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Sexual Selection Studies: A NESCenC Catalyst Meeting

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Abstract
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Disciplines
Animal Sciences | Behavior and Ethology | Biology | Evolution | Population Biology

Comments
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Sexual Selection Studies:
A NESCent Catalyst Meeting

By

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

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

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

This discrepancy between the selection and response to selection meanings of the phrase “sexual selection” surfaced during discussion of the badge in male collared flycatchers (Qvarnström et al., 2006). Here sexual selection apparently exists for the trait, but the relevant heritabilities are negligible, so an evolutionary response to sexual selection is not occurring. To reconcile this fact with a belief that sexual selection nonetheless explains the evolution of the badge, some participants argued that the badge is a “ghost of sexual selection past”, and that the absence of present-day heritabilities is merely an indication of past genetic variation having become exhausted during the selection process. Alternatively, the hypothesis that sexual selection caused the evolution of the badge might be false. The hypothesis that the badge represents a ghost of sexual selection past might someday become testable in light of increasingly available genomic estimates of past selection, for 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 heritabilites 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
offspring to which that gene pool refers.

**Sexual Selection Defined.** These considerations lead to proposing the following definitions for sexual selection and evolution by sexual selection:

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

**DEFINITION:** Evolution by sexual selection is a change in the genetic composition of a population caused by a differential probability of the genotypes within a sex being incorporated into fertilizations independent of a difference in total fecundity.

This definition highlights some points on which the participants did find agreement. Deliberately, this definition does not specify paradigmatic sex roles, does not specify the identity of processes that might produce sexual selection, and refers to fertilizations and not matings. 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. “Evolution” by sexual selection includes a requirement of significant heritability to account for evolutionary change.

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

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

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

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

The decompositions in the examples above might not be regarded as controversial. 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 that health can be compromised through sexually transmitted parasites. Females would presumably increase their own fecundity by remaining healthy, which requires their avoiding contact with unhealthy, parasitized males. Hence, mate choice in this context includes 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 of matings than unhealthy males. Thus the mate choice by females in this case includes components of both fecundity selection and sexual selection.

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

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

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

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

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

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

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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

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

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

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

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

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

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

\[
W_f = e \tag{3}
\]

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

\[
W_m = m_f e \tag{4}
\]

If the male and female do not cooperate, then the time allocations satisfy a Nash Equilibrium where neither party can improve their fitness increment given the other’s time allocation. At this equilibrium the female forages throughout the entire day, leaving perhaps an infinitesimal receptive period to collect any sperm needed to fertilize her eggs. Meanwhile, at this equilibrium, the male does not contribute any help to the female. That is, the non-cooperative Nash Equilibrium mating system consists of the male and female time 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 $m_f = 1$.

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

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

$$NP = (W_f - c_0)(W_m - 0)$$

where $NP$ is the Nash Product.

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

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<th>$m_m$</th>
<th>$m_f$</th>
<th>$t_h$</th>
<th>$t_g$</th>
<th>$f$</th>
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<tr>
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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.
References


