

# Sexual selection

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It took more than a century before genetic models and experimental field work convinced biologists that Darwin's theory of sexual selection was both plausible and testable. With its many fascinating research problems, sexual selection has now become one of the most active areas in the field of evolutionary biology, and the subject of several recent books<sup>1-5</sup>. Here, we discuss studies from the past five years, emphasizing reviews and syntheses that provide a gateway to the vast literature in this field.

The idea of sexual selection grew out of Darwin's attempt to solve a major problem for his theory of evolution by natural selection: why have males of many animals evolved conspicuous traits that probably reduce survival? Sexual selection, Darwin's key explanation, was his shorthand term for selection that arises through competition over mates or matings. Ecological competition occurs whenever the use of a resource by one animal makes it harder for others to obtain that resource; in sexual selection, the resource is mates<sup>1</sup>. Competition over mates is the unifying aspect of all forms of sexual selection, including that occurring by mate choice, where individuals compete to be chosen by the other sex.

## Mechanisms of sexual selection

Two mechanisms of sexual selection have attracted most interest: mate choice and 'contests' or other overt male conflicts (often called intrasexual selection – unnecessarily, since all sexual selection is intrasexual as it occurs through competition among members of the same sex). Mate choice, and its evolution, has presented theoreticians with one of the most complex problems in evolutionary biology and empiricists with challenges that have only recently been tackled on a broad front.

There are, however, also other important mechanisms of sexual selection that have received less attention (Table 1). Since 1970, when Parker pointed to its importance, sperm competition has been found in many

**animals<sup>4,6</sup>, and corresponding processes have been found to occur in plants. Among the lesser known mechanisms is endurance rivalry<sup>1</sup>, where the ability to remain reproductively active at a lek or other mating site is favoured, since it increases the number of matings. Another mechanism of sexual selection is scrambling to find the mate before rivals do. This can be achieved by: (1) early emergence or maturation – males becoming reproductively active before females (protandry, occurring in some plants as well as animals); and (2) swift localization of potential mates – favoured, for instance, by well-developed sensory organs, mobility and spatial memory. Sexual selection, therefore, may have profound effects for the neurosensory system. In plants, pollination scrambles are likely to favour rapidly growing pollen tubes and pollinator-attracting traits such as conspicuous flowers, scent and nectar<sup>1,7-9</sup>.**

**Competition over mates takes many forms and has far-reaching consequences for many organisms. Recent work suggests that relative reproductive rates of males and females, sperm competition and quality variation among mates affect the strength of sexual selection. Song, other display, body size, visual ornaments and material resource offerings are often sexually selected. There is much empirical evidence of mate choice, and its evolution is clarified by mathematical models. Recent advances in theory also consider costs of choice, effects of deleterious mutations, fast and slow evolution of preferences and preferred traits, and simultaneous preferences for several traits. Contests over mates are important; so is sperm competition, scrambles, endurance rivalry, and coercion. The latter mechanisms have received less attention than mate choice. Sexual selection may explain puzzling aspects of plant pollination biology.**

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increase the chances that a female will mate with him and not with other males. Sequestering, harassment, intimidation and forced copulation belong in this category. Other tactics used later in the reproductive cycle are induced abortion or infanticide that makes a female receptive to a new male.

**Table 1. Some of the mechanisms of sexual selection, and traits likely to be favoured in the competing sex<sup>a</sup>**

Mechanism	Characters favoured in the competing sex
Scrambles	Early search for and swift location of mates; well-developed sensory and locomotor organs
Endurance rivalry	Ability to remain reproductively active during a large part of the season
Contests	(1) Traits that improve success in fights, such as large size, strength, weaponry, agility or threat signals (2) Alternative mating tactics of inferior competitors, avoiding contests with superior rivals
Mate choice	(1) Behavioural and morphological traits that attract and stimulate mates (2) Offering of nutrition, territories, nest sites or other resources needed by the mate for breeding (3) Alternative mating tactics, such as forced copulation
Coercion	(1) Similar traits as for contests (1) (above) (2) Morphological and other adaptations for forced copulation and other coercive behaviour
Sperm competition	(1) Mate guarding, sequestering, frequent copulation, production of mating plugs or other means of preventing rivals from copulating with the mate (2) Ability of displacing rival sperm; production of abundant sperm to outcompete those of rivals
Infanticide	Similar traits as for contests (1) (above)

<sup>a</sup>Modified from Ref. 1.

Several mechanisms of sexual selection may often occur together, presenting the difficult problem of assessing their relative importance.

**Sex roles, sex ratios and the strength of sexual selection**

One aspect of Darwin's problem concerns sex roles. Why is sexual selection usually more pronounced in males than females? Bateman's classic explanation, that the strength of sexual selection depends on the relationship between mating success and offspring production, which is usually steeper in males, has now been integrated with formal selection theory (Box 1). The relationship can be approximated by a regression line relating fecundity to mating success (numbers of mates)<sup>12,13</sup>. To avoid confusion with sexual selection gradients of ordinary phenotypic traits, we suggest calling the slope the Bateman gradient, as it quantifies the relationship whose fundamental importance he clarified (Box 1).

Two main concepts used for explaining differences in sexual selection between males and females are Trivers' parental investment (investment in an offspring that reduces the parent's ability to invest in other offspring), and Emlen and Oring's operational sex ratio (the ratio of males to females among individuals ready to mate)<sup>1</sup>. Parental investment theory helps explain why sexual selection is generally strongest in the sex that invests least resources in offspring, usually males. It even clarifies, for instance, subtle intraspecific variation in courtship roles in male and female bushcrickets (Tettigonidae)<sup>14,15</sup>. It does not, however, explain the variation in male and female sexual selection among species with male uniparental care. In some such animals, for example, some pipefishes and waders, sexual selection is stronger in females. In others, for example, sticklebacks (*Gasterosteus aculeatus*), sexual selection is stronger in males<sup>16</sup>.

The reason seems to be that, in spite of caring for the brood, stickleback males have higher potential reproductive rates than females (for example, because a male can tend broods from several females at the same time). This difference can bias the operational sex ratio towards males, making sexual selection stronger among them although they care alone for the brood<sup>16</sup>. Whether the operational sex ratio, the maximum reproductive rate of the sexes or some other aspect most closely reflects the strength of sexual selection is, however, still debated<sup>13,15-17</sup>. For example, sperm competition reduces the realized reproductive rate of males relative to females, and it might indirectly influence the strength of sexual selection in the two sexes<sup>15</sup>.

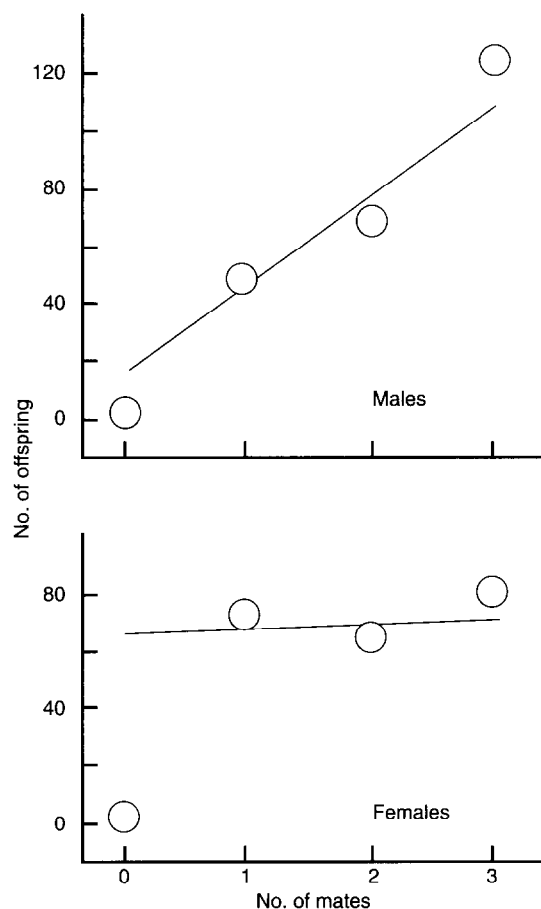
Another line of reasoning<sup>17</sup> suggests that optimal mate choice involves a trade-off between mate numbers and mate quality. Both sexes may be choosy. Sexual selection is usually strongest in the sex with the highest potential reproductive rate, and mate choice is exerted mainly by the other sex. If there is sufficiently high quality variation in the sex with the lowest rate, however, members of the most competitive sex might also be the most choosy. Both mate choice and competition over mates can then be strong in the same sex. A possible example is females in the role-reversed dotterel (*Charadrius morinellus*). Competition and mate choice within the same sex may be more common than previously thought<sup>17</sup>.

**Mate choice theory: the evolution of preferences and traits**

Most genetic models for the evolution of mate preferences consider a male trait and a corresponding female mate preference (reviewed in Refs 1,2,6 and 18). Male traits can become exaggerated in spite of a cost of reduced viability

**Box 1. The Bateman gradient and sexual selection in males and females**

In 1948, Bateman explained why sexual selection is usually strongest in males. In experiments with *Drosophila*, the number of offspring fathered by a single male increased in proportion to the number of females with which that male had mated. Female fecundity on the other hand did not increase if she mated with more than one male (see figures below). For this reason, there is a stronger premium among males than females on acquiring additional mates, leading to stronger competition over mates in males. The strength of sexual selection tends to increase with the Bateman gradient: the slope of the regression line relating offspring production to mating success for the sex in question. In the figure, weighted linear regression lines have been fitted to the data. Modified from Ref. 13, Fig. 3b.



The relationship between mating success and offspring production in the two sexes helps to explain the relative strength of sexual selection in males and females. Several kinds of relationships can occur<sup>13</sup>. With those relationships in the figures, sexual selection will be stronger in males, and the mating system is likely to be polygynous. With an exchange of the patterns for males and females, sexual selection tends to be stronger in females and the mating system to be polyandrous.

Many other relationships are possible. For example, if both sexes have steep Bateman gradients (such as the upper figure), they may both compete for mates, and the mating system may be polygamous. If both sexes have Bateman gradients close to zero (lower figure), the mating system may be monogamous and sexual selection weak. If there is large variation in quality and fecundity in one sex, however, sexual selection may be strong in the other sex, also in monogamous species.

This approach can also be used for studying sexual selection in hermaphroditic organisms, including plants<sup>12,42</sup>.

of the holder, if males with large ornaments enjoy higher mating success through attracting females. A major question still is why females choose males with such costly ornaments.

Two answers were suggested by Fisher in terms of indirect genetic benefits (although his name is usually only associated with one of them; see Ref. 1, p. 27): (1) females with a strong mate preference for the trait will have sons with higher mating success, which helps spread their choice genes through their sons; (2) the male trait indicates high heritable viability, which is inherited by the offspring of choosy females. These ideas have been formulated in major gene and quantitative genetic models (reviewed in Ref. 1). Among recent developments of mate choice theory are models where the realistic assumptions of costs of mate choice<sup>19</sup>, and effects of deleterious mutations, have been included<sup>20,21</sup>. These assumptions can greatly change the outcome (Box 2).

*Single versus multiple traits under sexual selection*

Many species have multiple sexual ornaments and displays. The condition for multiple or single sexual ornaments to evolve through Fisher's runaway process has been investigated in a polygenic model of two traits and two corresponding preferences<sup>22</sup>. Splitting the analysis into fast and slow dynamics (Box 2) gives equilibria in terms of selective pressures, independent of the genetic parameters.

The evolution of multiple female preferences in the model is controlled by joint cost, that is, by the extra cost for choice based on both traits instead of one of them. If the main cost of choice comes from lek attendance rather than time spent scrutinizing males, examining two aspects of a male's phenotype (e.g. tail length and eye colour) may not be costly. Runaway evolution then establishes several strong preferences. As the joint choice cost increases, the preference that dominates is the one that gives the female the greatest fisherian benefit (more attractive male offspring) relative to the cost of choice. At equilibrium there will always be a mixture of preferences and multiple male ornamentation.

In an indicator process with small joint choice costs, females evolve preferences for several male indicator traits<sup>23</sup> (Fig. 1a). If the joint

**Box 2. Genetic models of costly mate preference**

Early theoretical models assumed neutral mate preferences. That is, the time or energy invested to examine potential mates does not affect the lifetime reproductive success of the female. However, the evolutionary predictions change greatly if the realistic assumption of a cost of mate preference<sup>19</sup> is added<sup>20</sup>. A general polygenic model of trait and preference shows that the fitness of each sex is then maximized at the stable evolutionary equilibrium where female choice cost is minimal, that is, zero<sup>26</sup>, implying that Fisher's runaway process cannot occur with this set of assumptions.

Two ways of generating a stable equilibrium of exaggeration and costly mate preference have been proposed. The first is a model of fisherian self-reinforcing mate choice<sup>26</sup>, in which mutation bias works to reduce the male trait. Such a bias seems likely, as there will be many more mutational ways of disrupting a complex trait than improving it, but studies testing this assumption are needed. At equilibrium, the mutation bias is balanced by selection for a larger trait, but the trait will remain heritable, giving choosy females the indirect benefit of having sons with the preferred trait and a higher total fitness.

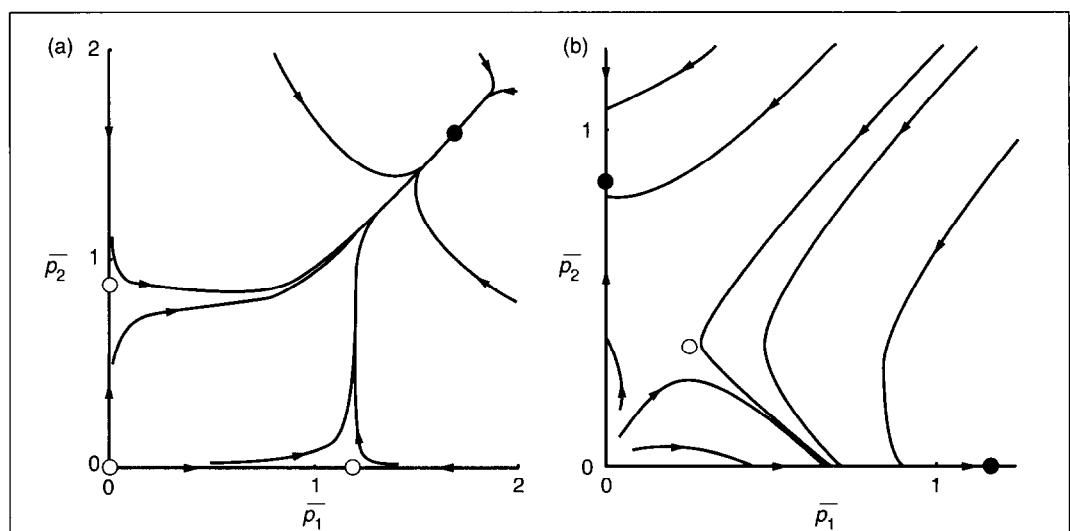
Second, indicator models assume that the male's trait reflects his general viability<sup>20</sup>. A three-trait polygenic model (including male's trait, female's preference and male's general viability) shows that an evolutionary equilibrium in which females engage in costly mate preference requires that two conditions are satisfied. First, mutational pressure or temporal or spatial variation in selection pressures causes a recurrent loss of general viability. Second, there is condition-dependence, that is, the male's realized signal increases with his general viability<sup>20</sup>. Condition-dependent expression of the signal is optimal if and only if producing a signal of given strength is more costly for weak males than for strong males (as is also concluded from a signalling game<sup>46</sup>).

In earlier analyses, it appeared that the evolutionary equilibrium depended both on selective and genetic parameters; how these were related was unclear. This problem has been tackled by analytical techniques based on the difference in the magnitude of parameters<sup>22</sup>. The evolutionary dynamics are split into 'fast dynamics', describing quick convergence to a line of equilibria, and 'slow dynamics', describing slow movement along the line. In addition, the genetic covariance between female preference and male ornament evolves very quickly towards the equilibrium value.

These techniques show that the equilibrium exaggeration in female preference is entirely defined by the ecological and behavioural parameters that give rise to selection, as all the genetic parameters cancel out<sup>22</sup>. The exact genetic mechanism controlling preference and trait is not important; neither is the absolute value of the genetic covariance. What matters is the effectiveness of the male ornament in creating preferential mating.

The same technique has also been used to analyse an indicator model in which the male's realized ornament size ( $s$ ) is a function of viability ( $v$ ), as  $s = t + t'v$ , where both a condition-independent component,  $t$ , and a condition-dependent component,  $t'$ , are polygenic traits that evolve<sup>23</sup>. The equilibrium is again independent of the genetic mechanisms; it is determined by ecology and behaviour. Female preference increases with the effectiveness of the male signal and the degree of condition-dependence in the cost of developing the trait, but decreases with the female cost of choice and the cost of the male ornament. Both the exaggeration of the male ornament size and its condition-dependence evolve in proportion to the level of female mate preference.

cost increases, however, the equilibrium with multiple preferences becomes unstable, whereas both of the single preference equilibria become locally stable (Fig. 1b). The evolutionary outcome now depends on initial conditions. Once a preference for a single male trait has evolved, other preferences cannot invade. The indicator process gives rise to local stability of existing preferences because, as Zahavi



**Fig. 1.** Slow dynamics and equilibria when there are two female preferences ( $\bar{p}_1$  and  $\bar{p}_2$ ) for two male indicator traits. Stable equilibria are shown as filled circles and unstable equilibria as open circles. The polygenic dynamics are seven-dimensional. The system first quickly converges onto a surface of quasi-equilibrium via fast dynamics, and then moves slowly, converging to the equilibrium. The figures describe this latter movement. On each axis there is an equilibrium where only a single preference is present. (a) Small joint costs of female choice. The mixture equilibrium is stable and there is evolution of multiple female preferences. Both single preference equilibria are unstable. (b) Large joint costs of choice. The mixture equilibrium is unstable and there is evolution of only a single female preference. The evolutionary outcome should depend on the history. From Ref. 23, with permission.

has pointed out, the reliability of a signal generally increases with its cost. An established preference thus leads to benefits that are likely to be greater than the benefits gained from choosing a novel, unexaggerated trait.

A review of sexual ornaments in birds<sup>24</sup> concluded that (1) there is no evidence of condition-dependent expression in multiple-ornamented birds, but rather of fisherian traits (but see Ref. 25), and (2) mate preferences are much weaker in such species than in birds with single ornaments, which show evidence of condition-dependent expression.

*Direct phenotypic benefit of mate preference*

Other genetic models have shown that a strong mate preference can evolve if it improves the total fitness of the female through direct phenotypic benefits, such as avoidance of disease transmission, inbreeding, mismating with another species, or through choice of a mate that gives better parental care or that is more fecund<sup>18,26,27</sup>.

*Sensory bias and neuro-computing models*

Females tend to prefer male traits of greater quantity<sup>28</sup>, which may be explained by fisherian or by indicator models. An alternative view, 'sensory exploitation', emphasizes that female mate-preference bias may occur without present adaptation, having arisen in some other context<sup>18,28</sup>. There is now evidence for such a bias from several species (e.g. Refs 25 and 28). Studies using neural network models support the possibility of sensory bias caused by developmental processes of sensory organs, rather than by adaptation through selection<sup>21,29</sup>.

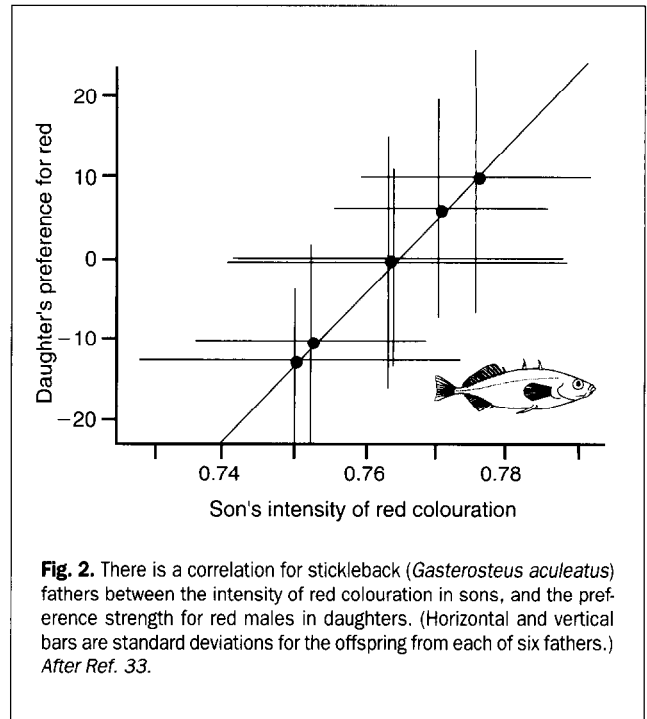
Symmetry preferences of females are often regarded as evidence for condition-dependent indicator mechanisms, because males with a higher general viability tend to be more symmetric (e.g. Ref. 24; see below). Neural network studies suggest, however, that symmetry preferences can also be a by-product of the need to recognize objects irrespective of their position and orientation in the visual field<sup>21,29</sup>.

**Empirical patterns**

Several large-scale patterns emerged from a review of 232 studies (186 species), each of which identified a mechanism of sexual selection and demonstrated a statistical relationship between some character and mating success (Ref. 1; also see Refs 24,28). Insects, birds, amphibians and fishes dominated among the species studied. Among the male traits most often shown to be sexually selected were song and display, body size, visual ornaments, and territory or other resources.

Female choice was found in 167 studies, so Darwin's once-controversial idea has been abundantly corroborated. (The strong predominance of mate choice is not necessarily representative for its relative importance, however: less attention has been paid to other mechanisms.) Also, male choice of mate is common (30 studies), mainly in animals with indeterminate growth, where males prefer large, highly fecund females. Another review, of mate choice based on visual and acoustic traits, showed that when females favour deviations from the mean trait size, they usually prefer more conspicuous, stronger signals given at higher rates, that is, deviations that elicit greater sensory stimulation<sup>28</sup>.

Male contests, the second main focus, were documented in 58 studies. Male scrambles or endurance rivalry were found in only 14 cases, probably because of a paucity of work on these mechanisms. There is, however, increasing evidence that endurance rivalry is important, for example, on leks and in other mating sites, where mating opportu-



**Fig. 2.** There is a correlation for stickleback (*Gasterosteus aculeatus*) fathers between the intensity of red colouration in sons, and the preference strength for red males in daughters. (Horizontal and vertical bars are standard deviations for the offspring from each of six fathers.) After Ref. 33.

nities increase with the time spent at the site<sup>30</sup>. Endurance rivalry favours the ability to remain reproductively active for long periods. Like contest competition, which usually favours large body size, endurance rivalry may also favour large body size, but for reasons of energetics rather than strength<sup>1</sup>.

DNA fingerprinting and related techniques (e.g. Ref. 31) have greatly increased the accuracy of paternity and maternity determination, showing that paternity often is not what the social pairing pattern suggests. Extra-pair fertilizations are common in many species<sup>4</sup>. For example, in the socially monogamous reed bunting (*Emberiza schoeniclus*), 55% of the young had fathers who were not the male who was bonded to their mother and feeding the young. Male contribution of parental care increased with his degree of paternity<sup>32</sup>. One of the possible reasons why females seek extra-pair copulations is heritable advantages to offspring fathered by high-quality males<sup>4</sup>, but this remains to be shown. The great variation in extra-pair paternity among species also remains to be explained.

*The genetics of sexually selected traits and preferences*

Fisherian as well as genetic indicator models assume that there is sufficient heritability of the preferred trait, which usually seems to be the case<sup>1</sup>. The models also predict a genetic correlation between the preferred trait and the preference, demonstrated in sticklebacks (*G. aculeatus*) (Fig. 2), guppies (*Poecilia reticulata*) and stalk-eyed flies (*Cyrtodiopsis dalmanni*)<sup>33-35</sup>. These results suggest that sexual selection by mate choice has substantial genetic consequences. A genetic correlation alone does not reveal, however, which mechanism is at work. A correlation is predicted by fisherian runaway, indicator and species recognition mechanisms. Developing critical tests for distinguishing among them, and estimating their relative importance in particular cases, remains a major challenge.

In the seaweed fly (*Coelopa frigida*), a preferred character (male size) is strongly heritable owing to a chromosomal inversion that also influences larval viability; inversion heterozygotes have a higher survival. The ingredients for a genetic

indicator mechanism therefore seem to be present<sup>36</sup>. There is now evidence for such a mechanism from several species<sup>1,25</sup>. On the other hand, the widespread, rapid, divergent evolution of male intermittent genital organs among insects and other animals seems best explained by fisherian runaway evolution, combined with sensory bias<sup>37</sup>. Although it presently receives less attention than indicator mechanisms, fisherian runaway selection remains a possible factor in many cases<sup>1,37,38</sup>.

#### Fluctuating asymmetry

Much interest is presently focused on fluctuating asymmetry of secondary sex traits (side-wise random deviations from perfect bilateral symmetry)<sup>2,39,40</sup>. The degree of asymmetry is likely to reflect the ability of the genome to counteract genetic and environmental stress and produce an harmonious phenotype. This opens the possibility for a genetic indicator process, with a mating preference for symmetry. There are several supporting results, but the role of fluctuating asymmetry in sexual selection is debated, and its analysis contains many pitfalls<sup>21,29,39,41</sup>.

#### Phenotypic benefits of mate choice

Direct phenotypic benefits such as male contribution of territory, nutrition or parental care may explain female choice of mate in many species (reviewed in Refs 1–3,18). There are, however, usually no obvious direct benefits of mate choice in lekking species, where females visit males only for copulation. Genetic advantages of mate choice therefore have often been suggested for such species. But some direct benefits such as avoidance of disease, or protection from other coercive males, are possible also on leks<sup>5,18</sup>. Female preferences have been identified in a few lekking species. Possibly, male contest competition is also responsible for much of the selection of male secondary sex traits in lekking animals<sup>5</sup>.

#### Sexual selection in plants

In spite of early work in the 1970s by pioneers such as Willson and Charnov, sexual selection ideas did not become widespread in botany until recently. Yet the fundamental aspect of sexual selection, that is, competition over mates, matings, fertilizations and, ultimately, offspring production are probably as important in some higher plants as in animals. Botanists as well as zoologists may therefore benefit from insights gained by application of sexual selection ideas to plants<sup>1,7–9,12,42</sup>.

A major form of sexual selection in plants is scrambles among pollen to reach stigmas and fertilize ovules. Such competition favours attraction and reward of pollinators by conspicuous inflorescences, scent and nectar<sup>1,8,9</sup>. Sexual selection via male function may partly explain why many cosexual plants have more flowers than needed for full seed set. The extra flowers may increase reproductive success through pollen export. It may also explain why species with separate sexes usually have more and larger flowers in males than females.

Sexual selection in plants can operate also via female function. Seed set seems to be limited by insufficient pollination in some plants, so females may compete over matings<sup>1,8,9,12,42</sup>. Quantifying the relative importance of male versus female sexual selection in plants is a challenging empirical problem.

Comparison with animals opens interesting perspectives. Some plants have enormous flowers (Fig. 3) that seem as extreme as the largest ornaments in animals. Yet, genetic runaway or indicator processes seem highly unlikely in these plants. Genetic coupling between trait and preference can-

not normally arise when their determination resides in the separate genomes of plant and pollinator. Genetically simpler mechanisms, such as direct attraction to the strongest signal, may be responsible. Focus on complex genetic mechanisms has perhaps made us partly overlook the importance of simpler processes in animals as well<sup>1</sup>.

Post-pollination events might influence male success in plants. There is some evidence for 'female choice' of pollen in the style, but post-fertilization choice of embryos to mature seems more likely to be important<sup>7,43</sup>. Such processes are part of parent-offspring relations rather than sexual selection. The two types of processes show several similarities as well as differences<sup>43</sup>.

#### Costs of sexual selection

Several costs can limit the expression of secondary sex traits (e.g. reviewed in Refs 1–3,19,44–46). Signalling or searching for mates can lead to higher predation in males; fights over territories or females may cause injury or death. Sexually selected larger body size makes males more prone to starve than females during the growth period in birds and mammals. Secondary sex traits can also impose energetic and foraging costs. Several types of natural selection may therefore limit secondary sex traits. But sexual selection can also be self-limiting, if a trait favoured by one sexually selected fitness component reduces success in another component. For example, large male body size in the red-wing blackbird (*Agelaius phoeniceus*) is advantageous in male contests, but larger males spend more time foraging and have less time to defend their territory and attract females<sup>3</sup>.

No experimental study of secondary sex traits has yet produced a quantitative fitness account of the predicted balance between sexual selection advantages and natural (or sexual) selection disadvantages. With few exceptions<sup>19,46</sup>, costs of mate choice are still to be measured.

#### Advances in related fields

Species recognition, sexual selection and speciation are processes that may interact<sup>1,47</sup>. Sexual selection and divergence of secondary sex signals has probably played a major role in the profuse speciations of some taxa, such as fruit flies and crickets in Hawaii, cichlids in African lakes, and anurans, passerine birds and even angiosperm plants<sup>1</sup>. More work is required to test this possibility; modern comparative approaches are likely to be of great help in this as in many other contexts.

Sexual selection shares several research problems with animal communication. In particular, the extent to which signals are reliable indicators of quality or intentions is debated in both fields (e.g. Ref. 48).

Sexually selected traits form part of the effort an animal expends in order to reproduce. Analyses of the development and cost of such traits may therefore benefit from application of a life history perspective, an opportunity that largely remains to be exploited (but see Ref. 49; reviewed in Refs 1 and 2).

#### Conclusions

The present eruptive phase in the study of sexual selection has produced massive evidence of its importance for

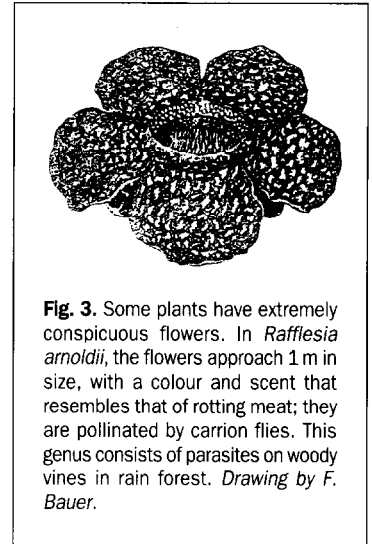


Fig. 3. Some plants have extremely conspicuous flowers. In *Rafflesia arnoldii*, the flowers approach 1 m in size, with a colour and scent that resembles that of rotting meat; they are pollinated by carrion flies. This genus consists of parasites on woody vines in rain forest. Drawing by F. Bauer.

many characteristics of higher animals and plants. Mate choice, as well as sexual contest competition, has been abundantly demonstrated, but several probably common mechanisms of sexual selection, such as scrambles and endurance rivalry, remain poorly investigated. Further empirical work is needed on these mechanisms, on the causes of the great variation in sex ornaments among species, and on the nature, costs, benefits and genetics of mating preferences.

**Acknowledgements**

We thank Staffan Andersson, Frank Götmark, Andrew Pomiankowski, Adrian Thomas, Jerry Wilkinson and a referee for helpful suggestions on the manuscript. Financial support was provided by the Swedish Natural Sciences Research Council to M.A., and by a grant-in-aid from the Ministry of Education, Science and Culture, Japan to Y.I.

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