with higher extrapair paternity rates show stronger sexual

305   dichromatism, are more migratory, and have reduced male care at the initial stages of the

306   breeding cycle (nest-building and incubation). However, effect sizes were small and the direction

307   of causality obscure. For example, the relationship with sexual dichromatism was largely due to

308   changes in female, not male, coloration, which might be explained by plumage adaptations in

309   females to promiscuous behaviour (i.e. more crypsis). Similarly, males may respond to high

310   extrapair paternity rates by allocating more effort to extrapair mating than to parental care at the

311   early stages of the nesting cycle when more females are available for extrapair copulation

312   (Westneat et al. 1990). Hence, patterns of association may reflect consequences rather than

313   causes of variation in extrapair paternity. These results imply a sobering conclusion that neither

314   factors associated with social opportunities, ecology and life history variation, nor male

315   secondary sexual traits, can explain the large variation in genetic polyandry documented among

316   bird species in general or among songbirds in particular. Additionally, rates of extrapair paternity

317   carry a rather weak phylogenetic signal (Lifjeld et al. 2019), which suggests that the behaviour is

318   an evolutionarily labile trait that responds rapidly to changing selection pressures.

319   How then can the diversity in avian genetic mating systems be explained? Extrapair

320   mating is an arena for sexual conflict where females might be better positioned to win in terms of

321   controlling the process of internal fertilization, despite the higher value of winning for males

322   (Lifjeld & Robertson 1992). Petrie and Kempenaers (1998) argued that variation in this behavior

323   can only be understood by considering the benefits, costs and constraints to female choice. Their

324   paper is a timely reminder, since some more recent studies seem to dismiss an adaptive role for

325   female extrapair mating due to a lack of empirical evidence for female genetic benefits (e.g.

326   Arnqvist & Kirkpatrick 2005; Forstmeier et al. 2014). Clearly, if female extrapair mating is

327   adaptive, the benefits must either be direct (fertility insurance) or indirect ('good', 'sexy' or

328   compatible genes), since females seem to obtain nothing but sperm through extrapair copulation.

329   An implication of this assertion is that female genetic benefits could be small or non-existent in

330   species with low rates of extrapair paternity, and that evidence for female genetic benefits should

331   primarily be sought among species with extensive female extrapair mating. There is indeed

332   evidence for genetic benefits, such as a higher cell-mediated immune response, (Arct et al. 2013;

333   Fossoy et al. 2008; Garvin et al. 2006; Johnsen et al. 2000), increased heterozygosity (Foerster et

334   al. 2003; Fossoy et al. 2008; Stapleton et al. 2007; Tarvin et al. 2005) and enhanced reproductive

335   success for offspring sired by extrapair males (Foerster et al. 2003; Gerlach et al. 2012) in

336   passerine species with high extrapair paternity rates.

337   There is evidence to indicate a key role for genes involved in immune function. Passerine

338   birds have higher rates of extrapair paternity than other clades of birds (Griffith et al. 2002).

339   They also have much more polymorphic and duplicated MHC genes (Hess & Edwards 2002;

340   Minias et al. 2018; O'Connor et al. 2016; Westerdahl 2007), which play an important role in the

341   adaptive immune system. These patterns could be causally linked. A study on eight species from

342   the passerine sister families Muscicapidae and Turdidae found a positive correlation between

343   extrapair paternity rates and sequence diversity at the peptide-binding sites of MHC class II

344   molecules (Gohli et al. 2013). In one of these species with high extrapair mating, the bluethroat

345   *Luscinia svecica,* individuals can have up to 56 different alleles and thus a minimum of 28

346   duplicated loci (Rekdal et al. 2018). Gene duplications ensure a high within-individual allelic

347   repertoire and can be favoured under high pathogen pressure (Bentkowski & Radwan 2019;

348   Minias et al. 2018). Mate choice for resistant mates or mates that enhances the pathogen

349   resistance in offspring will reinforce the natural selection for gene duplications. The positive

350   correlation between extrapair mating and MHC diversity and duplication would therefore

351   suggest that species that face strong pathogen-mediated selection evolve an extrapair mating

352   strategy for immunogenetic benefits.

353   In a 'Red Queen' (Table 1) coevolutionary dynamic between pathogens and host

354   immunity, the strength of pathogen-mediated selection may fluctuate within a species over time,

355   and also vary among species with similar ecology and distribution at any point in time. If social

356   mate choice does not provide enough options for females to choose the better genes, extrapair

357   mating might evolve as an alternative mating strategy. Once most individuals have acquired an

358   effective allelic repertoire to fight off pathogens, or social mate choice offers sufficient options,

359   the benefit of female extrapair mating will be reduced and the mating system will revert towards

360   sexual monogamy. This 'Promiscuous Red Queen' hypothesis (Fig. 2) can therefore explain why

361   divergence in extrapair mating systems evolves rapidly among closely related species.

362   Genotyping of hypervariable and highly duplicated genes like the passerine MHC with

363   next generation sequencing methods holds a great potential for testing predictions of the

364   Promiscuous Red Queen hypothesis in species with extensive extrapair mating and highly

365   diversified immune genes (Lighten et al. 2014; O'Connor et al. 2016; Sebastian et al. 2016).

366   Many sets of samples utilized previously for paternity studies should be readily available for

367   testing of MHC diversity.

368   Female extrapair mate choice for immune genes can result in different non-random

369   combinations of parental alleles. Females might prefer specific beneficial alleles (good genes) or

370   alleles that make a good match to her own alleles (compatible genes). What constitutes a

371   favourable allelic match should be investigated by analyzing the fitness of individuals with

372   different allelic repertoires (Milinski 2006). If maximum allelic diversity (in terms of number or

373   sequence diversity of alleles) yields the highest fitness, females should choose males with

374   dissimilar alleles (Strandh et al. 2012). If an intermediate allelic diversity is optimal, as too

375   many alleles can lead to autoimmunity, then females should choose a mate that gives an

376   intermediate allelic diversity in the offspring (reviewed in Milinski 2006). Regardless of what the

377   optimal allelic diversity for individuals could be, the model predicts that extrapair offspring

378   should have an allelic diversity closer to the population optimum than that of within-pair

379   offspring. If the optimum lies close to the population mean, then observed choices may not differ

380   from each other or from a random model in mean values, only in variances. Even if the mate

381   choice optimum lies close to the population mean and there is stabilising selection (reduced

382   variance) around this optimum in an ecological time frame, MHC diversity can still increase over

383   evolutionary time if the optimum moves (Estes & Arnold 2007).

384   A further challenge will be to reveal a possible mechanism for the mating preference;

385   either there could be pre-copulatory cues for a behavioral discrimination among males, or cryptic

386   female sperm selection mechanisms in the oviduct or at the ovum (Firman et al. 2017). A recent

387   study reported that the chemical composition of preen wax reflects similarity at MHC II

388   genotypes in a songbird (Slade et al. 2016), which opens up the possibility for pre-copulatory

389   mate choice based on olfactory cues in passerine birds, as previously documented in seabirds

390   (e.g. Strandh et al. 2012) (section 1a).

391

392   *1d. Inbreeding and mate choice – when are relatives preferred?*

393   Inbreeding affects fitness negatively in a wide range of taxa (Crnokrak & Roff 1999;

394   Keller et al. 1994; Keller & Waller 2002), with an increase in genome-wide homozygosity in the

395   offspring of related parents. Resulting effects on fitness can arise through partial dominance or

396   overdominance; the result of either being the promotion of inbreeding avoidance mechanisms

397   (Charlesworth & Charlesworth 1987; Marr et al. 2002). However, inbreeding may not

398   systematically result in selection for inbreeding avoidance, and it is challenging to predict when

399   an organism avoids, tolerates or even prioritizes consanguineous matings (Szulkin et al. 2013).

400   Building on well-developed theory that underpins similar phenomena in organisms such as

401   plants, where selfing is common, a consideration of both the costs of inbreeding avoidance and

402   benefits of inclusive fitness is necessary. If inbreeding costs are sufficiently low, both sexes can

403   be selected to inbreed (Kokko & Ots 2006; Parker 1979; Parker 2006) as a means to promote

404   gains in inclusive fitness among related individuals. This can be achieved through extrapair

405   copulations, although such mating decisions may come at the cost of a decrease in the fitness of

406   extrapair relative to within-pair young (Lehtonen & Kokko 2015). However, although an

407   increase in inclusive fitness was suggested as an explanation for matings among related

408   individuals as long as four decades ago (Parker 1979), it has remained widely ignored by animal

409   ecologists. More recent advances in evolutionary genetic theory have restored interest in

410   questions related to inbreeding biology (Kokko & Ots 2006), and empirical data show refined

411   mate choice based on female inbreeding status. In burying beetles, only females that are inbred

412   themselves, with greater risk of a genetic compromise by inbred partners, choose outbred males

413   (Pilakouta & Smiseth 2017).

414   Future work should address the relationship between sexual selection and inbreeding in

415   wild animal populations (section *1e*). Recent software developments, such as Rhh (Alho et al.

416   2010), have proven very useful to investigate large data sets focusing on the effects of inbreeding

417   on the process of sexual selection and other components of fitness (Bebbington et al. 2017;

418   Forstmeier et al. 2012). Furthermore, progress in genomic and theoretical investigations of

419   inbreeding (Hedrick & Garcia-Dorado 2016) and sexual selection (Anthes et al. 2017) provide a

420   thorough foundation for future work on aspects of sexual selection and inbreeding biology in the

421   wild. In the next section we take a closer look at how individuals may avoid inbreeding.

422

423   ***1e. Inbreeding avoidance: when markers matter***

424   Inbreeding avoidance can occur through polyandry (Bretman et al. 2004; Firman &

425   Simmons 2008; Foerster et al. 2003; Olsson et al. 1996; Simmons et al. 2006; Tregenza &

426   Wedell 2002), dispersal (Bollinger et al. 1993; Greenwood 1980; Pusey 1987), and kin

427   recognition (Gerlach & Lysiak 2006; Hoffman et al. 2007). In the latter, MHC haplotypes have

428   been proposed as a cue associated with kin discrimination, due to potential correlations between

429   the degree of shared MHC alleles and genome-wide relatedness (Brown & Eklund 1994; Penn &

430   Potts 1999; Potts & Wakeland 1993). Individuals that mate with MHC dissimilar partners are

431   then expected to avoid potential fitness costs associated with inbreeding, while optimizing

432   (Kalbe et al. 2009; Madsen & Ujvari 2006; Reusch et al. 2001) or maximizing offspring MHC

433   heterozygosity, via heterozygote advantage (Doherty & Zinkernagel 1975) or negative frequency

434   dependence (Hedrick 2002; Milinski 2006; Slade & McCallum 1992).

435   MHC genes encode glycoproteins that bind pathogen-derived peptide fragments on cell

436   surfaces, and thus play an important role in the immune system (Janeway et al. 2001; section 1c).

437   Therefore, two selective forces may underlie MHC-based mate discrimination, inbreeding

438   avoidance and enhanced immunocompetence. The function of MHC in mate choice and the

439   importance of disentangling these two fitness-related phenomena has been demonstrated in wild

440   Atlantic salmon (*Salmo salar*) (Landry et al. 2001), and in the Swedish sand lizard (*Lacerta*

441   *agilis*) (Olsson et al. 2003). Specifically, mated salmon pairs showed greater dissimilarity at

442   their functional MHC class II β proteins than expected under random mating, but did not exert

443   mate discrimination according to genetic relatedness or inbreeding avoidance.

444   Although MHC loci may still act as a cue for kinship in some systems (reviewed by Penn

445   & Potts 1999; Spurgin & Richardson 2010), MHC similarity between mated pairs should be

446   interpreted with a degree of caution. It is essential to distinguish between degree of kinship and

447   MHC similarity, and avoid generalization with regards to the genetic mechanisms underlying

448   differential reproductive investment in vertebrates. In other words, a sound scientific approach in

449   studies of disassortative mating patterns relies on an adequate choice of genetic marker.

450   *1f. Research on broadcast-spawning invertebrates can advance the field of sexual selection*

451   While Darwin (1871) dismissed the 'lowest classes' from sexual selection, it is now

452   appreciated that sexual selection can indeed operate in such taxa, albeit in different ways

453   (Levitan 1998). There is every reason to suppose that even in sedentary broadcast spawners,

454   sexual selection can affect gamete traits (Evans et al. 2012; Evans & Sherman 2013), gonads and

455   even life history traits (Parker et al. 2018). For example, eggs exposed to experimental sperm

456   mixtures can discriminate between sperm from different male genotypes (Palumbi 1999), and

457   sperm move preferentially towards more genetically compatible ova (Evans et al. 2012).

458   Gonadosomatic indices of conspecific males and females can vary considerably as a result of

459   sperm competition and sperm limitation levels, relative costs to the sexes of gonad tissue and

460   gamete production, and the trade-off between growth and reproduction (Parker et al. 2018).

461   One of the benefits of studying broadcast spawning invertebrates in the context of sexual

462   selection is that they represent an early stage in the sexual cascade (Parker 2014; Parker &

463   Pizzari 2015) (Table 1), capturing a phase before the evolution of enhanced mobility and

464   behavioural complexity, which, as Darwin realized, was essential for the evolution of adaptations

465   through pre-copulatory sexual selection. Since it is often difficult to separate pre-and post-

466   copulatory components of sexual selection, sedentary broadcast spawning invertebrates present a

467   unique opportunity to study the type of adaptation that can arise through sexual selection and

468   sexual conflict at the gametic level, eliminating pre-copulatory considerations. A question that

469   arises is why these taxa have remained 'frozen' at a sedentary level, without selective forces

470   favouring increased mobility and female targeted gamete release, since traces of such behaviour

471   are seen in 'pseudo-copulation' in some echinoderms (Keesing et al. 2011) and pairing behaviour

472   in certain cnidarians (Tiemann et al. 2009).

473

474   **(2) Sender and receiver mechanisms shaping signal design**

475   The proximate physiological and neurological mechanisms for production, emission and

476   perception of signals are essential keys to both adaptive and non-adaptive aspects of sexual

477   communication. In particular, the design and evolutionary trajectories of signals are shaped by

478   both *content (*e.g., accuracy and honesty of quality advertisements), and *efficacy* (e.g., sensory

479   ecology and receiver psychology). In the sections below, we discuss developments and

480   challenges in these two areas.

481   First, the mediation of signal honesty in many study systems likely depends on a dynamic

482   and complex integration of social and physiological costs, which may be both spatially and

483   temporally variable. It can be a formidable empirical challenge to measure the "right" parameters

484   at the right time, but for detailed understanding of honest signaling, this is the way forward.

485   Second, and especially relevant to the biodiversity theme of our workshop, we address

486   the increasingly appreciated impact of receiver biases (sensory, perceptual or cognitive) on both

487   design and diversification of sexually selected traits (see e.g. Cummings & Endler 2018; Ryan &

488   Cummings 2013; ten Cate & Rowe 2007). Here also lie great empirical challenges, for example

489   to objectively identify and quantify the relevant dimensions of signal traits, signaling conditions

490   and sensory tuning, to experimentally demonstrate receiver biases, and, in appropriate cases, to

491   phylogenetically reconstruct the origins and contingencies of these traits.

492

493   *2a. Mediation of signal honesty in a dynamic framework: integration of social and*

494   *physiological costs*

495   Several models of sexual selection predict that signal traits are honest indicators of

496   individual quality (Andersson 1986; Folstad & Karter 1992; Grafen 1990; Hamilton & Zuk

497   1982; Zahavi 1975). An implicit prediction of these models is a consistency in the physiological

498   mediation of honesty, that is, the costs associated with the trait should be fairly constant over

499   time. This assumption is likely unrealistic given that physiological condition can change

500   drastically, even over short periods of time (e.g. changes in physiology due to illness or a

501   variable environmental context), while many signal traits are produced once and are fairly static.

502   Further, the expression of signal traits is relative in the sense that the same signal can be viewed

503   as more or less exaggerated, depending upon the social context, such as the signal intensity of

504   conspecifics in the population. The mechanisms that allow morphological signal traits to convey

505   relevant information within a changeable social context is an interesting puzzle, especially in

506   cases where traits are developed and then fixed for a set period of time during which

507   reproductive transactions take place, such as horns and many aspects of plumage that are

508   developed annually. For dynamic traits that can be modulated in real-time, such as song rate or

509   acrobatic courtship display, the problem becomes a bit less complicated because signalers can

510   behaviorally adjust to changing physiological conditions and social context.

511   There is recent appreciation that even static signal traits have an active rather than

512   constant relationship with physiology and behavior, which likely has important implications for

513   determining how these signals remain coordinated with behavior as social contexts change (e.g.

514   Merrill et al. 2014; Safran et al. 2008; Tibbetts 2014; Vitousek et al. 2014). Still, questions

515   remain about if and how these interactions maintain the transmission of honest information to

516   conspecifics.

517   A cornerstone of both physiological and social cost models of honest signaling is that

518   signal costs are less steep for high-condition compared to low-condition individuals, which

519   creates variation in optimal signal expression (Grafen 1990). Social challenge of signal

520   expression is relatively robust to this assumption (for a review see Webster et al. 2018), but

521   necessarily reliant on frequency of challenge and either potential or realized social costs.

522   Physiological costs can also vary conditionally, for example, both testosterone-induced

523   immunosuppression and glucocorticoid-related ectoparasite load differ based on the quality of

524   the signaler in blue tits (Roberts & Peters 2009) and sand lizards respectively (Lindsay et al.

525   2016). Webster and colleagues (2018) argue that physiological costs, although subject to

526   intensive scrutiny in the last few decades, may be a less evolutionarily stable mechanism for

527   honest signal mediation than social costs. Where selection for social punishment of cheaters

528   should increase as the benefits of social status become higher, selection should favor a

529   decoupling between costly physiological processes and trait expression, such as through

530   upregulation of target sensitivity to hormonal stimulus. However, the limited empirical support

531   for physiological cost models of honest signal mediation (i.e. immunocompetence handicap

532   hypothesis, Roberts et al. 2004) may instead reflect the challenges of detecting these costs.

533   These challenges include the following. 1) The pleiotropic actions (Table 1) of key

534   biomarkers of physiological state, such as pro- and antioxidants, testosterone, and

535   glucocorticoids, can have contradictory effects on different body systems, requiring

536   measurement of a broad panel of physiological costs. For example, simultaneous and opposing

537   relationships have been detected between hormone titre and endo- vs. ectoparasite load (Fuxjager

538   et al. 2011; Lindsay et al. 2016). 2) Time-lags between when biomarkers are elevated and when

539   they exert their influence can obscure detection of costs and necessitate repeat sampling and a

540   knowledge of multiple interacting physiological systems. For example, a direct link between

541   oxidative stress and telomere length has been difficult to establish (Boonekamp et al. 2017), but

542   when this relationship was examined across multiple sampling periods, it became clear that

543   telomere length near the end of life is strongly predicted by measurements of oxidative stress

544   experience earlier in life whereas simultaneously measured oxidative stress was unrelated

545   (Olsson et al. 2018). 3) Physiological production costs are presumably accrued during a brief

546   time-window of ontogeny, often distinct from the period in which the signal is utilized in socio-

547   sexual interactions. This necessitates researchers to have a deep knowledge of how and when

548   signals are formed and requires application of appropriate experimental procedures during these

549   critical time frames.

550   The degree to which social enforcement vs. physiological costs mediate signal honesty

551   likely varies with social context (gregariousness, presence of dominance hierarchies, population

552   density) and it is clear that social costs can have physiological outcomes and vice versa. For

553   example, testosterone stimulates aggressive behavior, and social aggression itself can increase

554   testosterone further ("challenge hypothesis", Wingfield et al. 1990). Such aggressive social

555   engagement can simultaneously influence production of glucocorticoids (Creel 2001; Creel et al.

556   2013), which, in turn, can impact investment in reproductive behaviors and testosterone

557   production (Sapolsky et al. 2000). Both hormones have been causally and correlationally linked

558   to signal expression in multiple systems (Cote et al. 2010; Cox et al. 2008; Fernald 1976; Leary

559   & Knapp 2014; Lendvai et al. 2013; Lindsay et al. 2016; Lindsay et al. 2011; Mougeot et al.

560   2004; Peters et al. 2000) and the relationship between signal and hormone titre itself can be

561   bidirectional (Laubach et al. 2013; Safran et al. 2008; Tibbetts et al. 2016). If an individual is in

562   poorer condition than when the signal was produced (and any production costs accrued),

563   secondary physiological costs associated with carrying and defending an elaborate signal may

564   accumulate. An emerging mismatch then, between the intensity of the signal and the behavior

565   and apparent health of the signaler, allows the receiver to assess true condition (i.e. "integrative

566   incongruence hypothesis",   Tibbetts 2014), despite the fact that the signal itself may remain

567   seasonally static.

568   Ideas for future questioning and caveats to this type of research have been addressed

569   elsewhere (Tibbetts 2014; Vitousek et al. 2014; Webster et al. 2018). Studies that include

570   observations of trait and behavior combinations with explicit full-factorial tests that adjust signal

571   intensity, behavior, and measure consecutive and simultaneous social and physiological costs are

572   needed. Such research should be paired with examination of long-term fitness consequences of

573   potential costs.

574

575   *2b. Receiver mechanisms and biases that shape signal design*

576   "Sensory biases may cause elaboration in the absence of the Fisherian process... and

577   more reasonably be the null hypothesis and primitive model on which to build other components

578   of sexual selection" (Price et al. 1987).

579   Flowers, fruit, aposematism, mimicry, begging, and, not least, socially and sexually

580   selected threat signals: nature is full of spectacular signals that have evolved without genetically

581   correlated preferences, and by simply exploiting a biased detection, preference or aversion in the

582   intended receiver. Such receiver biases can be sensory, perceptual or cognitive (Ryan &

583   Cummings 2013), hardwired or learning-based (ten Cate & Rowe 2007), adaptive or neutral, or

584   even maladaptive if compensated by benefits in another context in which the bias is adaptive and

585   perhaps originated.

586   Like all communication signals, sexual displays can be deconstructed into two defining

587   properties: information content, and efficacy (Andersson 2000; Guilford & Dawkins 1991).

588   Traditionally, models of sexual selection were concerned with the adaptive significance of

589   female choice and whether the information content of male ornaments conveyed direct or

590   indirect (genetic) fitness consequences (Andersson 1994; see also section 1a, above). In contrast

591   to such 'sender-precursor models' (see Bradbury & Vehrencamp 2011) of signal evolution,

592   'receiver-precursor models' shift focus to efficacy aspects such as signal conditions (background,

593   attenuation) and receiver properties, by exploring how signal design may originate and be

594   exaggerated to exploit sensory or cognitive receiver biases (collectively termed 'perceptual

595   biases' by Ryan & Cummings 2013). Empirically this was triggered by classic studies of

596   preferences and biases that phylogenetically seemed to pre-date the visual or acoustic signal trait

597   (Basolo 1990; Ryan et al. 1990). Additionally, exploitation of pre-existing biases has been

598   suggested as a common origin of sexual signal evolution (Arnqvist 2006). Yet, despite the

599   obviously crucial importance that receiver properties must have for signal design and evolution

600   (Guilford & Dawkins 1991; Guilford & Dawkins 1993; Jansson & Enquist 2005), studies of

601   sexual signal evolution have, with some notable exceptions (Arak & Enquist 1993; Enquist &

602   Arak 1993), largely neglected receiver psychology (Table 1), and studies of receiver psychology

603   have rarely interpreted results in an evolutionary context.

604   While most studies of receiver biases in sexual selection have focused on mate choice,

605   the application of receiver precursor models to agonistic (threat) signaling systems presents a

606   very different context. Firstly, agonistic signals have the potential to be emancipated from the

607   constraints of direct linkage to male quality; some mechanism must maintain signal honesty, but

608   this maintenance may be achieved through socially mediated costs. Thus, agonistic signals may

609   be more evolutionarily labile than epigamic signals, potentially allowing for higher rates of

610   change in signal form. Secondly, the time scale for signal information to manifest can be much

611   shorter for agonistic signals; a male can test the honesty of another male's signal directly. This

612   interaction also sets the stage for a learning signal function, essentially representing a

613   discrimination task analogous to those shown to generate 'generalization' in the psychology

614   literature (Ghirlanda & Enquist 2003; ten Cate & Rowe 2007; Table 1). Therefore, agonistic

615   signaling systems may be ideal candidates for investigating the influence of receiver biases on

616   the evolution of signal form. Indeed, recent studies have revealed ongoing selection by receivers

617   on agonistic signal design, compatible with patterns of convergent evolution in the direction of a

618   receiver preference (Ninnes & Andersson 2014; Ninnes et al. 2015; Ninnes et al. 2017).

619   One of the primary challenges for research into this field is to tidy up the definitions and

620   terminology used in regard to receiver psychology. Whereas the environmental constraints and

621   selective forces on both senders and receivers are well covered and structured in the Sensory

622   Drive model (Cummings & Endler 2018; Endler & Basolo 1998), there is some confusion

623   regarding the terms used to describe the neurological mechanisms of receiver biases (e.g.

624   sensory, perceptual, cognitive), as well as the implications for signal selection (e.g. supernormal

625   stimulus, generalization, peak-shift) (Endler & Basolo 1998; Ghirlanda & Enquist 2003; Ryan &

626   Cummings 2013; ten Cate & Rowe 2007). Figure 3 is an attempt to distinguish some of these

627   terms and how they relate to each other, but many questions remain. For example, are 'pre-

628   existing biases' inherent hard-wired preferences, or a function of the psychology of

629   discrimination tasks (i.e. generalization; Ghirlanda & Enquist 2003; ten Cate & Rowe 2007)?

630   Future work should seek to integrate conceptual frameworks from biology and psychology to

631   help elucidate mechanistic processes. For example, an examination of 'pre-existing biases' in

632   signal design should include methods standard to the field of psychology such as the generation

633   of response gradients by testing responses at multiple points on a signal dimension. Second, is

634   the impact of receiver psychology on sexual signal design, through selection on signal efficacy,

635   underappreciated? 'Virtual evolution' experiments have suggested that receiver biases similar to

636   empirically demonstrated generalization gradients (Jansson & Enquist 2003), are sufficient to

637   drive signal exaggeration (Jansson & Enquist 2005). This aligns with for example the consistent

638   and pre-existing receiver biases found in closely related widowbirds and bishops (*Euplectes* spp),

639   displaying varying degrees of signal exaggeration (Ninnes & Andersson 2014; Ninnes et al.

640   2015; Ninnes et al. 2017; Pryke & Andersson 2002). Echoing previous researchers including

641   Endler (1992), Ryan & Cummings (2013) and West-Eberhard (2014), we suggest that intensified

642   attention to the origins, mechanisms and response gradients of receiver biases will bring us

643   closer to the neuroethology of signal selection and the design and diversity of sexual signals. In

644   *section 4a* we also discuss some of the implications of evolving receiver preferences on

645   speciation.

646   Lastly, the notions of 'aesthetic preferences' and 'beauty, used in both Darwins and

647   Fishers writings on female choice, have been treated as objective biological traits (Prum 2017;

648   Renoult et al. 2016), leading to heated debate (e.g. Borgia & Ball 2018; Patricelli et al.). Renoult

649   and Mendelson (2019) argue that aesthetic preferences represent neurobiologically efficient and

650   thereby adaptive cognitive processing, strongly resembling the 'inevitable signal recognition

651   biases' suggested by the artificial neural network models of Enquist and Arawk (1993). Most

652   controversy has been instigated by Prum (2012; 2017) who argues not only that the Fisherian

653   process should be the null model of the evolution of mating preferences, but that any hereby

654   evolved cognitive bias is the 'aesthetic sense' while the exaggerated signal properties define

655   'beauty'.   These assertions received several critical responses (e.g. Borgia & Ball 2018;

656   Patricelli et al.), also from quarters that agree with Prum that "mate choice for indicators is often

657   assumed as an explanation for the evolution of elaborate displays without sufficient

658   consideration of other processes" (Patricelli et al. 2018).

659   In our own view, perceptual and cognitive biases are likely to be key components of the

660   'aesthetic sense' that Darwin (1871) attributed to choosy females (see also Renoult 2016;

661   Renoult et al. 2016). Moreover, since perceptual biases may drive ornament or armament

662   exaggeration without involving any sender-receiver genetic covariance or the Fisher process

663   (Price et al. 1987), it may be a simpler, and more testable, 'null model' of signal selection in

664   general, and as regards sexual selection, it would apply to both mate choice and contest

665   competition.

666

667   **(3) Genetic architecture of sexual selection**

668   Understanding the genetic architecture of sexual selection, and thus evolvability and

669   constraints on sexually selected traits, is a long-term goal of the field and one where substantial

670   progress has been made in recent years. Notable examples include advances in our understanding

671   of the genetic basis of stripes in cichlid fish (Kratochwil et al. 2018), QTL loci underlying song

672   in Hawaiian crickets (Ellison & Shaw 2013) and other insects (Gleason et al. 2016),

673   morphological traits known to be targets of sexual selection in birds (Hansson et al. 2018), and

674   genes involved with conversion of red carotenoid pigments in birds (Lopes et al. 2016; Mundy et

675   al. 2016). There is an increasing number of studies that demonstrate convincing heritability of

676   key sexually selected traits, like copulatory organs or chemical signaling, and there are several

677   examples demonstrating the evolutionary *consequences* of sexual selection, such as

678   incompatibilities between species (Rose et al. 2014). However, the great progress in identifying

679   genes associated with morphological, coloration and signaling traits known to be under sexual

680   selection has not been accompanied by similar demonstrations of predicted evolutionary

681   signatures in many such genes. Specifically, no example exists, to our knowledge, in which the

682   genetic basis of a sexually selected trait has been shown to evolve rapidly in response to recent

683   or ongoing sexual selection, either experimentally in the lab or in nature.

684   In contrast, rapid evolution is easier to detect in reproductive genes such as accessory

685   gland and reproductive proteins (Finn & Civetta 2010; Hurle et al. 2007; Wyckoff et al. 2000)

686   and many gene systems associated with interactions between sperm and egg as well as

687   copulatory proteins have been identified in *Drosophila*. Proteomic approaches are adding detail

688   to our understanding of the complex chemical cocktails exchanged during mating in flies,

689   primates and other groups (Claw et al. 2018; Gotoh et al. 2018; Wilburn et al. 2018). The

690   predicted rapid evolution of genes involved in co-evolutionary interactions between the sexes,

691   and between hosts and parasites, has been demonstrated repeatedly. For example, immune genes

692   that may serve as 'good genes' such as MHC genes (see section *1c*) undergo a type of cycling

693   characterized by rapid evolution (Eizaguirre et al. 2012). A greater understanding of the

694   evolutionary dynamics of genes underlying signaling and performance traits therefore stands as a

695   major gap in our field.

696

697   ***3a. What genes underlie variation in performance?***

698   A goal of contemporary research in the field of sexual selection is the identification of

699   candidate loci for performance. Detailed and often time-intensive field studies of sexual selection

700   are required to identify the phenotypes associated with display or mating success. When

701   combined with modern sequencing techniques, these types of data make it possible to contrast

702   the expression levels or genotypes of the successful individuals with the unsuccessful, revealing

703   key loci underlying measures of performance. Although in principle straightforward, almost no

704   published studies have used such a protocol (but see Johnston et al. 2013). While sequencing on

705   a large scale can still be cost prohibitive, perhaps more importantly, the type of detailed

706   behavioral observations producing reliable individual data on complex parameters like "mating

707   success" are expensive in terms of investment in time and in effort. Field studies on the great

708   snipe (*Gallinago media*) illustrate the latter point (Höglund et al. 2017). To obtain reliable

709   sample sizes, the field work has been conducted over many years under sometimes harsh field

710   conditions and the data is subject to problems inherent to all multi-season datasets, such as

711   observer, site and year effects.

712   Importantly, genotype effects on mating success may be context dependent, as appears to

713   be the case in great snipes. The effect of candidate SNPs (Single Nucleotide Polymorphism) on

714   great snipe mating success depended on whether birds were infected with avian malaria, as

715   revealed by significant interaction terms among infection status and genotype in a few loci

716   (Höglund et al. 2017). Genomic studies of sexual selection are emerging (see section *4e*), and

717   more such are required to make general conclusions. For this to be possible, long term studies

718   with careful observations and detailed knowledge of natural history combined with genomic data

719   is the only remedy.

720

721   ***3b. Genic capture and ongoing sexual selection***: *how many genes are enough?*

722   A classic question in sexual selection theory is to what extent the evolution of secondary

723   sexual traits is constrained by the exhaustion of genetic variation resulting from the process of

724   selection itself ('the lek paradox'; Andersson 1994; Kirkpatrick 1982; Table 1). In some cases

725   trait expression is dictated by allelic variation at a single locus, whereas in others trait expression

726   is polygenically determined. If genetic variation limits exaggeration of secondary sex traits, this

727   effect should decrease with the number of loci dictating trait development. For example, mating

728   with close relatives contributes to loss of genetic variation and thus, inbreeding opposes

729   sustained sexual selection and secondary sex trait evolution (Keller & Waller 2002). Empirical

730   research in the fields of sexual selection and evolutionary genetics are inconsistent in terms of

731   the generality of these fundamental processes.

732   Much discussion has been directed toward the investigation of genetic architecture of

733   multilocus signaling traits with the underlying idea that strongly condition-dependent traits

734   capture all the genetic variance in condition ('genic capture', Rowe & Houle 1996; Tomkins et al.

735   2004; Table 1). Since many loci provide a large target for mutations, genetic variation could

736   persist over time despite strong directional selection. Work on genic capture has until recently

737   been largely theoretical, because the genotypes of few phenotypic traits are usually unknown in

738   natural populations. An example demonstrates how genetic variation for a strongly polymorphic

739   secondary sex trait, horn type in Soay sheep, is maintained by a trade-off between natural and

740   sexual selection in a single gene (*RXFP2*) (Johnston et al. 2013). Horn shape is under strong

741   sexual selection in males, but not in females, so another hypothesis, intra-locus sexual

742   antagonism (see section *3c*) could also be rejected (Johnston et al. 2013). Work on field caught

743   *Drosophila,* however*,* showed that even with substantial genetic variance in a secondary sex trait,

744   cuticular hydrocarbons, the vast majority of this variation was not closely associated with the

745   direction of sexual selection (Hine et al. 2004). Despite condition-dependence of traits, genetic

746   variation underlying trait expression can be depleted by sexual selection in the wild and thus

747   genic capture did not offer a resolution to the lek paradox in this system. In an interesting

748   empirical example of genic capture, chemical mutagenesis of the male guppy (*Poecilia*

749   *reticulata*) germline negatively affected courtship displays but not colouration, indicating that the

750   former is a large mutational target (Herdegen & Radwan 2015). Such mutagenic approaches,

751   when complemented with whole-genome sequencing to verify affected loci, offer a robust

752   approach to study mutational targets, but are limited in their applicability to sexual selection on

753   polygenic traits in the wild. Although the presence of only a few genes can be adequate for

754   evolution of secondary sexual characters to proceed in some systems, multiple and variable

755   genes may not be enough to sustain character evolution in other systems.

756

757 *3c. How do genome processes impact sexual selection and sexual conflict?*

758   Although much empirical research related to sexual selection has been conducted

759 extensively at the organismal level, little progress has been made in identifying the genomic

760 mechanisms responsible for various sexually selected traits (but see Johnston et al. 2011).

761 Because sexual dimorphism is often the evolutionary outcome of sex-specific selective patterns

762 such as sexual selection, understanding the molecular basis of sexually dimorphic traits is key to

763 understanding evolution by sexual selection. Whereas sex-biased gene expression has been

764 documented in various tissues in many taxa, demonstrating dimorphism at the molecular level

765 (e.g. Leder et al. 2010; Mank et al. 2010; Zhang et al. 2007), it is unclear in many cases whether

766 sex-biased genes are actually antagonistic or if they are a result of current or past antagonistic

767 effects (Parsch & Ellegren 2013). Additionally, although there are numerous theoretical papers

768 connecting the evolution of sex chromosomes, sex-biased expression and sexual antagonism (e.g.

769 Kirkpatrick & Guerrero 2014; Mank et al. 2014; Parsch & Ellegren 2013), it has been difficult to

770 test hypotheses in the wild (but see empirical advances by Hollis et al. 2014; and review by

771 Mank 2017). Much of the difficulty in identifying the genomic bases of sexually selected traits is

772 due to our limited understanding of the genome. It is increasingly feasible to gather DNA,

773 mRNA and protein sequence data, yet understanding genomic and proteomic modifications, such

774 as epigenetics or protein phosphorylation, and the details of interactions among molecules is also

775 necessary to understand the final phenotype.

776   It has become widely accepted that regulatory variation is the likely source for much of

777 the observed phenotypic variation among and within species (e.g. Carroll 2008), and regulatory

778 differences have been implicated as a mechanism resulting in sexual dimorphism (Williams et al.

779 2008). If one considers the concept of intra-locus conflict, where males and females exhibit

780   different fitness optima at a genomic locus, conflict may be resolved by differential regulation of

781   that gene in males and females without dramatic changes in the genome. As suggested by Rice

782   (1984), the sex chromosomes may be hotspots for sexually antagonistic genes, but they also

783   provide a potential mechanism for resolving both intra- and inter-locus conflict through the

784   maintenance of sex-specific alleles. In effect these alleles must be largely regulatory, since there

785   is little unique information on the sex chromosomes in many known systems, and recent work

786   shows that noncoding regulatory sequences alone are sufficient to drive sex reversal in mice

787   (Gonen et al. 2018). Consistent with this idea, replacement of Y chromosomes between species

788   of flies results in genome-wide changes in gene expression, mediated by regulatory factors

789   encoded on the Y chromosome (Branco et al. 2013; Sackton et al. 2011). Additionally,

790   organisms without sex chromosomes still exhibit sex differences, most basically in gonad

791   formation and physiology, but also in behaviour. Thus differential regulation leading to sexual

792   dimorphism must be achieved through regulatory cascades that in some cases can be initiated by

793   one or few genes, or even by the environment (Bachtrog et al. 2014).

794   Another question is which ontogenetic or polyphonic stage to sample individuals in order

795   to understand the genetic basis of a sexually selected trait. Much of the obvious morphological

796   and behavioral differences between the sexes are studied in sexually mature organisms, yet the

797   molecular bases for many of these differences, particularly morphology or coloration, are likely

798   due to differential expression initiated early in development before the trait becomes obvious

799   (Hubbard et al. 2015). This is the case with sexually dimorphic abdominal pigmentation in *D.*

800   *melanogaster* (e.g. Williams et al. 2008), and most studies that identify differences in gene

801   expression between species or ontogenetic stages are in fact identifying regulatory differences

802   (Mallarino et al. 2016). This early development of dimorphism makes it difficult to associate the

803   phenotypic differences observed in adult organisms with specific DNA differences or mRNA

804   expression that may underlie the trait. Studies examining the molecular basis of sexually selected

805   signals in birds often focus on the seasonal elaboration of traits such as plumage color in an

806   effort to identify relevant genes (Lopes et al. 2016; Mundy et al. 2016). New epigenetic

807   techniques, such as ATAC-seq, can identify regions of the genome with open chromatin,

808   unwound from nucleosomes and available for binding by transcription factors, and promise to

809   identify new ways in which the genome can be differentially modulated between the sexes

810   without requiring differences in DNA sequence (Buenrostro et al. 2015).

811   Molecular pleiotropy and the physical location and recombination environment of a gene

812   may constrain its evolvability and ease of study (see 'pleiotropy', Table 1). For example, many

813   proteins form complexes with other proteins or bind to DNA or RNA in order to carry out their

814   function. These interactions limit the mutations that a given gene can accumulate before it is

815   non-functional (Papakostas et al. 2014). Additionally, many genes are pleiotropic and may

816   influence several, even quite different biological processes by being expressed at different times,

817   in different tissues or by forming complexes with different protein partners. Linkage and

818   recombination can also affect the evolvability of genes (Table 1). Genes that are in close

819   proximity on a chromosome will likely be inherited together, thus linked allelic combinations of

820   these genes will tend to be inherited together. In some cases linked loci can even become fixed,

821   as when a chromosomal inversion occurs, creating a 'supergene' with diverse effects on the

822   breeding phenotype (Kupper et al. 2016; Lamichhaney et al. 2016; Tuttle et al. 2016). Clearly, a

823   better understanding of genome processes as well as how genes interact and are expressed in

824   both sexes will aid in the understanding of sexually selected traits and sexual antagonistic genes.

825

826 **(4) Sexual selection and sexual conflict as drivers, or obstacles, of speciation**

827   Sexual selection is an important evolutionary force in the context of speciation (e.g.

828 Kraaijeveld et al. 2011; Panhuis et al. 2001; Ritchie 2007; Schaefer & Ruxton 2015).

829 Traditionally, research in this field has focused on the role of sexual selection during early

830 phases of population divergence, because divergence in display traits and preferences can

831 quickly cause pre-zygotic isolation (Coyne & Orr 2004). This focus is not surprising given the

832 huge variation we observe in sexually selected traits among relatively newly formed, closely

833 related species. However, sexual selection through mate choice is unlikely to lead to speciation

834 by itself (Ritchie 2007; Servedio & Burger 2014), an argument that has resulted in a growing

835 interest in understanding sexual selection in the broader context of ecological speciation (Martin

836 & Mendelson 2014; Scordato et al. 2014).

837   There is also a growing awareness that cryptic forms of female choice, i.e. post-

838 mating/post-spawning processes resulting in conspecific sperm precedence, may be important

839 sources of reproductive isolation (Howard 1999; Palumbi 2009; Swanson & Vacquier 2002; Van

840 Doorn et al. 2001). In addition, male-male competition (Qvarnström et al. 2012; Tinghitella et al.

841 2018) and sexual conflict (reviewed by Parker 2006) are becoming increasingly recognized as

842 important mechanisms of speciation. Below, we discuss these novel lines of progress in our

843 understanding of the role of sexual selection in speciation. Additionally, we provide some

844 suggestions for use of genomic methods in testing current controversies in the field.

845

846 *4a. Mate choice and ecological speciation*

847   The vast majority of theoretical models evaluating the role of sexual selection in

848 speciation are based on *Fisherian* processes of sexual selection (Lande 1981). Why has the

849   interest in benefit-driven mate choice been so slow in being transferred from research on sexual

850   selection within populations to research on the role of sexual selection in speciation processes?

851   At least one identified potential "problem" with benefit-driven mate choice in the context of

852   speciation is associated with the unidirectional nature of choice. Disruptive selection is

853   considered to be a prerequisite for population divergence under gene flow but disruptive

854   selection on benefit-driven mate choice is generally not expected. Moreover, while differences in

855   natural selection experienced by geographically separated populations may quickly lead to

856   divergence in male display traits (Maan & Seehausen 2011), mating preferences (Table 1) may

857   not change in a similar manner. For example, when a long bird tail signals some type of quality

858   and males have evolved shorter tails in one population due to high local costs (e.g. strong

859   predation pressures), females from that population would not be expected to prefer males with

860   relatively short tails. Females from this population of short-tailed males should instead be

861   expected to prefer to mate with males from long-tailed populations whenever they have a chance

862   to do so.

863   There are several possible solutions to this "problem". First, female mate preferences

864   may actually experience corresponding natural selection pressures as male display traits. Segami

865   Marzal et al. (2017) found that cryptic female poison frogs experienced elevated predation risk

866   when associating with an aposematic partner. Hence, predation may act directly on female

867   choice favoring the evolution of preferences for less conspicuous males. Second, female mate

868   preferences may be exposed to other environment-specific natural selection pressures that target

869   their sensory system, resulting in population specific mate choice targets ('sensory drive', Table

870   1, Boughman 2002; Endler 1992). In short, if a sensory trait, for example vision, is locally

871   adapted and also involved in finding mates or assessing their quality, this functional linkage may

872   result in divergence in male display traits (Boughman 2002; see also section 2b where we discuss

873   how receiver mechanisms and biases shape signal design). Moreover, Schluter and Price (1993)

874   suggested that several male traits may reveal the same type of benefits but the perception of these

875   traits may differ between environments resulting in different traits being the prime targets for

876   benefit-driven mate choice in different environments. Empirical evidence suggest multiple

877   effects of female sensory traits causing divergence in male courtship traits (Boughman 2001;

878   Boughman 2002; Fuller & Noa 2010; Seehausen et al. 2008). Finally, a third possible solution is

879   that mate preferences remain the same but assortative mating between populations that are

880   adapted to different environments is still possible (Kopp et al. 2018). For example, immigrant

881   males that lack genes underlying local adaptation are unable to develop large ornaments, such as

882   bright coloration, enabling females to discriminate against them (van Doorn et al. 2009). Males

883   that are well adapted to the local environment will therefore be more attractive to females, and

884   offer direct benefits (e.g. territory quality) or genes that are related to local adaptation (reviewed

885   in Safran et al. 2013). Thus, under certain prerequisites, genes that contribute to adaptation will

886   spread in the population through both natural and sexual selection. In some systems, however,

887   rare immigrants to a population appear to achieve enhanced survival and lower parasite loads

888   compared to residents (Bolnick & Stutz 2017). In section *4d* below, we discuss how genomic

889   approaches can be used to test the prerequisites for sexual and natural selection to jointly

890   promote speciation.

891

892   *4b. Cryptic female choice and post-copulatory reproductive isolation*

893   Choice mechanisms directly based on conspecific sperm traits rather than species-specific

894   secondary sexual traits are known from external fertilizers, like abalones, sea urchins and oysters

895   (Vacquier & Swanson 2011) and fish (Yeates et al. 2013). Post-copulatory reproductive barriers

896   are much less known in internal fertilizers, at least partly because of the difficulty of studying

897   what goes on within the female reproductive tract (Birkhead & Brillard 2007). However, there is

898   increasing evidence for such "cryptic" mechanisms of female choice, where heterospecific sperm

899   is discriminated against also in internally fertilizing animals, like insects (Coyne & Orr 2004)

900   and non-passerine birds (Birkhead & Brillard 2007).

901   Although pre-copulatory mate choice based on plumage and song traits is well known in

902   passerine birds, little attention has been paid to possible post-copulatory reproductive barriers.

903   Passerine sperm morphology is known to evolve rapidly (e.g. Hogner et al. 2013) and the rate of

904   evolution is positively related to the risk of sperm competition (Rowe et al. 2015). One emerging

905   question is therefore whether sperm divergence could be causally involved in reproductive

906   isolation between incipient species pairs with sperm competition, through differential

907   fertilization success of conspecific over heterospecific sperm. At the mechanistic level, this could

908   work via co-evolution between sperm length and sperm storage tubule length (Briskie &

909   Montgomerie 1992). In other words, sperm of a heterospecific male might be selected against

910   because they are not the right size to fit in the sperm storage tubules. Alternatively, reproductive

911   proteins in seminal- and ovarian fluid, which are known to evolve rapidly in other taxa (Turner

912   & Hoekstra 2008), but see (Rowe et al. 2018), may be the key molecules involved in post-

913   copulatory selection mechanisms also in passerines.

914   A recent study of two sympatric *Ficedula* flycatchers, suggests that female pied

915   flycatchers (*F. hypoleuca*) that are constrained to pair with heterospecific males, are more prone

916   to perform extra-pair copulations with conspecific males and able to exert cryptic choice in

917   favour of their sperm, thereby reducing the risk of producing unfit hybrid offspring (Cramer et

918   al. 2016a). By *in vitro* testing of sperm velocity from males of each of the two species against

919   cloacal fluid collected from females of both species, the authors found an asymmetric pattern:

920   sperm from collared flycatcher (*F. albicollis*) males experienced a higher velocity reduction in

921   pied flycatcher female fluid than in collared flycatcher fluid, but not vice versa. Furthermore, this

922   effect was strongest for pied flycatcher females with a high likelihood of previous exposure to

923   sperm of collared flycatcher males. Such effects were not seen in studies of four other, non-

924   hybridizing passerine species pairs, with a range of divergences in genetic distance and sperm

925   morphology (Cramer et al. 2014; Cramer et al. 2016b), suggesting that selection against

926   hybridization may have favored the evolution of this cryptic barrier in flycatchers.

927   Future studies, targeting the molecular mechanisms underlying sperm performance within

928   conspecific and heterospecific female reproductive environments, will shed novel light on the

929   type of selection acting at this cryptic level of female choice and the relative importance of pre-

930   and post-copulatory mate choice in speciation processes.

931

932   *4c Male-male competition and niche segregation*

933   When males compete over females or resources needed to attract females, they often bias

934   their aggression towards the most common male phenotype in the population (Qvarnström et al.

935   2012; Tinghitella et al. 2018). This means that both the invasion of, for example, new color

936   morphs and stable polymorphism within populations become much more likely than in cases

937   when mate choice acts as the main mechanism of sexual selection (reviewed in Qvarnström et al.

938   2012; Tinghitella et al. 2018). One may argue that such negative frequency-dependent selection

939   driven by male aggression could promote divergence in e.g. color morphs with little divergence

940   in niche use. In agreement with this line of reasoning, Seehausen and Schluter (2004) found that

941   sibling species of cichlid fishes in Lake Victoria were ecologically similar but markedly different

942   in coloration. Closely related species of cichlids with similar color were also less likely to

943   occupy the same habitat patches (Seehausen & Schluter 2004). Should we then expect the

944   diversifying aspects of male-male competition to be unrelated to ecological speciation?

945   There are at least three main reasons to expect that divergence in sexually selected traits

946   used in male contest competition may often be associated with divergence in niche use. First,

947   dominance hierarchies are often asymmetric between color morphs and population divergence in

948   traits used in combat (e.g. horns, large bodies) is often directly associated with dominance

949   strategies and thereby access to other resources than females (Forsgren et al. 1996; Qvarnström

950   et al. 2012). We therefore predict population divergence in sexually selected traits used in male-

951   male competition and population divergence in niche use to often be associated. Second, at

952   secondary contact between young species, selection against heterospecific aggression may

953   contribute to increased niche segregation. Ongoing habitat segregation was for example observed

954   in a recently formed hybrid zone between collared and pied flycatchers on the Swedish island,

955   Öland. An asymmetry in male contest competition ability over nesting sites needed to attract

956   females resulted in male pied flycatchers being displaced from deciduous forests patches into

957   less preferred mixed forest habitats (Vallin et al. 2012). As a consequence of this habitat

958   segregation, the access to resources used to feed nestlings declined dramatically in breeding

959   territories used by pied flycatchers but the risk of hybridizing with collared flycatchers also

960   declined (Rybinski et al. 2016). Thus, habitat segregation not only led to reduced aggressive

961   interactions between the two flycatcher species, but also to reproductive isolation. Third,

962   environmental effects on the efficiency of different signaling traits may not only affect which

963   traits become targets of female choice by being relatively more detectable or reliable (Schluter &

964 Price 1993) but also which traits become targets of male competition. Lacky and Boughman

965 (2013) compared limnetic and benthic species of threespine stickleback fish across different

966 habitats. They found that mixed habitats favored two trait combinations and thereby likely

967 divergence and reproductive isolation while homogenous open habitats favored only one trait

968 combination and thereby likely hindered trait divergence and reproductive isolation (Lackey &

969 Boughman 2013).

970

971 **4d. How does sexual conflict impact speciation processes?**

972 In contrast to sexual selection, less research has targeted the consequences of sexual

973 conflict on speciation. Several approaches concur with the notion that sexual conflict will also

974 catalyse speciation, others suggest the reverse (see reviews by Gavrilets 2014; Parker 2006). The

975 hypothesis that selection favours restriction of gene flow when hybrids between ecotypes have a

976 fitness disadvantage relies on the tacit assumption that female interests will prevail in mating

977 decisions. However, unless the hybrid disadvantage is sufficiently great, it will be in male

978 interest to mate (Kokko & Ots 2006; Parker 1974; Parker 1979; Waser et al. 1986); a wide

979 parameter zone exists over which sexual conflict applies and in this zone selection on females

980 acts as a force favouring speciation by restricting gene flow, but selection on males acts as a

981 force resisting speciation by promoting gene flow. While some empirical studies suggest that

982 sexual conflict promotes speciation, others do not (Gavrilets 2014; Plesnar-Bielak et al. 2013).

983 Extending this argument, Parker & Partridge (1998) suggested that under sexual conflict,

984 'female win' resolutions in given taxa may result in high species numbers and low genetic

985 variation per species, whereas 'male win' resolutions may result in taxa with low species

986 numbers and high genetic variation per species. Which solution prevails depends on the value of

987   winning (generally greater for males) and 'power', a measure related to the fitness costs of

988   overcoming the current defense by the opposite sex (costs for females of preventing mating may

989   often be less than the costs for males of imposing matings). Similarly, Magurran (1998) proposed

990   that sexual conflict and male interests may be key to explaining the absence of speciation in

991   Trinidadian guppies, *Poecilia reticulata*, where population differentiation is nevertheless high

992   and female choice appears to reinforce divergence. Sneak mating by males is common, and may

993   generate sufficient gene flow to prevent reproductive isolation. Early comparative attempts to

994   establish a link between speciation rate and possible proxies for sexual conflict (sexual size

995   dimorphism, polyandry) in mammals, butterflies and spiders were unsuccessful (Gage et al.

996   2002), but recent work on shorebirds also gives some support to the notion that male interests

997   (measured in terms polygamy) can act against speciation (D'Urban Jackson et al. 2017).

998   The role of sexual conflict in speciation certainly deserves further investigation. An

999   interesting complication is that if two subpopulations, A and B, have diverged sufficiently, the

1000   fitness consequences to males and females of A and B can become asymmetric, e.g. the relative

1001   hybrid disadvantage in (i) male A x female B matings may differ from that in (ii) female A x

1002   male B matings. Additionally, the balance for the sexes between the fitness value of winning (i.e.

1003   between mating or not mating) and 'power' (the fitness cost of overcoming defences) may differ

1004   in these two possible pairings (Parker 1979; Parker & Partridge 1998). Such asymmetries could

1005   hypothetically lead to a variety of situations: for example, sexual conflict could occur in case (i)

1006   but not in case (ii), so that (depending on the 'value of winning value'/'power' balance) selection

1007   could favour speciation in one population but not the other, a form of "speciation conflict".

1008

1009   ***4e. Genomic properties of speciation through sexual selection***

1010   Genomic approaches may help to bridge several important gaps in our current

1011   understanding of the role of sexual selection in speciation. Detailed information about the

1012   genomics underlying sexually selected phenotypes can be used to test key assumptions of

1013   theoretical models on sexual selection (Wilkinson et al. 2015, see also section 3 above) and then

1014   be placed into the context of speciation. Because, as mentioned above, divergent sexual selection

1015   alone rarely causes speciation (Ritchie 2007), one particularly interesting aspect of 'the context

1016   of speciation' deals with how traits involved in several different aspects of reproductive isolation

1017   can remain in linkage disequilibrium under gene flow (Butlin & Smadja 2018; Coyne & Orr

1018   2004; Seehausen et al. 2014; Table 1). Hybridization can easily break up crucial trait-

1019   combinations through recombination and segregation (Table 1, Felsenstein 1981). The

1020   completion of speciation under gene flow is therefore considered to be more likely when traits

1021   involved in reproductive isolation have dual functions (Gavrilets 2004; Slatkin 1982; Smadja &

1022   Butlin 2011). The completion of speciation occurs because, when a single trait is under divergent

1023   natural selection and also involved in mate choice, the association between these two functions

1024   cannot be easily broken by recombination. There are numerous examples of putative multiple

1025   effect traits ('magic' traits) involved in population divergence, many focusing on the signaling

1026   side of sexual selection (Servedio et al. 2011; Smadja & Butlin 2011). One of the best examples

1027   is from *Heliconius* butterflies, where the mimicry pattern also has a signaling function when

1028   acquiring mates (Kronforst et al. 2006; Merrill et al. 2011). However, mate preferences can also

1029   function as 'magic' traits with dual functions. For example, in the context of sensory drive

1030   speciation (Table 1) in teleost fishes. In short, if a sensory trait, for example vision, is locally

1031   adapted and also involved in finding mates or assessing their quality, this means a functional

1032   linkage between niche use and mate choice. Given the difficulties in unravelling the genetic

1033   background of especially mate choice, these systems could be good candidates for studies of

1034   genetic architecture of mate preferences (Table 1). In *Pundamilia* cichlid fish and *Heliconius*

1035   butterflies, where gene flow is evident and multiple effect traits have been invoked to be

1036   instrumental in the speciation process, empirical results are consistent with few genes having a

1037   major effect on female assortative mating (Haesler & Seehausen 2005; Kronforst et al. 2006;

1038   Merrill et al. 2011; Svensson et al. 2017).

1039   When several different traits contribute to reproductive isolation, linkage disequilibrium

1040   among the underlying loci may shelter against the homogenizing effects of gene flow. Barton

1041   (1983) introduced the term 'coupling' to refer to a process where buildup of linkage

1042   disequilibrium between loci under divergent selection promotes speciation (Flaxman et al. 2014).

1043   Such coupling occurs because each locus with an effect on reproductive isolation is then not only

1044   influenced directly by selection acting on itself but also by indirect selection acting on the other

1045   coupled loci leading to stronger overall isolation. Much scientific attention has been directed to

1046   possible genetic coupling by physical linkage between isolation loci through proximity on

1047   particular chromosomes (e.g. sex chromosomes, Qvarnstrom & Bailey 2009), particular parts of

1048   chromosomes with low recombination rates (e.g. centromeres Ortiz-Barrientos et al. 2016) or

1049   within recently formed chromosomal rearrangements (Noor et al. 2001). Empirical studies

1050   suggest that differentiated loci are indeed enriched in genomic regions with reduced

1051   recombination (Wolf & Ellegren 2017) but such patterns alone need to be interpreted with

1052   caution. Genomic studies need to be tightly intertwined with knowledge about phenotypic effects

1053   to reveal which differentiated loci that have effects on reproductive isolation as differentiation

1054   *per se* does not impose a key function in the speciation process. To achieve this goal several

1055   different methods need to be combined. First, ecological and behavioral studied are needed to

1056   reveal the function of phenotypic traits and their role in niche use, mating and most importantly

1057   their barrier effects - their role in causing reproductive isolation. Second, the genetic variants

1058   underlying these traits need to be revealed with genome wide association studies or similar

1059   (GWAS, Rockman 2012). Finally, Butlin and Smadja (2018) recently suggested that more

1060   scientific attention also needs to be directed towards the coupling processes themselves and that

1061   the term 'coupling' should be extended to include any process that generates coincidence of

1062   barrier effects. Reaching these three goals is a challenging empirical undertaking but would

1063   reveal key information about the speciation process, including the role of sexual selection in

1064   driving reproductive isolation.

1065

1066   **CONCLUSIONS**

1067   Our survey of emerging questions in sexual selection, while necessarily incomplete,

1068   shows that the field is on the cusp of a major revolution. In many ways the theoretical framework

1069   for the study of sexual selection and sexual conflict is robust, having been refined since the late

1070   1960s. What is needed now are bold empirical attempts to understand the diverse molecular and

1071   ecological mechanisms that could modulate the outcomes of sexual selection and sexual conflict.

1072   One obvious frontier of sexual selection resides in increased understanding of the

1073   molecular genetic and physiological mechanisms of traits subjected to or contributing to sexual

1074   selection and sexual conflict, an understanding that next-generation molecular methods will help

1075   achieve. Although interesting in its own right, it is perhaps even more important what these

1076   mechanisms imply about the history, constraints and evolvability of traits, allowing several

1077   outstanding issues in sexual selection and sexual conflict to be addressed. A molecular

1078   understanding of sexually selected traits will help the field discriminate between alternative

1079 hypotheses for the maintenance of variability in those traits, for example, whether they have

1080 evolved via good genes mechanisms or by more arbitrary or neutral processes (Prum 2010; Prum

1081 2017). A good example is the recent elucidation of the genes involved with carotenoid

1082 metabolism in birds (Lopes et al. 2016; Mundy et al. 2016; Toews et al. 2017). With a clear

1083 understanding of the genes that process ingested carotenoids, we can gain better estimates of the

1084 true costs and constraints on those traits, which in turn can help predict their evolutionary

1085 trajectories within and between species.

1086   It would, however, be short-sighted to conclude that molecular mechanisms alone will

1087 bring a holistic understanding of sexual selection and conflict. Genetic mechanisms only have

1088 meaning when appropriately placed in the context of the natural history and ecological and social

1089 constraints that characterize different systems exhibiting sexual selection. Recent examples show

1090 how molecular methods achieve their biggest impact when deployed in the context of large-scale

1091 ecological and behavioral studies of naturally occurring variation in the wild (e.g. Bosse et al.

1092 2017). And although an understanding of the historical origins of traits, i.e. ancestral constraints

1093 and exaptations, is (or should be) the very essence of modern evolutionary biology, there is still a

1094 striking lack of 'tree-thinking' that would facilitate understanding such constraints in biology in

1095 general, and sexual selection in particular (Price et al. 2011). This trend is particularly true in the

1096 study of the many micro- and macroevolutionary consequences of sexual selection (but see Prum

1097 1997).

1098   Advances at the interface of molecular, ecological, behavioral and theoretical research

1099 will require collaborations between experts in divergent areas, a goal that we hope our workshop

1100 in Gothenburg has fostered.

1101

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1115 **Author contributions**

1116 SE organized the project, and SA, CK, WRL, and MO organised the workshop. WRL compiled

1117 and coordinated writing the manuscript. All authors participated in the "Origin of Biodiversity

1118 Workshop: Sexual Selection and Sexual Conflict" in Göteborg (Sweden), contributed to writing

1119 the manuscript, read and approved the final version submitted for publication. Lead author

1120 contributions to various sections are as follows (alphabetized by author surname): section 1- BB,

1121 CK, JTL, MO, GAP, TP: section 2 - SA, WRL, CEN, RJS: section 3 - SE, JH, EHL, MO: section

1122 4 - AJ, GAP, AQ, RJS, OS.

1123

1124 **Competing interests**

1125   We are unaware of any conflicting interests.

1126

1127   **FIGURES**

1128   **Figure 1. Results of trade-offs between pre- and post-copulatory investment in polyandrous**

1129   **species.** A male's reproductive success (i.e. the total number of offspring produced, *T*) is

1130   determined by: (a) the number of females with whom he mates successfully (mating success, *M*)

1131   and their fecundity (i.e. average number of ova produced, *N*), and (b) the proportion of these that

1132   he fertilises (*P*). When reproductive resources are limited, males face a trade-off between

1133   investment in precopulatory (a) and postcopulatory competition (b). Under some conditions,

1134   such trade-off can have alternative optima for different male types, setting the scene for

1135   alternative mating tactics, in which a discrete phenotype, which invests preferentially in

1136   attracting and monopolising females (e.g. territorial), co-exists and competes with phenotypes,

1137   which invest preferentially in sperm competition (e.g. sneaker or satellite). Adapted from Parker

1138   (1998).

1139

1140   **Figure 2. A graphical illustration of the "Promiscuous Red Queen" hypothesis for the**

1141   **evolution of immune gene diversity and variation in female promiscuity.** The diversity of

1142   immune genes in a population is shaped along two selection pathways, both subject to the Red

1143   Queen dynamics of host-parasite coevolutionary cycles (see text box). The first one, which is

1144   relevant for all species, is natural selection caused directly by pathogens resulting in differential

1145   survival of alleles. The strength of selection is determined by the abundance, diversity and

1146   virulence of pathogens in the environment, primarily exposed through diet and habitat-specific

1147   variables. The second pathway, sexual selection, kicks in when random mating (with respect to

1148   immune genes) is an inferior strategy compared to a mating preference for certain alleles. For

1149   species that form pair bonds, mating preferences can theoretically be exerted both in the pairing

1150   process and in subsequent extrapair matings, and can either target specific alleles (good genes) or

1151   alleles that make a good match to the female's own genotype (compatible genes). Pathogen-

1152   mediated selection can therefore act directly on organisms through a natural selection pathway,

1153   and indirectly through a sexual selection pathway, under a "Red Queen" scenario. When social

1154   mate choice is largely driven by non-genetic resource benefits and is random with respect to

1155   genes, genetic preferences can be exerted in extrapair mate choice. Females can thereby get the

1156   best (resources and genes) out of two separate choice situations. When social monogamy

1157   constrains female choice of genes, extrapair mating will evolve. The stronger the genetic benefits

1158   through pathogen-mediated selection on offspring fitness, the more effort females should devote

1159   to extrapair mating. When beneficial alleles increase in frequency and pathogens become less

1160   harmful, extrapair mating becomes less important. The "Promiscuous Red Queen" model is thus

1161   a possible explanation to the variation in extrapair mating systems observed among species and

1162   populations, especially in passerine birds.

1163

1164   **Figure 3: Generalization gradients and origins of receiver bias.** (A) Receiver biases exert

1165   directional selection on a signal trait (e.g. tail length in birds) and may create heightened

1166   responsiveness to supernormal stimuli. The blue curve depicts responsiveness by an unbiased

1167   receiver. Peak shift (orange line), area shift (green line), and open-ended (red line)

1168   'generalization gradients' (Table 1) are generated by discrimination learning, which here is

1169   illustrated by a negative (S-) and a positive (S+) training stimulus. (B) Other receiver biases can

1170   also derive directly from a peripheral sensory bias (e.g. in the retina), or from the higher level

1171   'Perceptual' processing of the sensory input (e.g. visual cortex). The general increase in

1172   phenotypic plasticity from peripheral to higher level neural processing is indicated.

1173

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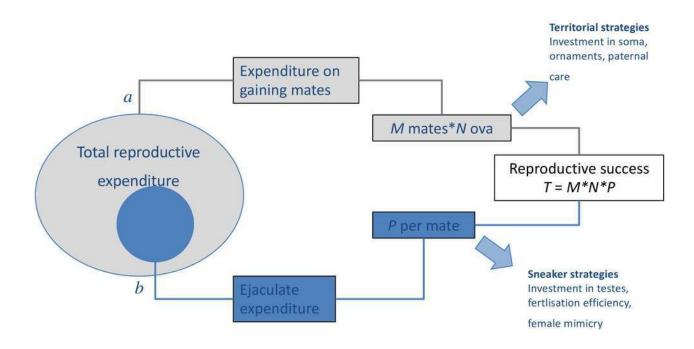
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Figure 1

Figure 1.Results of trade-offs between pre- and post-copulatory investment in polyandrous species.

A male's reproductive success (i.e. the total number of offspring produced, T) is determined by: (a) the number of females with whom he mates successfully (mating success, M) and their fecundity (i.e. average number of ova produced, N), and (b) the proportion of these that he fertilises (P). When reproductive resources are limited, males face a trade-off between investment in precopulatory (a) and postcopulatory competition (b). Under some conditions, such trade-off can have alternative optima for different male types, setting the scene for alternative mating tactics, in which a discrete phenotype, which invests preferentially in attracting and monopolising females (e.g. territorial), co-exists and competes with phenotypes, which invest preferentially in sperm competition (e.g. sneaker or satellite). Adapted from Parker (1998).
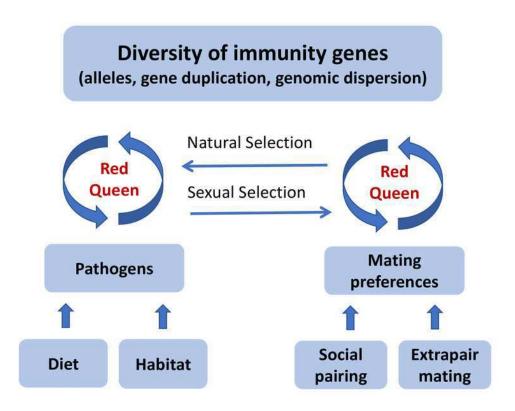
Figure 2

Figure 2.A graphical illustration of the "Promiscuous Red Queen" hypothesis for the evolution of immune gene diversity and variation in female promiscuity.

The diversity of immune genes in a population is shaped along two selection pathways, both subject to the Red Queen dynamics of host-parasite coevolutionary cycles (see text box). The first one, which is relevant for all species, is natural selection caused directly by pathogens resulting in differential survival of alleles. The strength of selection is determined by the abundance, diversity and virulence of pathogens in the environment, primarily exposed through diet and habitat-specific variables. The second pathway, sexual selection, kicks in when random mating (with respect to immune genes) is an inferior strategy compared to a mating preference for certain alleles. For species that form pair bonds, mating preferences can theoretically be exerted both in the pairing process and in subsequent extrapair matings, and can either target specific alleles (good genes) or alleles that make a good match to the female's own genotype (compatible genes). Pathogen-mediated selection can therefore act directly on organisms through a natural selection pathway, and indirectly through a sexual selection pathway, under a "Red Queen" scenario. When social mate choice is largely driven by non-genetic resource benefits and is random with respect to genes, genetic preferences can be exerted in extrapair mate choice. Females can thereby get the best (resources and genes) out of two separate choice situations. When social monogamy constrains female choice of genes, extrapair mating will evolve. The stronger the genetic benefits through pathogen-mediated selection on offspring fitness, the more effort females should devote to extrapair mating. When beneficial alleles increase in frequency and pathogens become less harmful, extrapair mating becomes less important. The "Promiscuous Red Queen" model is thus a possible explanation to the variation in extrapair mating systems observed among species and populations, especially in passerine birds.

Figure 3

Figure 3: Generalization gradients and origins of receiver bias.

(A) Receiver biases exert directional selection on a signal trait (e.g. tail length in birds) and may create heightened responsiveness to supernormal stimuli. The blue curve depicts responsiveness by an unbiased receiver. Peak shift (orange line), area shift (green line), and open-ended (red line) 'generalization gradients' (see Table 1: Glossary) are generated by discrimination learning, which here is illustrated by a negative (S-) and a positive (S+) training stimulus. (B) Other receiver biases can also derive directly from a peripheral sensory bias (e.g. in the retina), or from the higher level 'Perceptual' processing of the sensory input (e.g. visual cortex). The general increase in phenotypic plasticity from peripheral to higher level neural processing is indicated.
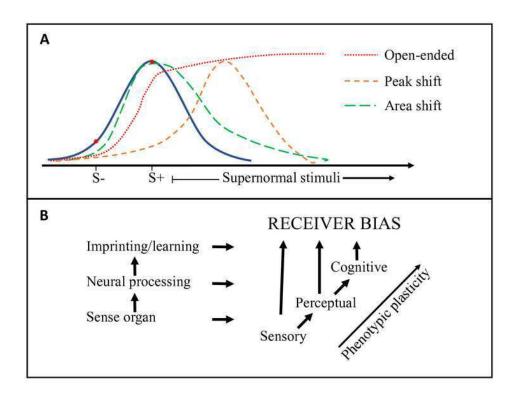
Table 1(on next page)

Table 1: Glossary

1 **Table 1:**
2 **Glossary**

Anisogamy	The within-species occurrence of gametes of two different sizes, which results in two sexes, males and females. Females produce the larger and males the smaller gametes.
Bateman Gradient	The slope of the linear regression of the number of offspring produced by an individual (reproductive success, or 'fertility') on the number of its reproductive partners (mating success). This represents the multiplicative component of the gradient of precopulatory sexual selection acting on a trait. It is named after the seminal study of Bateman (1948), which used fruit flies, *D. melanogaster*, to suggest that the relationship between fertility and mating success is stronger in males, and argued that in an anisogamous population males can have higher potential reproductive rates than females, resulting in more intense intrasexual competition over mating opportunities in males.
Benefits of mate choice	**'Direct' benefits** of mate choice are 'non-genetic' and include resources that will benefit the choosing parent or its offspring, for example access to food, a safe territory, or parental care. **'Indirect' benefits** are 'genetic' in the sense that by choosing a mate, a parent will secure 'good' (viability-related) genes or 'sexy' genes (genes for traits that are attractive to the opposite sex) for its offspring, or genes that are compatible to the parent's own genotype.
Generalization	Responsiveness (preference or aversion) to novel stimuli, generated by discrimination learning, and along the dimension(s) of the training stimuli. The resulting **generalization gradients** (e.g. a preference function) can be either a **Peak shift** (peak response to stimuli stronger than the positive training stimulus), or an **Area shift** (peak not shifted, but function asymmetric and biased towards the reinforced direction). Finally, if the gradient does not show a decrease within the interval considered, the preference or aversion can be called **Open-ended** (see e.g. Ghirlanda & Enquist 2003; ten Cate & Rowe 2007, and Fig. 3).
Genic capture	Female preferences for costly male traits results in the evolution of a genetic covariance between male condition, dictated by many genes, and a target male trait expression
Lek paradox	The problem, commonly relating to female choice of males on leks, of how genetic variation for mate choice can persist despite directional selection for the trait in the other sex, this genetic variation forming the basis for the choice. Under directional selection, the favoured genes should fixate, so that all individuals of the selected sex should have the gene(s) making them attractive, thus removing the basis for the choice.
Linkage disequilibrium (LD)	LD is the non-random association of alleles at different loci. The term often causes confusion and LD may exist without physical linkage or allele frequencies in equilibrium. The speciation-with-gene-flow process is characterized by the build up of LD and genome-wide LD is the footprint of speciation. LD in specific genomic regions reflects the history of selection, gene conversion and other forces that cause gene-frequency evolution.

Mating preference	A bias during mate choice which results in a skew towards mating with individuals that express specific phenotypic traits.
Mating system	**Monandry** – females mating with one male. **Monogamy** – both sexes mating with one mate. **Monogyny** – males mating with one female. **Polyandry** – females mating with multiple males. **Polygamy (or polygynandry)** – both sexes mating with multiple mates. **Polygyny** – males mating with multiple females.
Pleiotropy	One gene affects two or more traits (**genetic pleiotropy**), or one hormone affects two or more traits (**hormonal pleiotropy**).
Receiver bias	Used here and by some other authors (ten Cate & Rowe 2007) to include all biased responses (preferences or aversions), whether generated by peripheral sensory systems (**sensory bias),** neural processing (**perceptual bias**) or learning or imprinting (**cognitive bias**). Ryan and Cummings (2013) suggest that Sensory and Cognitive bias should be included in Perceptual bias. See Fig. 3
Receiver psychology	A phrase coined by Guilford and Dawkins (1991) "to encompass the cognitive mechanisms in signal receivers that process incoming information and could potentially influence signal evolution"(Rowe 2013).
Recombination	The production of offspring with different combination of alleles at different loci than their parents. Recombination often refers to the exchange of genetic material between homologous chromosomes during meiosis (chromosomal crossover).
Red Queen	A theory proposing that organisms must constantly evolve in response to their ever-changing environment. The "Red Queen" analogy is derived from Lewis Carroll's fantasy novel "Through the Looking-Glass" (1871) where the Red Queen tells Alice that "it takes all the running you can do, to keep in the same place". The Red Queen theory has been applied to many forms of coevolution among species, for example the antagonistic interactions between parasites and their hosts, and the benefit of sex. In sexual selection theory, Hamilton and Zuk (1982) proposed that sexual ornaments signal the bearer's resistance to parasites, which is a "Red Queen" model assuming a female preference for good genes. The "Red Queen" logic can also be applied to explain female preferences for rare or dissimilar alleles at immune genes that give a broader allelic repertoire and better pathogen resistance in the offspring, as argued here (the "Promiscuous Red Queen" hypothesis, see Fig. 2.)
Segregation	Pairs of alleles segregate (separate) into different gametes during meiosis. This is referred to as Mendel's law of segregation.
Sensory drive	A model proposed by Endler (1992) which encompasses evolutionary interactions between the (abiotic and biotic) environment, sensory system and courtship signals, taking into account pre-existing bias and sensory exploitation. Sensory and signalling systems coevolve under the constraints of the environment which hence influence the evolutionary trajectory in a predictable direction (Cummings & Endler 2018; Endler 1992).
Sexual cascade	The set of sequential evolutionary transitions in sexual strategy of eukaryote organisms, each transition under appropriate conditions giving rise to the

	selective forces that generate the next. Some taxa remain 'frozen' at a given stage without further change. The cascade begins with isogamous syngamy in unicells. Development towards multicellularity favours anisogamy and generates a unity sex ratio. In early, sedentary marine organisms with broadcast spawning, sexual selection is restricted to sperm competition and sperm selection. Development of mobility permits diversion of expenditure on sperm into 'female-targeting' (moving to and release of sperm adjacent to spawning females), which may ultimately facilitate internal fertilization and the many forms of pre-copulatory sexual selection documented by Darwin (1871).
Sexual conflict	A situation in which the fitness of a male and a female cannot be both maximized separately and simultaneously, by the same trait or reproductive decision. This can arise as social conflict between prospective sexual partners, when a reproductive decision (e.g. whether to mate with each other or not) is adaptive for one individual but detrimental to the other. This conflict is often mediated by sex-limited traits and can give rise to sexually antagonistic patterns of intersexual coevolution in which the antagonistic effect of alleles at some loci is counteracted by the effect of alleles at other loci (*inter-locus*). Another form of 'conflict' can arise when there is a divergence in the male and female phenotypic optima, and gene expression is not sex limited. In this case a locus can segregate for different alleles which may have sexually antagonistic effects when expressed in males and females, i.e. an allele that is beneficial when expressed in females may be detrimental when expressed in males and *vice versa* (*intra-locus*).
Sexual selection	Selection that depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to mating and fertilization (Andersson 1994; Darwin 1871).

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