Sexual Selection Studies:
Progress, Challenges, and Future Directions

Final Report from a NESCent Catalyst Meeting
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1 Introduction

In a meeting held at the National Evolutionary Synthesis Center (NESCent) in Durham, NC, during July 15–17, 2013, 34 participants reflecting a diversity of ages, nationalities, and disciplines reviewed the status of sexual selection studies and indicated challenges and future directions. "Sexual selection studies" is used here as an umbrella phrase referring to studies of courtship and mating, parent-offspring relations, family organization, and the interrelations 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.

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

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

The meeting focussed more on present challenges and future directions than on celebrating decades of past sexual selection research.

2 Defining Sexual Selection Today

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

2.1 A Starting Definition

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

> "Sexual selection describes the selection of traits associated with competition for mates." Continuing, "More formally, sexual selection is the relationship between a trait and its effect on fitness through sexual competition." Further, Shuker (2009) surmised, "My perception is that the above represents the consensus among evolutionary biologists of what sexual selection is."

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

The meeting's consensus that sexual selection is independent of sex roles is important because sexual selection is often misunderstood in the academy and general public as providing a biological basis to traditional sex roles such as passionate males and coy females. It was further understood at the meeting that sexual selection does not generally require or underwrite claims that sperm are cheap and eggs expensive, or that males are necessarily more promiscuous than females or that females are necessarily more disposed to parental care than males. As one participant wrote, “We can’t simply keep going around saying the old tripe of ‘competitive males and coy females because of anisogamy’ ”.

2.2 Deliberations

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

1. “Sexual selection is also not just intersexual choice, let alone just female choice.” Some researchers at this meeting consider choice sufficient to conclude that sexual selection is occurring, whereas others further require that the traits being selected are heritable and also that both the direction and intensity of preference for those traits be heritable.

2. “Sexual selection is not the same thing as sexual conflict.” This statement was understood by some to imply that sexual conflict need not be manifested as behavioral conflict. Others feel the existence of competition for mates *ipso facto* implies a kind of conflict, as in a genetic conflict of interest.

3. “Sexual selection [is] a component of an overall natural selection process, and inclusive of both selection and heredity.” Two issues in this statement drew strong responses. First, many workers do not believe that heritability is a requirement of sexual selection. Drawing on the formula in quantitative genetics that the response to selection equals the heritability times the strength of selection ($R = h^2S$), some researchers feel that sexual selection refers to the behavioral selection taking place, and that this selection may or may not produce an evolutionary response depending on the degree of heritability. Others however, agree that sexual selection must include heritability. It is common usage to attribute the evolution of ornaments and armaments to sexual selection, as in statements like “These antlers evolved because of intrasexual selection or these colorful feathers evolved because of intersexual selection.” Because this usage is making both an evolutionary claim in addition to a behavioral claim, in this usage a significant heritability is implied along with behavioral choice. Thus, although many participants assert that heritability is distinct from sexual selection, others think that sexual selection includes both the selectional behavior and heritability. As one participant wrote, “I agree entirely that sexual selection must include selection and heritable variation.”

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

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

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

5. Many participants stated that sexual-selection processes might not be about access to mates as much as about access to fertilizable gametes. They stated that the criterion for success should be scored not in terms of matings as in the Shuker (2009) definition, but in terms of fertilizations.

6. Some participants unpacked the Shuker (2009) definition's reference to competition for mates into various specific processes, extending Darwin's (1871) original dichotomy of male-male competition and female choice of males: (1) scrambles (mate search and handling), (2) contests (including fights with and without weaponry), (3) endurance rivalry, (4) post-copulatory versions of 1 to 3, (5) competition to attract mates, (6) competition to obtain better mates, and (7) post-copulatory versions of 5 and 6. Other participants noted that those processes are zero- or negative-sum processes—they assume a given number of eggs is to be allocated or, in the case of sexual conflict, some number of eggs is to be destroyed.

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

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

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

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

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

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

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

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

Some participants however, object to this entire discussion of the genetic conditions underlying the LK runaway process because they do not consider the heritability (including its multivariate extension as the matrix **G** above) to be part of sexual selection's definition. One participant writes that this entire paragraph is “flawed” because it “conflates heritability and selection” even though the requirements on **G** for the LK process to operate are taken directly from the literature that proposes the LK process as a null model for the evolution of a trait and the preference for it by intersexual selection.

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

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

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

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

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

10. Participants debated the good-genes and sexy-sons processes in the sexual selection. (The phrase, "sexy sons", is being used here as shorthand for the indirect benefits of sexually attractive offspring.) Participants reviewed 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). Sexually selected traits not correlated with fitness cannot be used as the basis for mate choice based on the premise that good genes are thereby being passed on to offspring even though the traits themselves are often heritable.

    Some participants argued that the combination of the ornament being heritable together with an absence of an ornament to fitness correlation implies that the ornament must have evolved for its "sexiness" alone, consistent with the LK runaway "null" model.

Other participants objected to posing good-genes and sexy-sons as an either/or proposition because the LK model requires, as discussed above, not only that the ornament-viability correlation be zero and the heritability of the ornament be positive as observed, but also that both the heritability of the preference be positive and the genetic correlation between preference and ornament be positive. Roughly speaking, these requirements mean both that the female interest in having sexy sons should be inherited by her daughters and also that what females find to be sexy should not change in the next generation. Because the meta-analysis did not address the female-preference side of the question, these participants felt that the failure to support a good genes process of sexual selection could not be used as evidence for a sexy-sons process of sexual selection instead.

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

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

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

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

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

(3) "Direct fitness benefits resulting from mate choices must enhance female fitness within each generation; if they do not, traits associated with decreased fitness benefits within each generation will be removed from the population. This is the reason why 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 ± Standard Error of Mean)

h_o^2	Heritability of Male Badge Size	0.381 ± 0.028
h_v^2	Heritability of Male Fitness	0.031 ± 0.012
r_{ov}	Genetic Correlation Male Ornament and Male Fitness	0.154 ± 0.094
h_p^2	Heritability of Female Preference	0.026 ± 0.010
r_{op}	Genetic Correlation Between Badge and Preference	-0.015 ± 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 be heritable, but the daughter of a mother interested in sexiness might not herself be interested in the sexiness of her mate, and also an ornament sexy in one generation may not be perceived as sexy in the next generation.

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

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

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

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

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

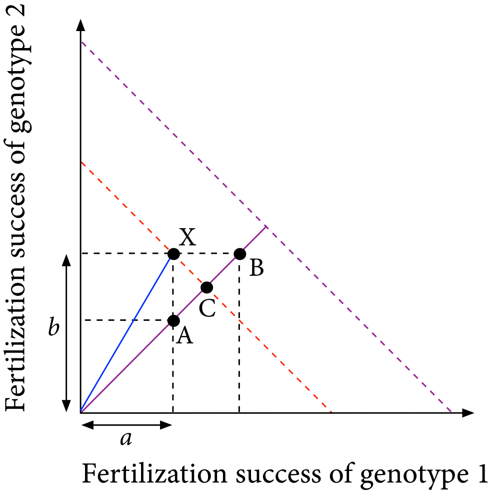
Definitions #2 and #3 (in one of their many versions) attracted the most adherents. Definitions #1 and #2 do not take a position on whether sexual selection is a component of natural selection and so can be supported by participants who regard them as distinct. Definitions #1 and #2 also do not require 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 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... [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." In the first scenario, grasping organs that expedite mating in ocean surf correspond to the outcome of fertility selection (increasing the size of the pie). In the second scenario, grasping organs that allow monopolizing a female to exclude other males correspond to the outcome of sexual selection. Darwin lumps fertility selection together with viability selection to form natural selection. So, in definition #3 sexual selection is distinct from fertility 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.

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.



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

3 Future Directions

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

1. Refining and Adopting a Definition. "I believe we should refine and work toward a near-universal adoption of a common definition and the development and testing of null models. We should clearly define at least one null model and show how it can be tested and accepted or rejected using at least one numerical example, based either on real (published) or hypothetical data."

2. Alternatives to Sexual Selection. "Given that a lot of mating is social and non-fertilizing, life history theory in ecology suggests an alternative approach to sexual selection studies. This approach starts at the end of the growing season and works back to the beginning of the life cycle through backward induction. The approach should first determine what the best social system is for the maturation of young—parental cooperation or not, social foraging or not, *etc.* Then taking a step backwards, the approach determines what negotiations will lead to the optimal end-of-season social system such as negotiations to set the degree of mutual support and the clutch size. Next, the approach works back from that to what type of signaling system in terms of ornaments and courtship behavior is needed to communicate the necessary information to carry out the negotiations. This approach is 'social infrastructure selection' (*e.g.* Roughgarden 2012b). It focusses on ornaments, courtship and mating as a social mechanism to achieve fertility selection, *i.e.*, on increasing the number of young—on increasing the pie rather than gaining a larger section of a fixed pie, using the terminology of definition #3."

3. Comparative Genomics and Sexual Selection. "Comparative genomic studies are showing that genes expressed in a sexually dimorphic manner show faster evolution between

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

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

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

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

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

8. Physical Intimacy to Realize Cooperative Outcomes. "Various forms of physical intimacy including mutual grooming, preening, and vocalizations as well as same-sex matings may all comprise mechanisms to coordinate and realize cooperative outcomes to situations involving non-congruent interests (*e.g.* Roughgarden 2012a). The role of social bonds in realizing a Nash bargaining outcome rather than a Nash competitive equilibrium outcome is a possible direction for future investigation."

9. Causes of Male Parental Investment. "Parental care evolution and sexual selection influence one another. Females have been thought to provide more parental care than males and sexual selection on males has been argued to disfavor the evolution of paternal care (*e.g.* Queller 1997, Kokko and Jennions 2008). If males provide any care, they are expected to invest less when females mate multiply and males are less certain of paternity. Yet, biparental care persists in many species despite female promiscuity, and also male-only care is found in a wide range of taxa despite multiple mating by females. Instead, female choice, male competition and parental effort coevolve as a result of interactions within and between the sexes (Alonzo, 2012). Inter-sexual selection arising from female choice can favor the evolution of paternal care and even lead to the loss of maternal care (Alonzo, 2012) and empirical patterns indicating that male ocellated wrasses with the lowest certainty of paternity are the most likely to provide paternal care (Alonzo and Heckman 2010, Alonzo, 2010)."

10. Game-Theoretic Analysis of Parental Care. "The parental investment hypothesis (Trivers 1972) links anisogamy with greater female parental care using arguments shown to be logically flawed (Kokko and Jennions 2008, Dawkins and Carlislie 1976). Self-consistent versions of Maynard Smith's parental care game (Maynard Smith 1977) show that anisogamy, in fact, selects for greater male parental care (Iyer and Shukla, in prep.), a result consistent with the first evolutionary transitions in parental care among ancestral fish and birds being from no-care to male-only care (Royle *et al.* 2012). Hence the mammalian pattern of greater female parental care appears to be derived, and may emerge from factors such as parentage differences between the sexes and patterns of sexual selection rather than anisogamy (Kokko and Jennions 2008, Iyer and Shukla in prep)."

11. Choice and Parental Investment. "Future work could usefully investigate choice for parental investment, which has received surprisingly little attention (see *e.g.* Royle *et al.* 2010). Such choice for parental care could vary in intensity depending on the choosers own phenotype, and their own level or style of care. It will also have important implications for behavioural consistency (see *e.g.* Royle *et al.* 2010) and negotiation (see Johnstone and Hinde 2006)."

12. Sexual Selection and Speciation. "A definition of sexual selection should be clarified as being distinct from a definition of natural selection because the role of sexual selection in speciation given the existence of so many different models of sexual selection in the literature. We organize the existing models of sexual selection into those that are likely to interact with environmental context (*e.g.* good genes or good parent traits)

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

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

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

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

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

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

4 Conclusion

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

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