

Sexual Selection Studies: A NESCent Catalyst Meeting

By

Joan Roughgarden¹, Elizabeth Adkins-Regan², Erol Akçay³, Jeremy Chase Crawford⁴,
Raghavendra Gadagkar⁵, Simon C. Griffith⁶, Camilla A. Hinde⁷, Thierry Hoquet⁸, Cailin
O'Connor⁹, Zofia M. Prokop¹⁰, Richard O. Prum¹¹, Sharoni Shafir¹², Samuel S. Snow¹³,
Daniel Taylor¹⁴, Jeremy Van Cleve¹⁵ and Michael Weisberg¹⁶

¹Hawaii Institute of Marine Biology, University of Hawaii, 5241 Wili Road, Kapaa HI 96746 USA, joan.roughgarden@hawaii.edu

²Department of Psychology/Department of Neurobiology and Behavior, 218 Uris Hall, Cornell University, Ithaca, NY 14853-7601 USA, erl2@cornell.edu

³Department of Biology, University of Pennsylvania, Philadelphia, PA, 19104 USA, eakcay@sas.upenn.edu

⁴Museum of Vertebrate Zoology/Department of Integrative Biology, University of California, Berkeley, 3101 Valley Life Sciences Building, Berkeley, CA 94720 USA, jeremy.crawford@alumni.duke.edu

⁵Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012 India, ragh@ces.iisc.ernet.in

⁶Department of Biological Sciences, Macquarie University, Sydney, NSW 2109 Australia, simon.griffith@mq.edu.au

⁷Behavioural Ecology Group, Wageningen University, Building 122, De Elst 1, 6708 WD, Wageningen, The Netherlands, camilla.hinde@wur.nl

⁸Faculty of Philosophy, University Jean Moulin Lyon 3, 1 rue de l'Université, BP 0638, 69239 Lyon Cedex 02 France, thierry.hoquet@univ-lyon3.fr

⁹Department of Logic and Philosophy of Science, University of California, Irvine, Social Science Tower 793, Irvine, CA 92697 USA, cailino@uci.edu

¹⁰Institute of Environmental Sciences, Jagiellonian University, Gronostajowa 7, 30-387 Kraków, Poland, zofia.prokop@uj.edu.pl

¹¹Department of Ecology & Evolutionary Biology, Yale University, New Haven CT 06520 USA, richard.prum@yale.edu

¹²Department of Entomology, The Hebrew University of Jerusalem, Rehovot 76100 Israel, sharoni.shafir@mail.huji.ac.il

¹³Department of Ecology & Evolutionary Biology, Yale University New Haven CT 06520 USA, samuel.snow@yale.edu

¹⁴Department of Computer Science, University of Bath, BA2 7AY, Bath, United Kingdom, djt20@bath.ac.uk

¹⁵National Evolutionary Synthesis Center, 2024 W. Main Street, Suite A200, Durham, NC 27705 USA, vancleve@nescent.org

¹⁶Department of Philosophy, University of Pennsylvania, 433 Cohen Hall, Philadelphia, PA 19104 USA, weisberg@phil.upenn.edu

Abstract

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.

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.

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 from the meeting for further comment by the community. This article offers the authors’ reflections on going forward and does not necessarily speak for other participants. The follow-

39 ing lists some of the points of disagreement and suggest accommodation where possible.
40 Some points of agreement were obtained and these are noted too.

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

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

56 This discrepancy between the selection and response to selection meanings of the phrase
57 “sexual selection” surfaced during discussion of the badge in male collared flycatchers
58 (Qvarnström et al., 2006). Here sexual selection apparently exists for the trait, but the rel-
59 evant heritabilities are negligible, so an evolutionary response to sexual selection is not
60 occurring. To reconcile this fact with a belief that sexual selection nonetheless explains
61 the evolution of the badge, some participants argued that the badge is a “ghost of sexual
62 selection past”, and that the absence of present-day heritabilities is merely an indication
63 of past genetic variation having become exhausted during the selection process. Alterna-
64 tively, the hypothesis that sexual selection caused the evolution of the badge might be false.
65 The hypothesis that the badge represents a ghost of sexual selection past might someday
66 become testable in light of increasingly available genomic estimates of past selection, for
67 example Nadeau et al. (2007). Readers should consult the full report for more detail.

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

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

The behavior occurring during courtship, mate choice, parent-offspring dynamics and so forth may involve both increasing the size of the pie and increasing the share of the pie. Hence the authors recommend identifying sexual selection with processes that increase the share of the gene pool, and fecundity selection with processes that increase the number of

98 offspring to which that gene pool refers.

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

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

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

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

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

121 For example, from a quantitative genetic tradition, a conjecture is that the variance in
122 fitness resulting from variation in some behavior might be partitioned into a component
123 pertaining to variance in zygote number produced and a component pertaining to variance

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

in probability of being incorporated into those zygotes. If so, the component of variance explained by zygote number could be taken as a measure of the fecundity selection and the component explained by zygote incorporation could be taken as a measure of sexual selection. The methods of Shuster et al. (2013) might be extended to accomplish this task. Also, quantitative approaches from population genetics and other theoretical traditions might provide additional measurement protocols.

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

The distinction between sexual selection as a frequency dependent process and fecundity selection as a density dependent process is consistent with a possible reading of Darwin’s 1871 passages intended to clarify the distinction between sexual selection and natural selection:

“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 these animals being washed about by the waves of the open sea, they absolutely require these organs in order to propagate their kind, and if so, their development has been the result of ordinary or natural selection” [Vol. I, p. 256]. But, “if the chief service rendered to the male by his prehensile organs is to prevent the escape of the female before the arrival of other males, or when assaulted by them, these organs will have been perfected through sexual selection, that is by the advantage acquired by certain males over their rivals. But in most cases it is scarcely possible to distinguish between the effects of natural and sexual selection.” [Vol. 1, p. 257]

In Darwin’s first scenario, grasping organs that prevent being washed out to sea while mating in ocean surf correspond to the outcome of fecundity selection (increasing the size of the pie). In Darwin’s second scenario, grasping organs that allow monopolizing a female

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

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

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

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

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

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

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

199 Contributions from political science emphasize that competition and conflict are eco-
200 nomically inefficient. Much theoretical political-science research seeks to explain the para-
201 dox of why conflict exists in spite of its inefficiency, presumably resulting from a breakdown
202 of institutions, a hoarding of private information, and/or a mis-estimation of each party's
203 interests and bargaining position. Political science also dwells at length on how human
204 evolutionary processes, both cultural and presumably biological, have led to increasingly
205 complex political and economic institutions that enable realization of common interests by
206 individuals following their own interests. In other words, self-interest, even when there
207 are material trade-offs and thus potential for conflict, does not necessarily imply realized
208 conflict. This calls into question the undiscussed but opposite presumption in evolutionary
209 biology that competition and conflict are unavoidable and social cooperation a derived con-
210 dition requiring special explanation. There is no reason why the perspective from political
211 science should not also apply to biology where efficiency in fitness production substitutes
212 for efficiency in economic utility (Akçay et al., 2013).

213 Contributions from humanists emphasize the special obligation of sexual selection re-
214 searchers to attend not only to the precision of their scientific claims but also to the ethi-

215 cal dimensions of their research. The humanists invite interdisciplinary engagement with
216 scholars in the history, philosophy, sociology, and gender studies of science as one route to
217 meeting this responsibility.

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

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Appendix. Fecundity Selection vs. Sexual Selection : An Illustration

Joan Roughgarden, Erol Akçay, Jeremy Van Cleve

A mathematical sketch is offered to illustrate the behavioral distinction between fecundity selection and sexual selection.

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

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

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

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

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

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

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

where m_m is the number of male mates a female has, m_f is the number of female mates a male has, and c_0, c_1, c_2 are coefficients. (These coefficients are typically assigned as $c_0 \rightarrow 1, c_1 \rightarrow 1$, and $c_2 \rightarrow \frac{1}{2}$.) This formula says that the daily egg production by a female increases with her own foraging time and from male contributions. Each of the m_m

265 males provides an assistance that reflects his total helping time divided by the m_f females
 266 among whom he is apportioning that time. Assuming $c_2 < 1$ implies that the contribution
 267 to female fecundity from male helping shows a decreasing return to scale.

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

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

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

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

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

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

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

280 If the male and female do not cooperate, then the time allocations satisfy a Nash Equi-
 281 librium where neither party can improve their fitness increment given the other's time al-
 282 location. At this equilibrium the female forages throughout the entire day, leaving perhaps
 283 an infinitesimal receptive period to collect any sperm needed to fertilize her eggs. Mean-
 284 while, at this equilibrium, the male does not contribute any help to the female. That is,
 285 the non-cooperative Nash Equilibrium mating system consists of the male and female time
 286 allocations, $\{t_h, t_g, t_f, t_r\} \rightarrow \{0, 1, 1, 0\}$. This mating system leads to the female and male

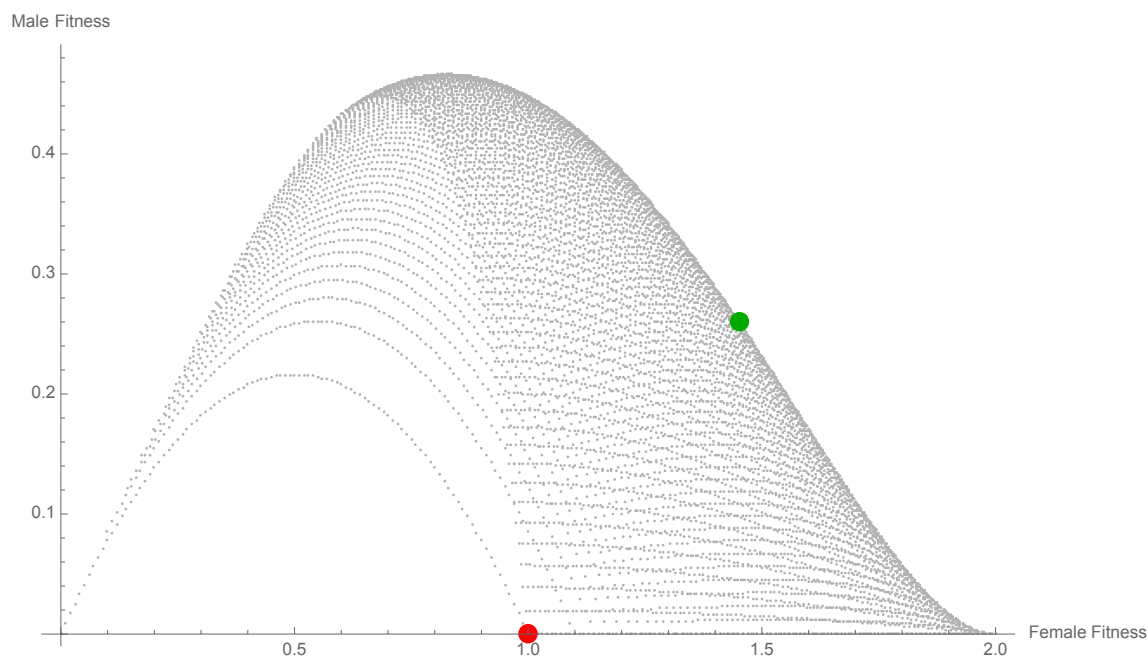


Figure 1: Payoff Space. Fitness pairs resulting from all combinations of male and female time-allocation strategies. Right edge of space is the Pareto boundary. Nash Equilibrium threat point is large dot on horizontal axis. Nash Bargaining Solution is large dot on Pareto boundary. Example for $m_m =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

287 fitness increments of $W_f \rightarrow c_0$ and $W_m \rightarrow 0$, regardless of the values assigned to the other
 288 parameters and coefficients.

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

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

293 where NP is the Nash Product.

294 Figure 1 presents an example of the payoff space for the male and female strategies
 295 illustrating the Nash Equilibrium threat point and the Nash Bargaining Solution. The

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

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

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

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

In general, the table shows that males should develop a balance between their alloca-

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

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

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

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

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

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

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