

1 **Sexual Selection Studies:**  
2 **Progress, Challenges, and Future Directions**

3 Final Report from a NESCent Catalyst Meeting  
4 Durham NC, July 15–17, 2013  
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41 **1 Introduction**

42 In a meeting held at the National Evolutionary Synthesis Center (NESCent) in Durham,  
43 NC, during July 15–17, 2013, 34 participants reflecting a diversity of ages, nationalities, and

44 disciplines reviewed the status of sexual selection studies and indicated challenges and future  
45 directions. “Sexual selection studies” is used here as an umbrella phrase referring to studies of  
46 courtship and mating, parent-offspring relations, family organization, and the interrelations  
47 among these. Two thirds of the participants brought special experience from their research  
48 and teaching in some area of sexual selection studies and one third brought perspectives  
49 from other areas of evolutionary biology and from the social sciences and humanities.

50 A special password-protected website was set up for the conference hosted at  
51 <http://sexualselectionstudies.drupalgardens.com>. Prior to the meeting participants  
52 posted essays on the meeting’s website describing each’s personal history, experience and  
53 professional perspective pertaining to sexual selection studies. During and after the meeting  
54 participants posted additional contributions to the meeting’s website. NESCent personnel  
55 video-taped the meeting and prepared archival movies showing the discussions during each of  
56 the three days. The discussions were wide ranging and the accumulated material voluminous.  
57 This report distills some of the meeting’s findings.

58 An initial draft of this report was circulated to all participants in September 2013. Accu-  
59 mulated comments and feedback were incorporated into a second draft that was circulated  
60 in November 2013. Typographic and other small corrections led to this third and final draft,  
61 dated December 11, 2013.

62 The meeting focussed more on present challenges and future directions than on celebrat-  
63 ing decades of past sexual selection research.

## 64 2 Defining Sexual Selection Today

65 The participants found that developing a contemporary definition of sexual selection was  
66 surprisingly difficult and time-consuming.

### 67 2.1 A Starting Definition

68 The meeting took as a starting point the definition of sexual selection from Shuker (2009):

69 “Sexual selection describes the selection of traits associated with competi-  
70 tion for mates.” Continuing, “More formally, sexual selection is the relationship  
71 between a trait and its effect on fitness through sexual competition.” Further,  
72 Shuker (2009) surmised, “My perception is that the above represents the consen-  
73 sus among evolutionary biologists of what sexual selection is.”

74 Almost all aspects of this definition turned out to be extensively debated. One point  
75 however, was generally accepted and agreed upon. Shuker (2009) wrote, “Sexual selection is  
76 not dependent on what have been termed ‘sex roles’... It is true that Darwin (1871) did not  
77 belabour this point, and that most of his writing on sexual selection prescribed male and  
78 female sex roles in a rather ‘traditional’ way.”

79 The meeting’s consensus that sexual selection is independent of sex roles is important  
80 because sexual selection is often misunderstood in the academy and general public as pro-  
81 viding a biological basis to traditional sex roles such as passionate males and coy females.  
82 It was further understood at the meeting that sexual selection does not generally require or

83 underwrite claims that sperm are cheap and eggs expensive, or that males are necessarily  
84 more promiscuous than females or that females are necessarily more disposed to parental  
85 care than males. As one participant wrote, “We can’t simply keep going around saying the  
86 old tripe of ‘competitive males and coy females because of anisogamy’ ”.

## 87 2.2 Deliberations

88 Discussion began with points raised in Shuker’s elaboration on his own definition and then  
89 continued on to additional issues (quotes taken from Shuker, 2009):

- 90 1. “Sexual selection is also not just intersexual choice, let alone just female choice.” Some  
91 researchers at this meeting consider choice sufficient to conclude that sexual selection  
92 is occurring, whereas others further require that the traits being selected are heritable  
93 and also that both the direction and intensity of preference for those traits be heritable.
- 94 2. “Sexual selection is not the same thing as sexual conflict.” This statement was un-  
95 derstood by some to imply that sexual conflict need not be manifested as behavioral  
96 conflict. Others feel the existence of competition for mates *ipso facto* implies a kind of  
97 conflict, as in a genetic conflict of interest.
- 98 3. “Sexual selection [is] a component of an overall natural selection process, and inclusive  
99 of both selection and heredity.” Two issues in this statement drew strong responses.  
100 First, many workers do not believe that heritability is a requirement of sexual selec-  
101 tion. Drawing on the formula in quantitative genetics that the response to selection  
102 equals the heritability times the strength of selection ( $R = h^2S$ ), some researchers  
103 feel that sexual selection refers to the behavioral selection taking place, and that this  
104 selection may or may not produce an evolutionary response depending on the degree  
105 of heritability. Others however, agree that sexual selection must include heritability.  
106 It is common usage to attribute the evolution of ornaments and armaments to sexual  
107 selection, as in statements like “These antlers evolved because of intrasexual selection  
108 or these colorful feathers evolved because of intersexual selection.” Because this usage  
109 is making both an evolutionary claim in addition to a behavioral claim, in this usage  
110 a significant heritability is implied along with behavioral choice. Thus, although many  
111 participants assert that heritability is distinct from sexual selection, others think that  
112 sexual selection includes both the selectional behavior and heritability. As one partici-  
113 pant wrote, “I agree entirely that sexual selection must include selection and heritable  
114 variation.”

115 Second, many participants do not accept that sexual selection is a component of natural  
116 selection but instead view natural selection and sexual selection as distinct processes  
117 and therefore do not agree with any statement claiming sexual selection to be a “com-  
118 ponent” of natural selection. We return to this point again later.

- 119 4. “For sexual selection not to occur in a population, there either has to be no scope for  
120 competition (partners as resources are not limiting, and all partners are of equal qual-  
121 ity), or the outcome of any competition for mates is totally random with respect to the  
122 traits expressed by individuals, such that successful partnerships represent a random

123 sample of pairs of individual phenotypes (and thus genotypes).” Although participants  
124 generally agreed that null hypotheses for sexual selection are needed, and that claims  
125 about whether sexual selection exists in particular cases should be empirically testable,  
126 they did not agree on which hypotheses constituted the appropriate null hypotheses.

- 127 5. Many participants stated that sexual-selection processes might not be about access to  
128 mates as much as about access to fertilizable gametes. They stated that the criterion  
129 for success should be scored not in terms of matings as in the Shuker (2009) definition,  
130 but in terms of fertilizations.
- 131 6. Some participants unpacked the Shuker (2009) definition’s reference to competition for  
132 mates into various specific processes, extending Darwin’s (1871) original dichotomy of  
133 male-male competition and female choice of males: (1) scrambles (mate search and  
134 handling), (2) contests (including fights with and without weaponry), (3) endurance  
135 rivalry, (4) post-copulatory versions of 1 to 3, (5) competition to attract mates, (6)  
136 competition to obtain better mates, and (7) post-copulatory versions of 5 and 6. Other  
137 participants noted that those processes are zero- or negative-sum processes—they as-  
138 sume a given number of eggs is to be allocated or, in the case of sexual conflict, some  
139 number of eggs is to be destroyed.

140 But other behavioral processes influence the number of fertilizations and thereby in-  
141 crease the size of the pie. Male-female cooperation such as nuptial gifts might increase  
142 the number of fertilized eggs produced, and parental care, social foraging or warning  
143 calls might increase the number of fertilized eggs that hatch, fledge or wean. Moreover,  
144 focussing on competition might miss the purpose of mating behavior. If a female is  
145 searching for a male who would cooperate with her in raising a large family, she might  
146 interview several males to see who was most behaviorally compatible. In this case the  
147 males might be seen as competing with one another for success in female choice but  
148 the outcome of a successful choice would be male-female cooperation.

- 149 7. Still other participants stated that the definition of sexual selection should not refer  
150 to specific processes at all but should consist of an operational protocol for measuring  
151 sexual selection independent of the mechanisms that bring about the sexual selection.  
152 One approach involves the differential “opportunity for selection” in the two sexes  
153 based on a population-genetic statistic for measuring the strength of natural selection  
154 (Crow 1958) and extended to measuring the strength of sexual selection (Arnold and  
155 Wade 1984a,b, Shuster and Wade 2003).

156 Let the opportunity for selection in males,  $I_m$ , be defined as the variance in fitness  
157 among males,  $V_m$ , divided by the square of the average fitness among males,  $W_m$ , *i.e.*,  
158  $I_m \equiv V_m/W_m^2$ . Similarly for females, let the opportunity for selection in females be  
159  $I_f \equiv V_f/W_f^2$ . Then the opportunity for sexual selection,  $\Delta I$ , is defined as the difference  
160 of these,  $\Delta I \equiv I_m - I_f$ . Sexual selection is absent, or equal in both sexes, if  $\Delta I$  is  
161 zero. These formulas assume the sex ratio is one; otherwise, a small correction is  
162 needed (p. 29, Shuster and Wade, 2003). However, a participant called attention to  
163 reservations about this approach that pertain to an interaction between stochasticity  
164 and the operational sex ratio (Jennions *et al.* 2012).

165 8. Participants considered at length the Fisher runaway process wherein a female’s pref-  
 166 erence for a male trait leads to an increase in the male trait that in turn leads to an  
 167 increase in the female preference for that trait, and so on (Fisher 1915, Lande 1981,  
 168 Kirkpatrick 1982, Fuller *et al.* 2005). The contemporary statement of this process,  
 169 termed by one participant as the LK model, has been asserted as a null model of  
 170 the evolution of trait and preference by intersexual selection (Prum 2010). Specifically,  
 171 consider three traits: male ornament,  $o$ , the female preference,  $p$ , and the organism’s vi-  
 172 ability,  $v$ . The additive genetic variance-covariance matrix among these traits (adapted  
 173 from Prum 2010, Appendix) is

$$\mathbf{G} = \begin{pmatrix} V_o & C_{op} & C_{ov} \\ C_{op} & V_p & C_{pv} \\ C_{ov} & C_{pv} & V_v \end{pmatrix} \quad (1)$$

174 where  $V_o$  is the additive genetic variance of the male ornament,  $V_p$  is that for the female  
 175 preference,  $V_v$  is that for viability,  $C_{op}$  is the additive genetic covariance between the  
 176 male ornament and the female preference for it,  $C_{ov}$  is that between the male ornament  
 177 and its viability, and  $C_{pv}$  is that between female preference and its viability.

178 A null model for whether the ornament connotes functional adaptation is simply that  
 179  $C_{ov}$  is zero, that is, the measure (size, color etc.) of the ornament is uncorrelated with  
 180 fitness. In this situation, the ornament’s measure cannot be used as signal of adaptive  
 181 functional quality. The ornament’s measure is arbitrary because it is uncorrelated with  
 182 any information about viability. It is neither honest nor dishonest because it cannot  
 183 be lied about. The ornament stands for itself and only for itself and might be preferred  
 184 in mating because of an arbitrary female preference for it.

185 However, the LK model itself is a model of a process, not solely a null model concerning  
 186 the adaptation-signaling potential of the ornament. In its entirety, the LK model  
 187 stipulates that two of the additive genetic variances,  $V_o$  and  $V_p$ , are both positive, that  
 188 both ornament and preference are not correlated with viability ( $C_{ov}$  and  $C_{pv}$  are both  
 189 zero) and the preference for the ornament,  $C_{op}$ , is positive. Hence, showing that  $C_{ov}$  is  
 190 not significantly different from zero is not sufficient to conclude that the LK process  
 191 is operating. In addition, a female must not suffer differential viability consequences  
 192 for expressing her preference ( $C_{pv}$  not significantly different from zero), whereas the  
 193 heritabilities for both the male ornament and the female preference must both be  
 194 significantly greater than zero, as must the genetic correlation between male ornament  
 195 and female preference, *i.e.*, the degree of preference should increase with the measure  
 196 of the male ornament.

197 Some participants however, object to this entire discussion of the genetic conditions  
 198 underlying the LK runaway process because they do not consider the heritability (in-  
 199 cluding its multivariate extension as the matrix  $\mathbf{G}$  above) to be part of sexual selec-  
 200 tion’s definition. One participant writes that this entire paragraph is “flawed” because  
 201 it “conflates heritability and selection” even though the requirements on  $\mathbf{G}$  for the LK  
 202 process to operate are taken directly from the literature that proposes the LK process  
 203 as a null model for the evolution of a trait and the preference for it by intersexual  
 204 selection.

205 9. Several participants argued that natural selection should be considered distinct from  
206 sexual selection. Four reasons were raised. First, natural selection and sexual selection  
207 are often spoken of as being in opposition—that ornaments driven by sexual selection  
208 to become ever larger encounter a push back from natural selection as the ornaments  
209 become unwieldy and deleterious to survival. This terminology could be replaced by  
210 stating that the sexual selection component of natural selection and the viability and/or  
211 fertility components of natural selection are in opposition, but the usage of viewing  
212 natural selection and sexual selection as being in opposition is widely used.

213 Second, one way of distinguishing between sexual and natural selection is by referring to  
214 who or what is doing the selecting. Indeed, going back to Darwin (1871), three distinct  
215 selectors can be envisioned. Selection by farmers is artificial selection, selection by the  
216 environment (both abiotic and social) is natural selection, and selection by mates or  
217 rivals is sexual selection.

218 Third, some participants emphasized the difference in outcome between natural se-  
219 lection and sexual selection. Natural selection leads to functional adaptation whereas  
220 sexual selection leads to non-functional and often aesthetic enhancement. These par-  
221 ticipants claimed that Darwin (1871) himself viewed natural selection as distinct from  
222 sexual selection because of this distinction between the evolution of functional and  
223 non-functional traits.

224 Fourth, research on a possible role for sexual selection in speciation would be furthered  
225 by distinguishing sexual selection from natural selection (Safran *et al.* 2013).

226 Nonetheless, other participants were not persuaded and continued to maintain that  
227 sexual selection is best viewed as a component of natural selection. One participant  
228 wrote, “whether natural selection is seen as arising from the total variation in fitness  
229 (including components due to fertilization success) or only fitness due to environmental  
230 sources of selection may often seem an unnecessary or perhaps even pedantic distinc-  
231 tion. . . casually talking of natural selection and sexual selection as independent can  
232 sometimes lead to logical inconsistencies. . . environmental selection on a mating signal  
233 will directly influence signal design and hence fertilization success. In reality, both  
234 interact to determine fitness, and interactions can be either positive or negative.” An-  
235 other wrote, “Viability selection and sexual selection are not always in opposition.  
236 Large body size in males may be favored by sexual selection but also may be useful in  
237 thermoregulation and/or predator deterrence.”

238 10. Participants debated the good-genes and sexy-sons processes in the sexual selection.  
239 (The phrase, “sexy sons”, is being used here as shorthand for the indirect benefits of  
240 sexually attractive offspring.) Participants reviewed a recent meta-analysis of 90 stud-  
241 ies on 55 species showing that sexually selected traits such as ornaments do not have  
242 a significant correlation with life history fitness traits (Prokop *et al.* 2012). Sexually  
243 selected traits not correlated with fitness cannot be used as the basis for mate choice  
244 based on the premise that good genes are thereby being passed on to offspring even  
245 though the traits themselves are often heritable.

246 Some participants argued that the combination of the ornament being heritable to-  
247 gether with an absence of an ornament to fitness correlation implies that the ornament

248 must have evolved for its “sexiness” alone, consistent with the LK runaway “null”  
249 model.

250 Other participants objected to posing good-genes and sexy-sons as an either/or propo-  
251 sition because the LK model requires, as discussed above, not only that the ornament-  
252 viability correlation be zero and the heritability of the ornament be positive as ob-  
253 served, but also that both the heritability of the preference be positive and the genetic  
254 correlation between preference and ornament be positive. Roughly speaking, these re-  
255 quirements mean both that the female interest in having sexy sons should be inherited  
256 by her daughters and also that what females find to be sexy should not change in the  
257 next generation. Because the meta-analysis did not address the female-preference side  
258 of the question, these participants felt that the failure to support a good genes pro-  
259 cess of sexual selection could not be used as evidence for a sexy-sons process of sexual  
260 selection instead.

261 However, an LK supporter rejoined that these reservations about the absence of data  
262 on female preference constituted “a ridiculous level of skepticism” and that the reserva-  
263 tions notwithstanding, “the meta-analysis has shown substantial support for heritable  
264 fitness advantages to sexiness only.”

265 Turning to the theoretical possibility of a good-genes process, one participant wrote,  
266 “I would say that on the whole there is theoretical support for good genes... for a  
267 summary of some of the older models see box 3.2.1 in Andersson (1994, p. 56–57)”.

268 However, another participant wrote at length detailing theoretical objections to a good-  
269 genes process:

270 (1) “Indirect selection on female fitness arising from good genes in offspring is nec-  
271 essarily weak because the intensity of selection diminishes by at least 1/2 and often  
272 as much as 1/8 or more of its original intensity with each generation, causing overall  
273 selection intensity to become vanishing small over even brief periods of evolutionary  
274 time. Parents are related to offspring by 1/2 and therefore selection on parental genes  
275 affecting the fitness of offspring is only half as strong as selection on zygotic genes  
276 (Wolf and Wade 2009).”

277 (2) “Non-genetic, direct effects on female fitness are sufficient to explain observed fe-  
278 male mate choices. While multiple mating by females is widely thought to enhance  
279 female fitness indirectly (by allowing females to increase the survivorship of their off-  
280 spring via ‘good genes’ or resources they receive from males), Arnqvist and Nilsson  
281 (2000) showed in a meta-analysis of 122 species that direct fitness benefits accrued by  
282 females (30-70%) were sufficient to account for patterns of multiple mating by females.  
283 They concluded that evidence of direct benefits to females arising from multiple mating  
284 were so pervasive that the presumed indirect effects on female fitness are unnecessary  
285 to account for the widespread occurrence of polyandrous mating (Shuster *et al.* 2013).”

286 (3) “Direct fitness benefits resulting from mate choices must enhance female fitness  
287 within each generation; if they do not, traits associated with decreased fitness benefits  
288 within each generation will be removed from the population. This is the reason why  
289 an early version of the “sexy son” hypothesis does not work. As stated by Kirkpatrick

(1985), ‘Decreased fecundity cannot be offset by the reproductive success of progeny. . . At any evolutionary equilibrium, the forces acting on the genes must equilibrate within each generation.’ Immediate, material forces that affect female survival or fecundity, may evolve by female choice but will not respond to any force that can be attributed to the fitness of descendants. The erroneous assumption that female traits will respond to cross-generational fitness benefits is the essence of the sexy son model as well as all other good genes arguments.”

This participant concludes that “the case against ‘good genes’ arguments for the evolution of female mate preferences is overwhelming.”

Finally, many participants noted that theoretically, if traits were to indicate good genes, the environment in which the genes are expressed must continue unchanged into the future.

All in all, both the theoretical possibility and empirical reality of the good-genes and sexy-sons mechanisms of sexual selection remained a subject of deep disagreement among participants.

11. The participants considered a study of collared flycatchers (Qvarnström *et. al.* 2006) as a test case for the ideas that had been discussed. The white badge on males has been considered to be a sexually selected character (*e.g.* Pärt and Qvarnström 1997). Based on 24 years of study with 8500 birds on the Swedish island of Gotland, the following table summarized the data on heritabilities of the badge (ornament), of fitness, and of female preference for the badge, as well as of the genetic correlation between preference and badge, using notation consistent with the genetic variance-covariance matrix above:

Genetic Components of Indirect Selection for Badge Size in Collared Flycatcher,  
(Qvarnström *et. al.* 2006) (Mean  $\pm$  Standard Error of Mean)

$h_o^2$	Heritability of Male Badge Size	$0.381 \pm 0.028$
$h_v^2$	Heritability of Male Fitness	$0.031 \pm 0.012$
$r_{ov}$	Genetic Correlation Male Ornament and Male Fitness	$0.154 \pm 0.094$
$h_p^2$	Heritability of Female Preference	$0.026 \pm 0.010$
$r_{op}$	Genetic Correlation Between Badge and Preference	$-0.015 \pm 0.169$

These data show that the ornament is moderately heritable but that male fitness is very weakly heritable, so that the genetic correlation between the ornament and male fitness is low. Furthermore, the heritability of female choice for the ornament is very low and the net result is that no genetic correlation exists between the male ornament and female preference. The low correlation between male badge size and male fitness limits the use of the badge size as an indicator of good genes because sons do not inherit much of their father’s fitness. The low heritability of female preference limits the use of the badge size as an indicator of sexy sons because daughters do not inherit an interest in sexiness that their mothers possess. An LK runaway process is further contraindicated because there is negligible genetic correlation between preference and ornament. That is, an ornament might be sexy now, and the ornament might indeed



327 be heritable, but the daughter of a mother interested in sexiness might not herself be  
328 interested in the sexiness of her mate, and also an ornament sexy in one generation  
329 may not be perceived as sexy in the next generation.

330 Participants found these data troublesome, although perhaps not unexpected theo-  
331 retically (Kirkpatrick and Barton 1997). Participants who feel that the definition of  
332 sexual selection does not include heritability stated that these data do not indicate  
333 whether sexual selection is occurring. One participant wrote, “Low heritability tells  
334 us nothing about sexual selection on badge size within any season, but does tell us  
335 that this selection will not effect change between seasons. This is a challenge for the  
336 KL and good-genes mechanisms, but does not tell us that badge size cannot be under  
337 sexual selection.” Similarly, another wrote, “These data measure heritability of fitness.  
338 They do not measure sexual selection on badge size. This would require data on male  
339 mating or fertilization success as a function of male badge size.”

340 Participants who do accept that heritability is included in sexual selection suggested  
341 that these data are consistent with the badge having evolved in the past from sexual  
342 selection (“ghost of sexual-selection past”) because bad genes have been weeded out by  
343 past female choice leading to present-day homogeneity in genetic quality (“paradox of  
344 the lek” realized). One participant wrote, “These correlations and heritabilities may be  
345 very hard to measure at equilibrium. These data are not relevant to the evolutionary  
346 process that brought the population to this point.” Similarly, another wrote, “It seems  
347 to me that if the system has low heritabilities for female preference as well as for male  
348 ornament, there really is no runaway process in place at the moment.” But another  
349 participant cautioned, “On the ‘ghost of sexual selection past’: Do we have good models  
350 of this with predictions? I don’t know of any. If we don’t this is dangerously close to  
351 being a just-so story.”

352 Other participants suggested that the data masked a fluctuating direction of sexual  
353 selection in different years. But a participant cautioned, “About fluctuating selection:  
354 as with other ‘context dependent benefits’ type explanations, this faces the problem  
355 that for the long-term evolution of a trait, there has to be positive selection on it  
356 averaged over the years. If a trait gets selected for one year and against the next, one  
357 cannot conclude that the trait evolves by sexual selection.”

358 The angst concerning this data set was expressed in the extreme by one participant who  
359 wrote, “I really don’t think we should include the dissection of the collared flycatcher  
360 studies. . . we really shouldnt focus too much attention on the findings of just one model  
361 system. If that work is incomplete or internally conflicting or inconsistent, it does not  
362 mean that the current empirical work on sexual selection can be said to be flawed in  
363 any way because it is after all just one species, and essentially one group of workers.”

364 Still other participants felt that the (Qvarnström *et. al.* 2006) data set on collared  
365 flycatchers in Gotland remains unparalleled for a natural population, encompassing as  
366 it does, 24 years of study and large sample size, and felt it must be taken into account  
367 in assessing the state of knowledge about sexual selection processes.

## 2.3 Towards a Final Definition

The deep differences in opinion evident in the deliberations above obviously precluded arriving at a consensus definition about what sexual selection is. One participant wrote, “To me the most striking thing of the meeting was that we all had very different views of how to define sexual selection.” Another participant wrote, “I absolutely don’t agree that there was a consensus reached as to which of the alternative definitions was the best.” The participants introduced a dozen or so possible definitions, of which here is a sample:

1. Sexual selection is the fraction of the sex difference in the variance in fertility owed to a combination of three factors: (a) the variance among males in fertilization numbers, (b) the variance among females in fertilization numbers per mating and/or (c) the covariance between male and female traits that affect fertilization numbers.
2. Sexual selection results on a trait when that trait has differential within-generation fitness due to differential fertilization success with gametes in the limiting sex.
3. Sexual selection is the component of selection that results from differential fertilization success among genotypes within a sex and that does not change total fertility.

Although these candidate definitions have important differences, they share common features: (1) they do not refer to sex roles at all, (2) they do not refer to the identity of the processes that might produce sexual selection, and (3) they do not refer to matings but to fertilizations. This later feature implicitly recognizes that many matings do not result in fertilizations and that the function of many instances of mating may be social rather than to effect a fertilization. Also the wording of all the candidate definitions departs considerably from the language, if not the intent, of Darwin’s (1871) characterizations of sexual selection.

Definitions #2 and #3 (in one of their many versions) attracted the most adherents. Definitions #1 and #2 do not take a position on whether sexual selection is a component of natural selection and so can be supported by participants who regard them as distinct. Definitions #1 and #2 also do not require that differences be heritable. Definitions #1 and #2 are largely behavioral. In contrast, definition #3 is the most explicitly genetical. It regards sexual selection as a component of a genetical selection process. In this definition the differences in fertilization success are assignable to different genotypes, implying that the differences are heritable. In this definition, the presence or absence of sexual selection is assayed in terms of genetical change and not in terms solely of behavior.

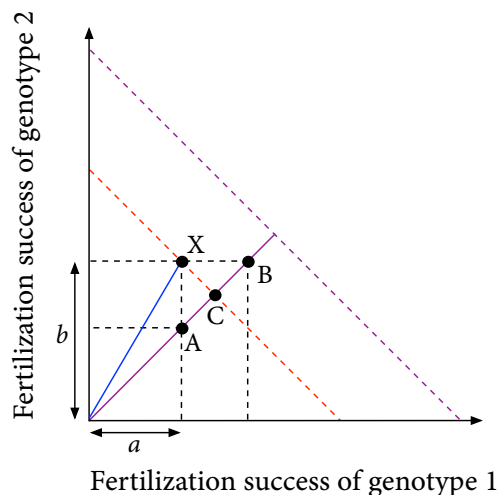
And definition #3 introduces a further issue: the distinction between a frequency-dependent process wherein genotypes differ in their share of a fixed reproductive pie *vs.* a density-dependent process wherein genotypes differ in the size of their reproductive pie. According to definition #3, sexual selection pertains solely to the change in the share of a fixed pie, and not to changing the size of the pie.

The origin for this distinction is a possible reading of Darwin’s (1871) saying that sexual selection “depends on the advantage which certain individuals over other individuals of the same sex and species, *in exclusive relation to reproduction*”. [Italics added.] In a passage intended to clarify the distinction between sexual selection and natural selection, he wrote, “The males of many oceanic crustaceans have their legs and antennae modified in an extraordinary manner for the prehension of the female; hence we may suspect that owing to

410 these animals being washed about by the waves of the open sea, they absolutely require  
 411 these organs in order to propagate their kind, and if so, their development has been the  
 412 result of ordinary or natural selection. . . [But] if the chief service rendered to the male by  
 413 his prehensile organs is to prevent the escape of the female before the arrival of other males,  
 414 or when assaulted by them, these organs will have been perfected through sexual selection,  
 415 that is by the advantage acquired by certain males over their rivals.” In the first scenario,  
 416 grasping organs that expedite mating in ocean surf correspond to the outcome of fertility  
 417 selection (increasing the size of the pie). In the second scenario, grasping organs that allow  
 418 monopolizing a female to exclude other males correspond to the outcome of sexual selection.  
 419 Darwin lumps fertility selection together with viability selection to form natural selection.  
 420 So, in definition #3 sexual selection is distinct from fertility selection, and thereby from  
 421 natural selection as well, but both sexual selection and natural selection are still components  
 422 of a common overall genetical selection process.

BOX 1. Supplement to Definition #3: Separating Sexual Selection from Fertility Selection

Suppose that two genotypes, 1 and 2, can compete for fertilizations. The total number of fertilizations possible (e.g., the total number of eggs a female has that can be fertilized by two competing males) is given by the dashed purple line. The diagonal purple line denotes equal fertilization success for both genotypes. At point X, genotype 2 obtains  $b$  fertilizations and genotype 1 obtains  $a$  fertilizations. Suppose also that genotypes 1 and 2 do not constructively or destructively interfere with one another when obtaining fertilizations; then, point A represents the total fertilization success of two individuals of genotype 1 and point B the success of two individuals of genotype 2. Genotype 2 obtains more fertilization success relative to genotype 1 and will be selected, but this is due to a combination of sexual selection and fertility selection where the latter causes the increase in total fertility from point A to point B. Now, suppose that point C represents the total fertility of two individuals when both are genotype 1 or 2. Genotype 2 still obtains a higher fertilization success relative to type 1 (point X) and will be selected, but when genotype 2 fixes in the population it does not increase the total fertility since both point X and point C both lie on the red dashed line. The relative fertility difference in this case causes only sexual selection.



423 Box 1 offers supplemental technical material concerning definition #3. More informally,  
424 consider a bird with a fixed clutch size. If the bird chooses one type of male over another  
425 because of its color, say, then sexual selection occurs, provided male color, female preference,  
426 and direction of female preference are all heritable. Alternatively, suppose the bird does not  
427 have a fixed clutch size but depends in part on courtship feeding to determine its clutch size.  
428 If the bird chooses one type of male over another because of its ability to contribute food,  
429 then fertility (natural) selection occurs, with perhaps some sexual selection mixed in too,  
430 provided male ability, female preference and female direction of preference are all heritable.  
431 Sexual selection refers to the part of fitness change owing solely to the female’s choice of one  
432 type of male over another, not taking into account any impact of that choice on the size of  
433 the pie. If this definition becomes widely adopted, statistical methodology will be deeded  
434 to partition the overall genetical selection process into its sexual-selection, fertility-selection,  
435 and viability-selection components.

### 436 3 Future Directions

437 Participants identified topics for research, some wholly within biology and others involv-  
438 ing interdisciplinary themes. Here is a sample of edited quotations from participants on  
439 future directions, presented in an arbitrary order more or less beginning with topics about  
440 sexual selection as such, then more general biological themes, and finally culminating with  
441 perspectives from the social sciences and humanities:

- 442 1. Refining and Adopting a Definition. “I believe we should refine and work toward a  
443 near-universal adoption of a common definition and the development and testing of  
444 null models. We should clearly define at least one null model and show how it can be  
445 tested and accepted or rejected using at least one numerical example, based either on  
446 real (published) or hypothetical data.”
- 447 2. Alternatives to Sexual Selection. “Given that a lot of mating is social and non-  
448 fertilizing, life history theory in ecology suggests an alternative approach to sexual  
449 selection studies. This approach starts at the end of the growing season and works  
450 back to the beginning of the life cycle through backward induction. The approach  
451 should first determine what the best social system is for the maturation of young—  
452 parental cooperation or not, social foraging or not, *etc.* Then taking a step backwards,  
453 the approach determines what negotiations will lead to the optimal end-of-season so-  
454 cial system such as negotiations to set the degree of mutual support and the clutch  
455 size. Next, the approach works back from that to what type of signaling system in  
456 terms of ornaments and courtship behavior is needed to communicate the necessary  
457 information to carry out the negotiations. This approach is ‘social infrastructure se-  
458 lection’ (*e.g.* Roughgarden 2012b). It focusses on ornaments, courtship and mating  
459 as a social mechanism to achieve fertility selection, *i.e.*, on increasing the number of  
460 young—on increasing the pie rather than gaining a larger section of a fixed pie, using  
461 the terminology of definition #3.”
- 462 3. Comparative Genomics and Sexual Selection. “Comparative genomic studies are show-  
463 ing that genes expressed in a sexually dimorphic manner show faster evolution between

464 species, strongly suggesting that sex-specific selection is a major cause of genetic evo-  
465 lution (*e.g.* Pröschel *et al.* 2006; Clark *et al.* 2007). This effect may be stronger in  
466 male-specific genes. Some of this effect probably lies in sexual selection (Ellegren and  
467 Parsch 2007; Mank and Ellegren 2009). Both artificial evolution in the laboratory and  
468 some field studies are also suggesting that sexual dimorphism in the transcriptome can  
469 evolve rapidly under sexual selection and predicts mating status (Pointer *et al.* 2013).”

470 4. Hormones and Sexual Selection. “Hormones such as steroids (gene transcription regu-  
471 lators) can produce sex differences through organization, activation or a combination  
472 of both, but it is not understood how these different processes are related to sexual  
473 selection. Gene-level mechanisms and genetic architecture of traits, along with hor-  
474 monal mechanisms, have the potential to help explain the phylogenetic distribution of  
475 sexually selected traits (Chenoweth and McGuigan 2010, Whitehead 2012, Cummings  
476 2012, Rosvall *et al.* 2012, Bergeon Burns *et al.* 2013.)”

477 5. Bounded Cognition and Mate Choice. “An animal’s cognitive abilities and limitations  
478 are important in shaping its behavior. In sexual selection, this view has been mostly  
479 applied for perceptual abilities and the evolution of signals (Rowe 2013), but may be  
480 extended more broadly to additional aspects of cognition (Guilford and Dawkins 1991;  
481 Miller and Bee 2012). Particularly, mate choice may be affected by context-dependent  
482 evaluations (Shafir *et al.* 2003; Bateson and Healy 2005)”

483 6. Signaling Theory and Sexual Selection. “Signaling games bear on sexual selection  
484 theory through the handicap model (Grafen 1990) that a signal’s cost helps maintain  
485 signal reliability between organisms with conflicting goals. Further research should in-  
486 vestigate common-interest signaling models (as, for example, outlined by Lewis 1969)  
487 to sexual signaling. Where mate interests strongly align, these models may be informa-  
488 tive. Evolutionary game theoretic investigations of common-interest signaling games  
489 indicate that populations can evolve informative signaling conventions that allow them  
490 to effectively coordinate behavior (Skyrms 1996, 2010).”

491 7. Same-Sex Social Bonds and Sexual-Selection Studies. “Describing, quantifying and  
492 testing the adaptive significance of same-sex sexual behaviour has clear conceptual  
493 connections to the field of sexual selection and social evolution (*e.g.* Bailey *et al.* 2013).  
494 As with opposite-sex social interactions, behaviours that appear to be sexual in origin  
495 because of their outward manifestation (*e.g.* courtship or attempted copulation) may  
496 arise from proximate mechanisms and ultimate functions that are not, in fact, sexual.  
497 An example might be cooperative breeding attempts engaging two individuals of the  
498 same sex when the opposite sex is in limited supply, as occurs in Laysan albatross  
499 (Young *et al.* 2008) and California gulls (Conover and Hunt 1984). However, sex-  
500 ual and non-sexual behaviours can clearly occur together; in the albatross example,  
501 female-female copulation attempts have been observed to occur in addition to affilia-  
502 tive behaviours such as mutual preening and cooperative nest-building. An affiliative  
503 role for same-sex sexual behaviour has also been postulated in a number of primate  
504 and mammalian species (Sommer and Vasey 2006).”

- 505 8. Physical Intimacy to Realize Cooperative Outcomes. “Various forms of physical intimacy including mutual grooming, preening, and vocalizations as well as same-sex  
506 matings may all comprise mechanisms to coordinate and realize cooperative outcomes  
507 to situations involving non-congruent interests (*e.g.* Roughgarden 2012a). The role of  
508 social bonds in realizing a Nash bargaining outcome rather than a Nash competitive  
509 equilibrium outcome is a possible direction for future investigation.”  
510
- 511 9. Causes of Male Parental Investment. “Parental care evolution and sexual selection  
512 influence one another. Females have been thought to provide more parental care than  
513 males and sexual selection on males has been argued to disfavor the evolution of pa-  
514 ternal care (*e.g.* Queller 1997, Kokko and Jennions 2008). If males provide any care,  
515 they are expected to invest less when females mate multiply and males are less certain  
516 of paternity. Yet, biparental care persists in many species despite female promiscuity,  
517 and also male-only care is found in a wide range of taxa despite multiple mating by  
518 females. Instead, female choice, male competition and parental effort coevolve as a re-  
519 sult of interactions within and between the sexes (Alonzo, 2012). Inter-sexual selection  
520 arising from female choice can favor the evolution of paternal care and even lead to  
521 the loss of maternal care (Alonzo, 2012) and empirical patterns indicating that male  
522 ocellated wrasses with the lowest certainty of paternity are the most likely to provide  
523 paternal care (Alonzo and Heckman 2010, Alonzo, 2010).”
- 524 10. Game-Theoretic Analysis of Parental Care. “The parental investment hypothesis  
525 (Trivers 1972) links anisogamy with greater female parental care using arguments  
526 shown to be logically flawed (Kokko and Jennions 2008, Dawkins and Carlisle 1976).  
527 Self-consistent versions of Maynard Smith’s parental care game (Maynard Smith 1977)  
528 show that anisogamy, in fact, selects for greater male parental care (Iyer and Shukla, in  
529 prep.), a result consistent with the first evolutionary transitions in parental care among  
530 ancestral fish and birds being from no-care to male-only care (Royle *et al.* 2012). Hence  
531 the mammalian pattern of greater female parental care appears to be derived, and may  
532 emerge from factors such as parentage differences between the sexes and patterns of  
533 sexual selection rather than anisogamy (Kokko and Jennions 2008, Iyer and Shukla in  
534 prep).”
- 535 11. Choice and Parental Investment. “Future work could usefully investigate choice for  
536 parental investment, which has received surprisingly little attention (see *e.g.* Royle  
537 *et al.* 2010). Such choice for parental care could vary in intensity depending on the  
538 choosers own phenotype, and their own level or style of care. It will also have important  
539 implications for behavioural consistency (see *e.g.* Royle *et al.* 2010) and negotiation  
540 (see Johnstone and Hinde 2006).”
- 541 12. Sexual Selection and Speciation. “A definition of sexual selection should be clarified as  
542 being distinct from a definition of natural selection because the role of sexual selection  
543 in speciation given the existence of so many different models of sexual selection in  
544 the literature. We organize the existing models of sexual selection into those that are  
545 likely to interact with environmental context (*e.g.* good genes or good parent traits)

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and those that are not (*e.g.*, sexual selection by the Fisherian runaway process) (Safran *et al.* 2013).”

13. Economic Theory of Marriage. “Mate selection theory in biology can likely draw upon ideas from the economic analysis of marriage based on Gary Becker’s (1973) theory of marriage. In particular, how sex ratios affect mate selection and how the resources each partner brings to the marriage influence the division of labor and of wages are topics treated in economic theories of marriage (Becker 1973, Grossbard-Shechtman 1993).”
14. Economic Theory of the Firm. “A social group of animals might be analogized to a firm in economics. Groups with social foraging and predator protection, as well as extended families, might be considered as ‘biological firms’ that produce offspring as their ‘product’. The theory of the firm in economics has models that show how to structure incentives to maximize group productivity (Coase 1937, Groves 1973, Milgrom and Roberts 1990, *c.f.* Kroszner and Putterman 2009). These models may be usefully adapted to biology to yield models in the behavioral tier of a two-tier theory needed for the evolution of social behavior (Roughgarden 2012b, Roughgarden and Song 2013).”
15. Economic Inefficiency of Conflict. “Whereas theoretical biologists generally start from the premise of zero-sum competition over shares in the next generation, political scientists and economists have a long tradition of seeing human interactions as a mix of common and conflicting interests. Even before Darwin, political philosophers and political economists argued that evolutionary processes, together with more deliberate or consciously coordinated efforts, lead to increasingly complex political and economic institutions that enable the realization of common interests. A substantial tradition of research since the 1950s, much of it using game theoretic concepts similar to those used in theoretical biology, has isolated and clarified a set of typical obstacles to cooperation that political and economic institutions may have evolved to overcome. These same obstacles frequently appear in interactions within and across non-human species. First, two members of one species, or members of two different species, might both be able to gain higher fitness if one of them could ‘commit’ to some particular behavior in an interaction. Second, members of one or more species might be able to increase their total fitness if information possessed by one animal could be credibly communicated to others. Just as we observe in human societies ranging from hunter-gatherers to advanced industrial economies, we see examples of arrangements within and across non-human species that can be naturally characterized as ‘institutions,’ and which seem to have evolved to allow credible commitment and the revelation of useful private information.”
16. Biological Institutions. “A biological institution is the context in which a biological interaction takes place that defines the allowable strategies and their consequences. In other words, biological institutions define the behavioral ‘game’ individuals are playing, or to use a term from a different perspective, a biological institution is the natural history of an interaction. The reason we use the term institutions is to make

588 analogy with the concept in social sciences, where institutions are designed to facilitate  
589 individuals behaving optimally for themselves to achieve mutually beneficial outcomes.  
590 In the same way, we hypothesize that many interactions in nature have evolved to be  
591 structured in such a way as to lead natural selection acting on individual behaviors  
592 (or to use a teleological phrasing, individuals following their own interests) to achieve  
593 mutually fitness-enhancing outcomes. The hammer-headed bat leks (Bradbury 1977)  
594 would be one example of a biological institution. The eventual reduction of aggression  
595 between individuals and non-interference with female choice represents a mutually  
596 beneficial arrangement that is compatible with individual incentives.”

597 17. History of Thought on Sexual Selection. “In the late nineteenth-century, many natural-  
598 ists reacted to Charles Darwins theory of sexual selection with great skepticism. They  
599 presumed that for sexual selection—through either mate competition or choice—to  
600 act as an effective means of evolutionary change, individuals must discern aesthetic or  
601 physiological differences in their rivals and potential mates, respectively (Milam 2010).  
602 Commensurate with the rise of ethology after World War II, zoologists increasingly  
603 described individual animals as active negotiators of their social environments. As  
604 biologists continue to deepen their understanding of the complexity of animal minds,  
605 the cognitive incapacity of animals is less frequently invoked as a factor limiting the  
606 operation of sexual selection. Thus, a historical perspective suggests that the fate of  
607 sexual selection as a biological theory has been, and continues to be, intimately linked  
608 to conceptions of animal mind.”

609 18. Sexual Selection’s Conceptual Evolution: “The major dramatic conceptual shifts listed  
610 in section 2 of this report, are indicators of tension within the concept of sexual se-  
611 lection. The sharp discrepancy between Darwin’s 1871 original insights, and the con-  
612 temporary notion of sexual selection, throw some doubts on the unity of the concept.  
613 While biologists constantly refer to Darwin’s views and depict themselves as the true  
614 heirs of Darwin’s mantle, there is little consistency in these claims of legacy. Darwin  
615 had no idea of mathematisation of sexual selection; he strongly suggested that sexual  
616 selection was linked to typical sex roles. It should be decided whether conflict, com-  
617 petition, and good genes are necessary assumptions of the evolutionary hypothesis, or  
618 not. Attention should be paid to animal models and systems. A consistent overview  
619 of the field should be undertaken, species per species, to summarize all data that have  
620 been gathered at this point, and assess their relevance to the issue of sexual selection  
621 currently operating in nature. Also, special care should be devoted to the mathemati-  
622 cal models that are currently used in biology, and whether other models should also be  
623 called for. This meeting also calls for more interdisciplinary work: for instance whether  
624 a different ‘evo-eco’ synthesis should be attempted: between evolutionary theory and  
625 economics (*cf.* Hoquet 2014).”

626 19. Sexual Selection and Public Discourse. “Sexual selection science operates within the  
627 charged space of ideas about nature and culture, mind and body, science and society,  
628 and biology and ideology. The evolutionary studies of mating and sexuality impact  
629 the general life sciences, the broader academy, public intellectual discussions, and pop-  
630 ular understandings of science. Examples include debates over human mating, dating,



631 and infidelity; rape and sexual aggression; sexual orientation; division of labor in the  
632 household and parenting; and the prospects for gender equality. These impacts im-  
633 ply a special responsibility for sexual-selection researchers to attend not only to the  
634 precision of their scientific claims but also to the ethical dimensions of their research.  
635 Interdisciplinary engagement with scholars in the history, philosophy, sociology, and  
636 gender studies of science provides one route to meeting this responsibility (Smith 2006,  
637 McCaughey 2008, Richardson 2013).”

## 638 4 Conclusion

639 A catalyst meeting of 34 participants was convened in July 2013 at NESCent (Durham,  
640 NC) to consider the progress, challenges and future directions of sexual selection studies.  
641 The meeting agreed that any contemporary definition of sexual selection should not specify  
642 characteristic sex or gender roles, should not specify particular processes that might produce  
643 sexual selection, and should not refer to matings but to fertilizations. However, the meeting  
644 did not identify a single definition of sexual selection that all or most participants found  
645 satisfactory. Differences of opinion coalesced around whether to include heritability in sexual  
646 selection’s definition or not, whether sexual selection is a component of natural selection or  
647 not, and whether data and theory support the existence of the good-genes and sexy-sons  
648 processes in nature or not. The meeting produced several candidates for a contemporary  
649 definition of sexual selection, of which three are presented in this report. The meeting  
650 participants also offered a suite of topics for future research including some involving solely  
651 new biology and others involving interdisciplinary collaboration with the social sciences and  
652 humanities.

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