

Sexual Selection Studies: A NESCent Catalyst Meeting

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9 **Abstract**

10 A catalyst meeting on sexual selection studies was held in July 2013 at the facilities of the National Evolutionary Synthesis Center (NESCent) in Durham, NC. This article by a subcommittee of the participants foregrounds some of the topics discussed at the meeting. Topics mentioned here include the relevance of heritability estimates to assessing the presence of sexual selection, whether sexual selection is distinct from natural selection, and the utility of distinguishing sexual selection from fecundity selection. A possible definition of sexual selection is offered based on a distinction between sexual selection as a frequency-dependent process and fecundity selection as a density-dependent process. Another topic highlighted is a deep disagreement among participants in the reality of good-genes, sexy-sons, and run-away processes. Finally, the status of conflict in political-economic theory is contrasted with the status accorded to conflict in evolutionary behavioral theory, and the professional responsibility of sexual-selection workers to consider the ethical dimension of their research is underscored.

24 **Introduction.** Thirty four participants reflecting a diversity of ages, nationalities, and disciplines met at the National Evolutionary Synthesis Center (NESCent) in Durham, NC, during July 2013 to review the status of sexual selection studies and to indicate challenges and future directions. “Sexual selection studies” is used here as an umbrella phrase referring to the study of evolutionary pressures arising from sexual reproduction, through processes such as courtship and mating, as well as parent-offspring relations, family organization, and the connections among these. Two thirds of the participants brought special experience from their research and teaching in some area of sexual selection studies and one third brought perspectives from other areas of evolutionary biology and from the social sciences and humanities.

34 The participants did not arrive at a consensus definition of sexual selection, and disagreed on many issues pertaining to sexual selection. The meeting’s final report documenting these disagreements was reviewed and endorsed by the participants and is provided as supplementary material (Roughgarden, J. et al., 2013). This article highlights some items

38 from the meeting for further comment by the community. This article offers the authors' re-
39 flections on going forward and does not necessarily speak for other participants. The follow-
40 ing lists some of the points of disagreement and suggest accommodation where possible.
41 Some points of agreement were obtained and these are noted too.

42 **Relevance of Heritability.** Considerable disagreement exists concerning whether heri-
43 tability is to be included in the definition of sexual selection. The phrase "sexual selection"
44 has an ambiguous usage. In some contexts, heritability is implied and in others not. The
45 authors recommend simply recognizing this state of affairs and advocate more cautious
46 terminology in the future.

47 This is more than a trivial matter of semantics: whether sexual selection is understood
48 to include heritability underpins the empirical conditions under which sexual selection is
49 understood to occur. Take the breeders' equation, where the response to selection, R , equals
50 the heritability, h^2 , times the strength of selection, S : $R = h^2S$. If sexual selection is
51 defined by analogy to this equation, the presence of sexual selection simply means that
52 S is significantly non-zero. But that does not imply that sexual selection will cause any
53 change in the trait, i.e. that R is significantly non-zero. A statement like "sexual selection
54 has caused trait X to evolve" requires both a significant S and a significant h^2 . However, a
55 statement like "sexual selection is acting on trait X" requires only a significant S . In this
56 context, whether the S is causing or has caused an evolutionary response is left unspecified.

57 This discrepancy between the selection and response to selection meanings of the phrase
58 "sexual selection" surfaced during discussion of the badge in male collared flycatchers
59 (Qvarnström et al., 2006). Here sexual selection apparently exists for the trait, but the rel-
60 evant heritabilities are negligible, so an evolutionary response to sexual selection is not
61 occurring. To reconcile this fact with a belief that sexual selection nonetheless explains
62 the evolution of the badge, some participants argued that the badge is a "ghost of sexual
63 selection past", and that the absence of present-day heritabilities is merely an indication
64 of past genetic variation having become exhausted during the selection process. Alterna-
65 tively, the hypothesis that sexual selection caused the evolution of the badge might be false.
66 The hypothesis that the badge represents a ghost of sexual selection past might someday
67 become testable in light of increasingly available genomic estimates of past selection, for

68 example Nadeau et al. (2007). Readers should consult the full report for more detail.

69 **Sexual Selection vs. Natural Selection.** Considerable disagreement also exists on whether
70 sexual selection should be considered a component of natural selection or distinct from
71 natural selection. Many participants initially felt that sexual selection is merely a subset
72 of natural selection. Upon further thought however, there is advantage to viewing them
73 as distinct in the following sense. If natural selection is regarded as consisting of fecun-
74 dity selection and viability selection, then sexual selection may be considered distinct from
75 these, although all three contribute to what might be termed the overall “genetical evolu-
76 tionary process”, provided the heritabilities for these components are significant. Everyone
77 acknowledges, of course, that evolution is proceeding via changes in the gene pool. But
78 it is also valuable to acknowledge that sexual selection, fecundity selection and viability
79 selection can each be brought about by substantially different processes and can lead to
80 qualitatively different results such as traits that are functionally adaptive vs. traits that are
81 not functionally adaptive.

82 **Distinguishing Sexual Selection From Fecundity Selection.** There may be advantages
83 to distinguishing sexual selection as a frequency-dependent process from fecundity selec-
84 tion as a density-dependent process. This distinction seems to underlie many of the dis-
85 agreements and differing perspectives among participants and as evident in the disputes
86 of recent literature. A perspective from life-history theory in population ecology focuses
87 on designing the survivorship curve, $l(x)$ and the maternity function, $m(x)$ to maximize
88 the intrinsic rate of increase, r . So it is natural from this perspective to see courtship and
89 the gene-sharing through sex as cooperative life-history traits that increase r , thereby in-
90 creasing the size of the pie, so to speak. Alternatively, a perspective focusing solely on
91 gene pool frequencies does not capture density dependent processes within and between
92 sexes that contribute to a total increase in fecundity. Without including density dependent
93 processes, courtship and sex can function only as purely competitive processes providing
94 mechanisms to gain a larger fraction of a pie whose size is fixed at unity.

95 The behavior occurring during courtship, mate choice, parent-offspring dynamics and
96 so forth may involve both increasing the size of the pie and increasing the share of the pie.

97 Hence the authors recommend identifying sexual selection with processes that increase the
98 share of the gene pool, and fecundity selection with processes that increase the number of
99 offspring to which that gene pool refers.

100 **Sexual Selection Defined.** These considerations lead to proposing the following defini-
101 tions for sexual selection and evolution by sexual selection:

102 DEFINITION: *Sexual selection* is a differential probability of the genotypes
103 within a sex being incorporated into fertilizations independent of a difference
104 in total fecundity.

105 DEFINITION: *Evolution by sexual selection* is a *change* in the genetic com-
106 position of a population *caused* by a differential probability of the genotypes
107 within a sex being incorporated into fertilizations independent of a difference
108 in total fecundity.

109 This definition highlights some points on which the participants did find agreement.
110 Deliberately, this definition does not specify paradigmatic sex roles, does not specify the
111 identity of processes that might produce sexual selection, and refers to fertilizations and
112 not matings¹. This later feature implicitly recognizes that many matings do not result in
113 fertilizations and that the function of many instances of mating may be social rather than to
114 effect a fertilization. “Evolution” by sexual selection includes a requirement of significant
115 heritability to account for evolutionary change.

116 The authors note this definition is not quantitative. It expresses in words an idea of
117 what sexual selection might be understood to mean, an idea that may be conceptually dis-
118 tinguished from that of fecundity selection. This definition implicitly calls for theoretical
119 research to be carried out on quantitative methods, protocols and criteria to partition the
120 data taken on mating dynamics and parent-offspring relations into their sexual-selection
121 and fecundity-selection components.

122 For example, from a quantitative genetic tradition, a conjecture is that the variance in
123 fitness resulting from variation in some behavior might be partitioned into a component

¹In theoretical population genetics, “mating” may sometimes be understood to refer specifically to mating events that yield fertilization.

124 pertaining to variance in zygote number produced and a component pertaining to variance
125 in probability of being incorporated into those zygotes. If so, the component of variance
126 explained by zygote number could be taken as a measure of the fecundity selection and the
127 component explained by zygote incorporation could be taken as a measure of sexual selec-
128 tion. The methods of Shuster et al. (2013) might be extended to accomplish this task. Also,
129 quantitative approaches from population genetics and other theoretical traditions might pro-
130 vide additional measurement protocols.

131 A conceptual issue to resolve is what the “pie” refers to, or in the definition above, to
132 what or whom does the phrase, “total fecundity”, refer. To illustrate an answer to these
133 questions, an appendix is supplied in which the “pie” from the perspective of a focal male
134 refers to the number of offspring produced by all the females he is mating with. The ap-
135 pendix shows how the distinction between fecundity selection and sexual selection might
136 be approached from a game-theoretic tradition in behavioral modeling.

137 The distinction between sexual selection as a frequency dependent process and fecun-
138 dity selection as a density dependent process is consistent with a possible reading of Dar-
139 win’s 1871 passages intended to clarify the distinction between sexual selection and natural
140 selection:

141 “The males of many oceanic crustaceans have their legs and antennae modified
142 in an extraordinary manner for the prehension of the female; hence we may
143 suspect that owing to these animals being washed about by the waves of the
144 open sea, they absolutely require these organs in order to propagate their kind,
145 and if so, their development has been the result of ordinary or natural selection”
146 [Vol. I, p. 256]. But, “if the chief service rendered to the male by his prehensile
147 organs is to prevent the escape of the female before the arrival of other males, or
148 when assaulted by them, these organs will have been perfected through sexual
149 selection, that is by the advantage acquired by certain males over their rivals.
150 But in most cases it is scarcely possible to distinguish between the effects of
151 natural and sexual selection.” [Vol. 1, p. 257]

152 In Darwin’s first scenario, grasping organs that prevent being washed out to sea while
153 mating in ocean surf correspond to the outcome of fecundity selection (increasing the size

154 of the pie). In Darwin's second scenario, grasping organs that allow monopolizing a female
155 to exclude other males correspond to the outcome of sexual selection (increasing the share
156 of the pie). Darwin lumps fecundity selection together with viability selection to form
157 natural selection. So, in this definition, sexual selection is distinct from fecundity selection,
158 and thereby from natural selection as well, but both sexual selection and natural selection
159 are still components of a common overall genetical selection process.

160 To take another example, consider a female bird with a fixed clutch size. If the female
161 chooses to mate with one type of male over another because of his feather colors, then evo-
162 lutionary sexual selection occurs, provided the intensity of male color, intensity of female
163 preference, and the direction of female preference are all heritable. Alternatively, suppose
164 the female does not have a fixed clutch size but depends in part on courtship feeding by
165 the male to determine its clutch size. If the female chooses one type of male over another
166 because of his ability to contribute food, then evolutionary fecundity selection occurs, with
167 perhaps some evolutionary sexual selection mixed in too, provided male ability, female
168 preference and female direction of preference are all heritable.

169 The decompositions in the examples above might not be regarded as controversial.
170 However, the definition involves subtleties. Consider females exerting mate choice us-
171 ing a male secondary sexual trait directly indicative of male health (an index signal) and
172 that health can be compromised through sexually transmitted parasites. Females would
173 presumably increase their own fecundity by remaining healthy, which requires their avoid-
174 ing contact with unhealthy, parasitized males. Hence, mate choice in this context includes
175 fecundity selection on the female. However, the female mate choice also brings about in-
176 tersexual sexual selection on the males to reveal their health and secure a higher percentage
177 of matings than unhealthy males. Thus the mate choice by females in this case includes
178 components of both fecundity selection and sexual selection.

179 Social infrastructure selection, *sensu* Roughgarden (2012), focuses on the fecundity
180 selection component of the genetical selection process resulting from reproductive social
181 behavior. Its empirical claim is that differential fertilization success of genotypes is rarely
182 the result solely of zero-sum processes that do not change total fecundity, but as a rule also
183 involves positive-sum (cooperative) processes that increase total fecundity.

184 Readers may consult the supplementary material to see other definitions that have been
185 considered.

186 **Reality of Good Genes etc.** Substantial disagreement emerged concerning the reality
187 of the good genes, sexy sons, and run-away processes. Some have concluded that these
188 processes simply do not exist at all. Although they can plausibly arise in verbal and mathe-
189 matical models, these processes are often unsupported or even contraindicated by data and
190 inconsistent with other theoretical arguments. Many however, still continue to believe these
191 processes do exist. This disagreement emerged during discussion of a recent meta-analysis
192 of 90 studies on 55 species showing that sexually selected traits such as ornaments do not
193 have a significant correlation with life history fitness traits (Prokop et al., 2012). See the
194 supplementary material for more detail. The authors cannot propose a middle ground or
195 reconciliation between these positions; the disagreement can only be worked out with new
196 data and careful meta-analyses. The authors merely observe that serious reservations exist
197 about the reality of these processes regardless of their venerable presence in the literature.

198 **Relation to Other Disciplines.** Two points made by participants from the social sciences
199 and humanities are now highlighted.

200 Contributions from political science emphasize that competition and conflict are eco-
201 nomically inefficient. Much theoretical political-science research seeks to explain the para-
202 dox of why conflict exists in spite of its inefficiency, presumably resulting from a breakdown
203 of institutions, a hoarding of private information, and/or a mis-estimation of each party's
204 interests and bargaining position. Political science also dwells at length on how human
205 evolutionary processes, both cultural and presumably biological, have led to increasingly
206 complex political and economic institutions that enable realization of common interests by
207 individuals following their own interests. In other words, self-interest, even when there
208 are material trade-offs and thus potential for conflict, does not necessarily imply realized
209 conflict. This calls into question the undiscussed but opposite presumption in evolutionary
210 biology that competition and conflict are unavoidable and social cooperation a derived con-
211 dition requiring special explanation. There is no reason why the perspective from political
212 science should not also apply to biology where efficiency in fitness production substitutes

213 for efficiency in economic utility (Akçay et al., 2013).

214 Contributions from humanists emphasize the special obligation of sexual selection re-
215 searchers to attend not only to the precision of their scientific claims but also to the ethi-
216 cal dimensions of their research. The humanists invite interdisciplinary engagement with
217 scholars in the history, philosophy, sociology, and gender studies of science as one route to
218 meeting this responsibility.

219 **Conclusion.** The authors close with editorializing remarks. Researchers in sexual se-
220 lection studies have a responsibility to proactively seek concepts and analogies in related
221 disciplines. Sexual selection studies does not stand alone as a self-contained and isolated
222 discipline. The field will die if it is defensive and backward looking. The field should cel-
223 ebrate the disagreements that have been taking place within it in recent years as a sign of
224 health. The field should look forward to a reframing of its content in terms that would be
225 unthinkable from perspectives that date to the 1970's.

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239 Appendix. Fecundity Selection vs. Sexual Selection : An Illustration

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242 A mathematical sketch is offered to illustrate the behavioral distinction between fecun-
243 dity selection and sexual selection.

244 Consider a focal male who allocates time during a day into two activities: helping the
245 females he is mating with to produce eggs vs. guarding those females to prevent other males
246 from mating with them. The sum of times allocated to these activities is 1. These two times
247 are t_h (helping time) and t_g (guarding time).

248 Next, consider a focal female who allocates time during a day into two activities: forag-
249 ing by herself to produce eggs vs. being receptive to mating. The sum of the times allocated
250 to these activities is 1. These two times are t_f (foraging time) and t_r (receptivity time).

251 In this setup, the reproductive “pie” for the male is the sum of the eggs produced by
252 all the females he is mating with. Fecundity selection favors increasing the size of that pie
253 by helping the females he is mating with to produce more eggs. Sexual selection favors
254 increasing the fraction of that pie that he sires. The scope of the pie refers to the number
255 of females the male is mating with.

256 The overall mating system that emerges can include, for the male, elements of both
257 fecundity selection and sexual selection, and for the female, varied amounts of foraging
258 activity and mating receptivity.

259 The theoretical problem is to determine the simultaneously optimal values for the vector
260 of time allocations for both the male and female, $\{t_h, t_g, t_f, t_r\}$. Consider then how this
261 problem might be investigated in the following scenario.

262 Let the female’s daily egg production, e , be

$$e = t_f c_0 + m_m c_1 \left(\frac{t_h}{m_f} \right)^{c_2} \quad (1)$$

263 where m_m is the number of male mates a female has, m_f is the number of female mates
264 a male has, and c_0, c_1, c_2 are coefficients. (These coefficients are typically assigned as
265 $c_0 \rightarrow 1, c_1 \rightarrow 1,$ and $c_2 \rightarrow \frac{1}{2}$.) This formula says that the daily egg production by a

266 female increases with her own foraging time and from male contributions. Each of the m_m
267 males provides an assistance that reflects his total helping time divided by the m_f females
268 among whom he is apportioning that time. Assuming $c_2 < 1$ implies that the contribution
269 to female fecundity from male helping shows a decreasing return to scale.

270 Let the fraction of the day's eggs sired by the focal male be

$$f = c_4 \left(\frac{t_r}{m_m} \right) \left(1 - e^{-c_3 \frac{t_g}{m_f}} \right) \quad (2)$$

271 where c_3 and c_4 are coefficients (typically, $c_3 \rightarrow 2$ and $c_4 \rightarrow 1$). If the female has m_m
272 mates, her receptivity time, t_r , is apportioned equally among these males. If the male has
273 m_f mates, his guarding time, t_g , is apportioned equally among these females. Increasing
274 guarding time yields increasing fertilization with a decreasing return to scale. Increasing
275 receptivity yields increasing fertilization linearly. In the scenario modeled here, all the eggs
276 on a given day may not be fertilized. (With the arbitrary coefficients of Table 1, f works
277 out in the top row to be only 17.9% and even less in the other rows.)

278 The fitness increment of a female is the number of eggs she produces during the day
279 taking into account her own foraging plus any help from the males she is mating with

$$W_f = e \quad (3)$$

280 whereas the fitness increment of the male is the number of eggs produced during the day
281 by all the females he is mating with times the fraction of those that he sires,

$$W_m = m_f f e \quad (4)$$

282 If the male and female do not cooperate, then the time allocations satisfy a Nash Equi-
283 librium where neither party can improve their fitness increment given the other's time al-
284 location. At this equilibrium the female forages throughout the entire day, leaving perhaps
285 an infinitesimal receptive period to collect any sperm needed to fertilize her eggs. Mean-
286 while, at this equilibrium, the male does not contribute any help to the female. That is,
287 the non-cooperative Nash Equilibrium mating system consists of the male and female time

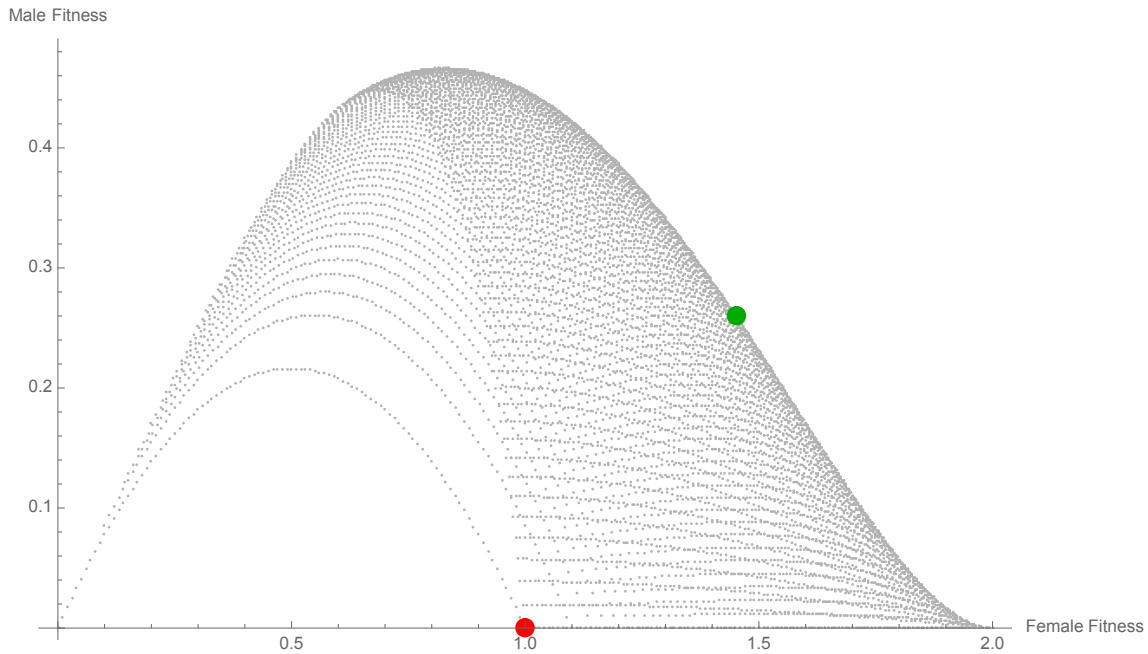


Figure 1: Payoff Space. Fitness pairs resulting from all combinations of male and female time-allocation strategies. Right edge of space is the Pareto boundary. Nash Equilibrium threat point is large dot on horizontal axis. Nash Bargaining Solution is large dot on Pareto boundary. Example for $m_m = 1$ and $m_f = 1$.

288 allocations, $\{t_h, t_g, t_f, t_r\} \rightarrow \{0, 1, 1, 0\}$. This mating system leads to the female and male
 289 fitness increments of $W_f \rightarrow c_0$ and $W_m \rightarrow 0$, regardless of the values assigned to the other
 290 parameters and coefficients.

291 This non-cooperative outcome may be taken as the threat point for negotiation during
 292 courtship to attain a cooperative alternative. The cooperative alternative, represented by
 293 the Nash Bargaining Solution, is the time-allocation vector that maximizes the product of
 294 the excess fitness increments relative to the threat point,

$$NP = (W_f - c_0)(W_m - 0) \quad (5)$$

295 where NP is the Nash Product.

296 Figure 1 presents an example of the payoff space for the male and female strategies

Table 1: Fecundity and Sexual Selection in Males, Foraging and Receptivity in Females.

m_m	m_f	t_h	t_g	t_f	t_r	f	W_f	W_m
1	1	0.630897	0.369103	0.65624	0.34376	0.179453	1.45053	0.260302
1	2	0.580645	0.419355	0.758275	0.241725	0.082798	1.29709	0.214793
1	3	0.559978	0.440022	0.802733	0.197267	0.0501526	1.23477	0.185781
2	1	0.644623	0.355377	0.35512	0.64488	0.164034	1.96089	0.321652
2	2	0.595429	0.404571	0.543045	0.456955	0.076023	1.63431	0.24849
2	3	0.574299	0.425701	0.624977	0.375023	0.046331	1.50004	0.208495
3	1	0.65237	0.34763	0.0675028	0.932497	0.155744	2.49059	0.387894
3	2	0.604939	0.395061	0.339318	0.660682	0.0718736	1.98923	0.285947
3	3	0.5842	0.4158	0.457103	0.542897	0.0438113	1.78096	0.234079

297 illustrating the Nash Equilibrium threat point and the Nash Bargaining Solution. The
 298 cooperative-solution fitness increments for both males and females are larger than the non-
 299 cooperative-solution fitness increments, implying that cooperation according to the Nash
 300 Bargaining Solution is a win-win solution relative to the non-cooperative solution given
 301 by the Nash Equilibrium. Accordingly the Nash Bargaining Solution lies on the Pareto
 302 boundary of the payoff space, as depicted in the figure.

303 Table 1 presents the numerical solution to this maximization for several cases, based on
 304 the coefficients noted above. (A script written in Mathematica (Wolfram Research, Inc.)
 305 to solve the maximization is included in the supplementary material.) The table shows the
 306 cooperative solution—the optimal allocation between helping and guarding in the male,
 307 and between foraging and being receptive for the female, based on the Nash Bargaining
 308 Solution. The table also shows the male’s fraction sired and the resulting fitness increments
 309 for both female and male.

310 The first three rows present the cases where the female mates with one male, and the
 311 male mates with one, two or three females. The next three rows present cases where the
 312 female has two male mates and each male has one, two or three female mates. The last
 313 three rows present cases where the female has three male mates, and the male has one, two
 314 or three female mates.

315 In general, the table shows that males should develop a balance between their alloca-
316 tion to helping their mates produce more eggs and defending their paternity of those eggs.
317 That is, a balance should develop between fecundity selection and sexual selection. The
318 table also shows that, at the same time, the females should develop a balance between solo
319 foraging to increase their egg production *vs.* being receptive to mating.

320 More specifically, the table shows that increasing polygyny for a given degree of poly-
321 andry (revealed by comparing the rows within each group of three cases) leads to less
322 helping and more guarding by males, and to more solo foraging and less reproductive re-
323 ceptivity by females. As a result, increasing polygyny for a given polyandry leads to a lower
324 male sire fraction and to lower fitness increments for both males and females.

325 The table also shows that increasing polyandry for a given degree of polygyny (revealed
326 by comparing corresponding rows across each group of three cases) leads to more helping
327 and less guarding by males, and to less solo foraging and more reproductive receptivity by
328 females. As a result, increasing polyandry for a given polygyny leads to decreased male
329 sire fraction and to higher fitness increments for both males and females.

330 The table shows that increasing polygyny and polyandry are antagonistic. The highest
331 fitness for both males and females occurs with maximum polyandry and minimum poly-
332 gyny. In this case, the male behavior represents the most fecundity selection with the least
333 sexual selection, while at the same time, female behavior represents the least solo foraging
334 with the most reproductive receptivity.

335 Increasing polyandry promotes higher fitness increments because of the additive effect
336 of having multiple males contribute to a female's fecundity. Increasing polygyny inhibits
337 higher fitness increments because guarding time must be increased to cover multiple fe-
338 males, lowering the time available for contributing to increased egg production.

339 Readers may wish to explore other social scenarios by modifying the Mathematica
340 script supplied with the supplementary materials.

References

- 342 Akçay, E., J. Roughgarden, J. D. Fearon, J. A. Ferejohn, and B. Weingast. 2013. Biolog-
343 ical institutions: the political science of animal cooperation. *Social Science Research*
344 *Network* <http://ssrn.com/abstract=2370952>.
- 345 Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: John
346 Murray.
- 347 Nadeau, N. J., T. Burke, and N. I. Mundy. 2007. Evolution of an avian pigmentation gene
348 correlates with a measure of sexual selection. *Proceedings of the Royal Society B: Bio-*
349 *logical Sciences* 274:1807–1813.
- 350 Prokop, Z., L. Michalczyk, S. Drobniak, M. Herdegen, and J. Radwan. 2012. Meta-analysis
351 suggests choosy females get sexy sons more than “good genes”. *Evolution* 66:2665–
352 2673.
- 353 Qvarnström, A., J. E. Brommer, and L. Gustafsson. 2006. Testing the genetics underlying
354 the co-evolution of mate choice and ornament in the wild. *Nature* 441:84–86.
- 355 Roughgarden, J. 2012. The social selection alternative to sexual selection. *Philosophical*
356 *Transactions of the Royal Society B: Biological Sciences* 367:2294–2303.
- 357 Roughgarden, J. et al. 2013. Sexual selection studies: Progress, challenges, and future
358 directions. Final Report from a NESCent Catalyst Meeting in Durham, NC, July 15–17
359 2013. Revision 1.1, reviewed and endorsed by 34 participants.
- 360 Shuster, S. M., W. R. Briggs, and P. A. Dennis. 2013. How multiple mating by females
361 affects sexual selection. *Philosophical Transactions of the Royal Society B: Biological*
362 *Sciences* 368:20120046.