

1

2 **Why aren't signals of female quality more common?**

3

4 DJ Hosken^{1*}, SH Alonzo² & N Wedell¹

5

6 ¹Centre for Ecology & Conservation, University of Exeter, Cornwall, Tremough, Penryn,
7 Cornwall TR10 9EZ UK

8 ²Department of Ecology and Evolutionary Biology, University of California Santa Cruz, 1156
9 High Street, Santa Cruz, Ca 95064, USA

10

11 *Corresponding author: d.j.hosken@exeter.ac.uk

12

13

14 Key words:

15 sexual selection, ornamentation, mate choice, sexual harassment, sexual conflict

16

17

18

19 Running head: Missing female ornaments

20

21

22 **Why aren't signals of female quality more common?**

23 One of the most striking patterns in nature is the sexual dimorphism in animal sexual
24 ornaments (Darwin 1874; Andersson 1994). Exaggerated ornamental traits are far more
25 common in males than females. Moreover, in at least some if not most of the species where
26 we see some female ornamentation, it is rudimentary and possibly due to inter-sexual genetic
27 correlations (Poisant et al. 2010; Tobias et al. 2012). Exaggerated traits are largely believed
28 to be favored in males because females tend to be choosy (as a result of their greater parental
29 investment: Trivers 1972) and males signal to attract choosy females (Andersson 1994). Yet,
30 this explanation for the prevalence of exaggerated male ornaments does not fully explain the
31 general absence of ornaments in females. We would argue that in many, if not most taxa, some
32 male mate-choice still occurs (e.g. Trivers 1972; Bonduriansky 2001), even if it is limited to
33 males selecting females of the right species to signal to and mate with. Additionally, we know
34 that males do make reproductive decisions based on direct indicators of female quality (such
35 as body size), at least in some taxa. For example, males adjust ejaculates based on assessment
36 of female quality (e.g. Simmons et al. 1993; Gage 1998; Wedell & Cook 1999; Martin & Hosken
37 2001) and even refuse to mate with low quality females or when mating opportunities are
38 likely to return few fertilizations (e.g. Simmons & Bailey 1990; Alonzo & Warner 1999). If we
39 accept the premise that males, while not as choosy as females, still exert some choice of mates,
40 then the question arises: why don't females signal their sexual quality via ornamental
41 secondary sexual traits like males do?

42 Taking typical sex-roles as a given, there are two classical explanations for this lack of female
43 ornamentation. One is that females need to be more camouflaged than males - natural
44 selection is stronger on them for cryptic colouration (Wallace 1889) - and the other is that the
45 fecundity costs born by a female signaling this way would not be repaid via male mate-choice,
46 and hence females with exaggerated sexual traits would have lower fitness (Gwynne 2001).
47 That is, the fitness cost of producing the exaggerated trait would be prohibitive and females
48 would do better to spend their limited resources on additional eggs. Our purpose here is to
49 suggest an additional explanation for the lack of ornamentation that also highlights an
50 interesting area of future research.

51 We suggest that female ornamentation may be disadvantageous if more attractive females
52 disproportionately attract male attention (Figure 1). There is abundant evidence that mating

53 and male sexual-harassment can be costly to females (e.g. Parker 1978; Le Boeuf & Mesnick
54 1991; Chapman et al. 1995; Crudginton & Siva-Jothy 2000; Hosken et al. 2003; Gay et al.
55 2009; reviewed in Arnqvist & Rowe 2005). If this were the case, then more attractive females
56 would have lower fitness because of increased male harassment and the costs associated with
57 that (Figure 1). Thus the high quality (most attractive) females most able to bear the costs of
58 trait exaggeration in the absence of male harassment would not gain fitness by signaling
59 because of disproportionate male harassment – all else being equal. Equally, it may not pay
60 lower quality females to signal attractiveness either as they may not be able to secure a mate
61 or bear the costs of signaling (as per arguments for low quality males: Kotiaho 2000. Also see
62 LeBas et al. 2003). Note that this does not imply intermediate females signals should be fitter,
63 instead there should be directional selection against trait exaggeration in females as males
64 target females who signal their quality resulting ultimately in no female trait exaggeration. So
65 in this instance, it is not the cost of trait production *per se* that is fitness reducing, rather it is
66 the unwanted attention generated by displaying attractiveness that is problematic, although
67 these things could well be additive. While, there have been previous suggestions that female
68 ornaments could reduce male harassment (Tobias et al. 2012), here we reverse that logic to
69 point out something that has not been widely considered previously. We suggest that sexual
70 conflict over male harassment and costs of mating provides an additional explanation for the
71 relative absence of ornamentation in females. This suggestion depends on the assumption
72 that female fitness does not increase continuously with number of mates or with male
73 attention, and there is evidence for this in a range of taxa (e.g. Bateman 1948; Hosken et al.
74 2003; Bjork & Pitnick 2006; Jones & Ratterman 2009; reviewed in Collet et al. 2014). We also
75 assume that males are somewhat selective of females, or would be if they could accurately
76 determine female quality, and there is also evidence for this (e.g. Simmons & Bailey 1990).

77 Just as there is ample evidence of male mate-choosiness, there is also abundant evidence that
78 females try to avoid male harassment and that they also signal their unattractiveness or lack
79 of receptivity. For example, females physically attempt to thwart unwanted copulations (e.g.
80 Parker 1972), disguise themselves as males (e.g. Cook et al. 1994; Van Gossum et al. 2001),
81 use anti-aphrodisiacs to signal lack of receptivity (Andersson et al. 2000), move to habitats
82 that contain no males (Darden & Croft 2008) and form aggregations that reduce male
83 harassment to individual females (Pilastro et al. 2003). Given that selection can favour female
84 signals that reduce male harassment (e.g. signals of low quality mating status), we argue it is

85 very likely that the costs of male harassment could also select against ornaments that
86 positively signal female quality, even if these ornaments would be adaptive in the absence of
87 sexual harassment.

88 The exact properties of the fitness function describing female fitness relative to female
89 attractiveness will be determined by the mating-benefits/costs obtained by females and the
90 rate at which male harassment increases with female attractiveness/quality. But we are
91 really only assuming that the fertility/fecundity costs of not remating and of male harassment
92 vary with female attractiveness, such that more attractive females would benefit more by
93 avoiding males than they would by exposing themselves to additional mating opportunities
94 (because of elevated male harassment). This clearly raises the issue of female attractiveness
95 and fitness. Do we actually see selection against highest quality females or intermediately
96 attractive females having higher fitness? We are aware of two studies showing that more
97 attractive females endure greater male attention and reduced fitness in a manner consistent
98 with our idea (Long et al. 2009; Chenoweth et al. 2015). In fact, as argued here, Long et al.
99 (2009) suggest this may well be an underappreciated cost of sexual selection, but they do not
100 make the link between the general rarity of female ornamentation and this cost of harassment.
101 Additionally, Chenoweth et al. (2007) find evidence of stabilizing selection on female
102 fecundity (body size) through male mate choice. Thus it is plausible that it doesn't pay for
103 females to signal because of the costs of harassment and mating. This in turn results in a lack
104 of female ornaments over evolutionary time and male mate-preferences that tend to be even
105 weaker than predicted by relative parental investment (Trivers 1972) because female quality
106 is ambiguous due to the lack of clear signals of quality.

107 One way to evaluate this idea would be to test whether females are more likely to be
108 ornamented in species where costs of male harassment are low or absent, or where mating
109 more is advantageous, as in some nuptial gift providing taxa. In species where male
110 harassment varies, it would also be possible to compare the direction of selection on a female
111 ornament signaling-quality in the presence and absence of male harassment. At present we
112 are not aware of any studies that have systematically addressed these topics. Furthermore, it
113 may be interesting to theoretically investigate the impact of different shaped harassment-
114 female quality curves and the types of costs and benefits female incur as a result, and how
115 levels of male choosiness impact female fitness. Additionally, including male fitness payoffs
116 to assess how their responses could influence our simplistic predictions could also be

117 revealing. For example, if females signaled quality, it could pay males to “allocate” their
118 harassment of them based on the number of competitors present (as per ideal distribution
119 logic) and this could impact female signals too. These could all be avenues for future
120 investigation.

121 Finally we should stipulate that we do not wish to imply that male harassment of attractive
122 females is the primary reason for the lack of female ornamentation. We only want to alert
123 researchers to the possibility that this could be a contributing factor, and as Long et al. (2009)
124 note, perhaps this is a pervasive hidden cost of sexual selection.

125

126 **References**

127 Alonzo, S. H., & Warner, R. R. (1999). A trade-off generated by sexual conflict: Mediterranean
128 wrasse males refuse present mates to increase future success. *Behavioral Ecology*, *10*, 105-
129 111.

130 Andersson, M. (1994). *Sexual selection*. Princeton, U.S.A.: Princeton University Press.

131 Andersson, J., Borg-Karlson, A-B., & Wiklund, C. (2000). Sexual cooperation and conflict in
132 butterflies: a male transferred anti-aphrodisiac reduces harassment of recently mated
133 females. *Proceedings of the Royal Society of London, B*, *267*, 1271-1275.

134 Arnqvist, G., & Rowe, L. (2005). *Sexual conflict*. Princeton, U.S.A.: Princeton University Press.

135 Bateman, A. J. (1948). Intra-sexual selection in *Drosophila*. *Heredity*, *2*, 349-368.

136 Bjork, A., & Pitnick, S. (2006). Intensity of sexual selection along the anisogamy-isogamy
137 continuum. *Nature*, *441*, 742-745.

138 Bonduriansky, R. (2001). The evolution of male mate choice in insects: a synthesis of ideas
139 and evidence. *Biological Reviews of the Cambridge Philosophical Society*, *76*, 305-339.

140 Chapman, T., Liddle, L. F., Kalb, J. M., Wolfner, M. F., & Partridge, L. (1995). Costs of mating in
141 *Drosophila melanogaster* females is mediated by male accessory gland products. *Nature*,
142 *373*, 241-244.

143 Chenoweth, S. F., Petfield, D., Doughty, P., & Blows, M. W. (2007). Male choice generates
144 stabilizing sexual selection on a female fecundity correlate. *Journal of Evolutionary Biology*,
145 *20*, 1745-1750.

146 Chenoweth, S. F., Appleton, N. C., Allen, S. L., & Rundle, H. D. (2015). Genomic evidence that
147 sexual selection impedes adaptation to a novel environment. *Current Biology*, *25*, 1860-
148 1866.

149 Collet, J. M., Dean, R. F., Worley, K., Richardson, D. S., & Pizzari, T. (2014). The measure and
150 significance of Bateman's principles. *Proceedings of the Royal Society, B*, *281*, 20132973

151 Cook, S. E., Vernon, J. G., Bateson, M., & Guildford, T. (1994). Mate choice in the polymorphic
152 African swallowtail butterfly, *Papilio dardanus*: male-like females may avoid sexual
153 harassment. *Animal Behaviour*, *47*, 389-397.

154 Crudgington, H. S., & Siva-Jothy, M. T. (2000). Genital damage, kicking and early death. *Nature*,
155 *407*, 655-656.

156 Darden, S. K., & Croft, D. P. (2008). Male harassment drives females to alter habitat used and
157 leads to segregation of the sexes. *Biology Letters*, *4*, 449-451.

158 Darwin, C. (1871). *The descent of man and selection in relation to sex*. London, U.K.: John
159 Murray.

160 Gage, M. J. G. (1998). Influence of sex, size and symmetry on ejaculate expenditure in a moth.
161 *Behavioral Ecology*, *9*, 592-597.

162 Gay, L., Eady, P. E., Vasudev, R., Hosken, D. J., & Tregenza, T. (2009). Costly sexual harassment
163 in a beetle. *Ecological Entomology*, *34*, 86-92.

164 Gwynne, D. J. (2001). *Katydid and bushcrickets: reproductive behavior and evolution of the*
165 *Tettigonidae*. Ithaca, NY: Comstock Publishers.

166 Hosken, D. J., Martin, O. Y., Born, J., & Huber, F. (2003). Sexual conflict in *Sepsis cynipsea*: female
167 reluctance, fertility and mate choice. *Journal of Evolutionary Biology*, *16*, 485-490.

168 Jones, A. G., & Ratterman, N. L. (2009). Mate choice and sexual selection: what have we learned
169 since Darwin? *Proceedings of the National Academy of Sciences U.S.A.*, *106S*, 10001-10008.

170 Kotiaho, J. S. (2000). Testing the assumptions of conditional handicap theory: costs and
171 condition dependence of a sexually selected trait. *Behavioral Ecology & Sociobiology*, *48*,
172 188-194.

173 LeBas, N. R., Hockham, L. R., & Ritchie, M. G. (2003). Linear and correlational sexual selection
174 on "honest" female ornamentation. *Proceedings of the Royal Society of London, B*, *270*, 2159-
175 2165.

176 Le Boeuf, B. J., & Mesnick, S. (1991). Sexual behaviour of male northern elephant seals. I.
177 Lethal injuries to adult females. *Behaviour*, *116*, 143-162.

- 178 Long, T. A. F., Pischedda, A., Stewart, A. D., & Rice, W. R. (2009). A cost of sexual attractiveness
179 to high fitness females. *PLoS Biology*, 7, e1000254.
- 180 Martin, O. Y., & Hosken, D. J. (2002). Strategic ejaculation in the common dung fly *Sepsis*
181 *cynipsea*. *Animal Behaviour*, 63, 541-546.
- 182 Parker, G. A. (1972). Reproductive behaviour of *Sepsis cynipsea* (L.) (Diptera: Sepsidae) I.
183 Preliminary analysis of the reproductive strategy and its associated behaviour patterns.
184 *Behaviour*, 41, 172-206.
- 185 Parker, G. A. (1978). Searching for mates. In J. R. Krebs & N. B. Davies (Eds), *Behavioral*
186 *ecology: an evolutionary approach* (pp 214-244) London, U. K.: Blackwells.
- 187 Pilastro, A., Benetton, S., & Biazzi, A. (2003). Female aggregation and male competition reduce
188 costs of sexual harassment in the mosquitofish *Gambusia holbrooki*. *Animal Behaviour*, 65,
189 1161-1167.
- 190 Poissant, J., Wilson, A. J., & Coltman, D. W. (2010). Sex-specific genetic variance and the
191 evolution of sexual dimorphism: a systematic review of cross-sex genetic correlations.
192 *Evolution*, 64, 97-107.
- 193 Simmons, L. W., & Bailey, W. J. (1990). Resource influenced sex roles of zaprochiline
194 tettigoniids (Orthoptera: Tettogonidea). *Evolution*, 44, 1853-1868.
- 195 Simmons, L. W., Craig, M., Llorens, T., Schinzig, M., & Hosken, D. (1993). Bushcricket
196 spermatophores vary in accord with sperm competition and parental investment theory.
197 *Proceedings of the Royal Society of London, B*, 251, 183-186.
- 198 Tobias, J. A., Montgomerie, R., & Lyon, B. E. (2012). The evolution of female ornaments and
199 weaponry: social selection, sexual selection and ecological competition. *Philosophical*
200 *Transactions of the Royal Society, B*, 367, 2274-2293.
- 201 Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed) *Sexual*
202 *selection and the descent of man, 1871-1971* (pp 136-179). Chicago U.S.A: Aldine
203 Publishing.
- 204 Van Gossum, H., Stoks, R., & de Bruyn, L. (2001). Frequency-dependent male mate harassment
205 and intra-specific variation in its avoidance by females of the damselfly *Ischnura elegans*.
206 *Behavioral Ecology & Sociobiology*, 51, 69-75.
- 207 Wallace, A. R. (1889). *Darwinism: an exposition of the theory of natural selection with some of*
208 *its applications* (2nd edn). London, UK: MacMillan.
- 209 Wedell, N., & Cook, P. A. (1999). Butterflies tailor their ejaculate in response to sperm
210 competition risk and intensity. *Proceedings of the Royal Society of London B*, 266, 1033-1039.

211

212

213

214

215

216 **Figure 1.** Female fitness and male harassment as a function of female attractiveness. The top
217 panel (a) shows that intermediate female attractiveness equates to highest fitness because the
218 most attractive females suffer greater male harassment (lower panel b). Thus it would not
219 pay high-quality attractive females to signal their quality to males even though they are the
220 females most able to afford signal costs in the absence of male harassment costs.

221

222

