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Sexual selection: an evolutionary force in plants

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Sexual selection: an evolutionary force in plants?

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ABSTRACT

Sexual selection has traditionally been used to explain exaggerated sexual traits in male animals. Today the concept has been developed and various other sexually related traits have been suggested to evolve in the same manner. In nearly all new areas where the theory of sexual selection has been applied, there has been an intense debate as to whether the application is justified. Is it the case that some scientists are all too ready to employ fashionable ideas? Or are there too many dogmatic researchers refusing to accept that science develops and old ideas are transformed? Maybe the controversies are simply a reflection of the difficulty of defining a theory under constant re-evaluation. Thus, we begin by summarizing the theory of sexual selection in order to assess the influence of sexual selection on the evolution of plant morphology. We discuss empirical findings concerning potentially affected traits. Although we have tried to address criticisms fairly, we still conclude that sexual selection can be a useful tool when studying the evolution of reproductive traits in plants. Furthermore, by including the evidence from an additional kingdom, a fuller understanding of the processes involved in sexual selection can be gained.

Key words: good genes, incompatibility, mate choice, parent–offspring conflict, pollen competition, pollinator attraction, secondary sexual character, selective abortion.

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I. INTRODUCTION

Over the last century Darwin’s ideas about sexual selection (Darwin, 1871) have been developed and extended. While the germ for his theory was the need to explain apparently non-adaptive traits such as the pheasant’s tail, the evolutionary mechanisms involved have, over time, been suggested to work on a wide range of features in species from different orders (reviewed in Andersson, 1994). In the early 1980s this framework of theories was further proposed to be applicable to plants (Charnov, 1979; Willson, 1979; Queller, 1983), a suggestion that has been met with much scepticism. Although an increasing number of studies investigating this issue have been published the debate is by no means settled (Lovett Doust, 1990; Arnold, 1994; Willson, 1994; Grant, 1995; Richards, 1997; Marshall, 1998). This is, in part, the result of how various scientists define evolution through sexual selection (Arnold, 1994; Cunningham & Birkhead, 1998). Theories of sexual selection are under constant re-evaluation: no consensus has been reached as to how exactly sexual selection works or what it should include. The definitions of the various concepts involved mirrors this confusion.

In this review, we aim to throw light on research concerning plant reproductive traits suggested to evolve through sexual selection. The review consists of three sections. First we present a theoretical framework. Here we discuss various definitions of sexual selection. The two major theoretical models of how sexual selection works are then summarised. Linked to these theories are discussions concerning the level of heritability of the selected traits that allows for ongoing selection. We also address how

sexual selection can act on hermaphroditic organisms. In the second section, we present data from studies on plants. Specifically, we will consider the evolution of flower physiology, pollen characteristics and abortion of fertilized ovules and fruits. We also address some of the major sources of debate, including for example the stochastic influence resulting from the process of pollination and how to distinguish empirically sexual selection from other sources of non-random mating (Lyons *et al.*, 1989; Marshall, 1998). In the third section, we will address borderline issues *viz.* parent–offspring conflicts and incompatibility systems. We will discuss the problem of separating choice among mates from choice among offspring (Marshall & Folsom, 1991) and whether cryptic incompatibility is different from female choice and sexual selection.

II. THEORETICAL FRAMEWORK

(1) Definitions of sexual selection

(a) *Darwin on sexual selection*

Darwin found that several animal traits, such as bright plumage in birds, could not be explained through his theory of natural selection (Darwin, 1871). Some traits that had obvious negative effects on survival ability, e.g. the long neck of the giraffe that makes the animal more vulnerable to predation, could still be selected through natural selection since they also confer advantages (e.g. increased foraging ability), i.e. they have a positive net effect on survival. Other traits, such as the tail of the peacock,

do not have obvious positive effects on survival. Darwin recognized that the evolution of a certain trait was not only determined by the survival of the bearer. Of greater importance was the number of offspring the bearer contributed to the next generation. In a sexual species, one sex usually limits the reproductive output of the other. Thus, Darwin realised that selection could exist on traits that increase the number of mates acquired. This would then compensate for any negative effect on survival of exhibiting these traits. Darwin (1871) considered that the male sex was most intensely affected by sexual selection, especially when considering the evolution of display, although he did mention sexual selection acting on female choice (p. 271) and in monogamous species (p. 261).

(b) Modern definitions

Since sexual selection has been studied more extensively in animals than in plants, much of the following discussion is based on the zoological literature.

In most species, female reproductive success is limited by the availability of nutrients. Male reproductive success, by contrast, depends on the availability of fertile females (Bateman, 1948; Trivers, 1972). Sexual selection is often defined as resulting from the difference in reproductive success caused by competition for mates (Arnold, 1994). Scientists studying visually obvious secondary traits, such as colourful display or large tails, often limit the definition to the quantity of mates (e.g. Andersson, 1994). By this definition only traits expressed by the sex limited by the number of mates can be sexually selected. It is therefore gender biased, since females are limited by the number of available mates only in a few ('sex-role reversed') species. Female choice in all other instances, while regarded as a mechanism driving sexual selection, is not *per se* a result of sexual selection. Instead, female choice is considered a result of natural selection acting on offspring quantity or quality. Scientists studying female choice, however, find that the ability to choose a mate differs between individuals (Majerus *et al.*, 1986; Bakker, 1993). If sexual selection includes competition over the quality of mates as well as the quantity, female choice can be included in sexual selection.

Arnold (1994) argues against the use of quality since it might lead to confusion with the effects of fecundity selection. The amount of pollen deposited, for example, could have a component that is sexually

selected: large pollen deposits cover the stigma so that pollen from other individuals cannot germinate. A larger pollen deposit will, however, also ensure that all available ovules are fertilized. In theory, these selection pressures could be distinguished by asking the question whether a male (pollen donor) does equally well irrespective of the presence of other males. In practice, however, this is more difficult. Charlesworth, Schemske & Sork (1987) conclude that it is sometimes a matter of taste whether one wants to use the term sexual selection in preference to fertility (or fecundity) selection.

In monogamous species, both males and females can exert mate choice based on quality and hence both sexes show traits that have evolved as a result of competition for mates (Darwin, 1871). In Darwin's discussion of sexual selection in monogamous species he proposes female fecundity as a preferred trait used in mate choice (Darwin, 1871: p. 261).

Scientists studying sperm competition advocate the use of competition for access to female gametes, while the study of cryptic female choice focuses on the evolution of female ability to choose the quality of sperm after copulation has taken place (Eberhard, 1996). The study of sperm competition includes selection on primary sexual characters, an area covered by natural selection. Even evolution of the more obvious secondary sexual traits has a component of natural selection (Kodric-Brown & Brown, 1984). However, sexual selection can be regarded as a subset of natural selection, unified by the basic mechanisms of mate choice and competition, while the expression of a trait depends on the relative gain acquired by possessing this trait (Andersson, 1994). In the case of lekking birds, for example, the variance in reproductive success of males is very high and is usually dependent on only one or a few traits. The potential gain of possessing the trait can thus compensate a very large cost. In a monogamous species, however, this variance is lower and is dependent on a larger number of traits. For any given trait the potential gain is thus lower and can only compensate a low cost. The intensity of sexual selection on a trait in a monogamous species will then be lower (Cunningham & Birkhead, 1998).

Our aim in this review is to consider the evolution of floral traits in relation to interactions between conspecifics. As can be seen above, the definitions are not neutral but are context-dependent. As Helena Cronin (personal communication) points out: 'the place for definitions in science (if at all) is at the end, not the beginning. They play the role of a handy abbreviation for a long and complicated theory;

they shouldn't be pressed to play the role of laying out the major features of the theory at the very outset – after all, that is the very thing that is to be discovered'.

(2) Theories developed to explain the mechanisms of sexual selection

A main goal of sexual selection theory has been to explain the evolution of secondary sexual characters and mating preferences (Darwin, 1871). Even so, the underlying mechanisms for the evolutionary processes involved are still debated (e.g. Pomiankowski & Møller, 1995; Andersson & Iwasa, 1996; Cunningham & Birkhead, 1998). The two major forces that have been suggested to drive this evolution are contest competition between males and female preference for these ornaments (Bateman, 1948). These processes are well documented in many animal species (reviewed in Andersson & Iwasa, 1996), although it is often difficult to separate their effects (Cunningham & Birkhead, 1998). How female choice *per se* evolves, is, even after much theoretical work, an unsettled issue. The most cited theories are run-away selection (female choice evolving as a response to selection on the male) (e.g. Fisher, 1958; Lande, 1981) and several variations on the 'good genes' theme (e.g. Zahavi, 1975; West-Eberhard, 1979; Hamilton & Zuk, 1982). Theoretically, both hypotheses have proved possible explanations for the evolution of male ornaments and female preference. There is, however, a lack of firm empirical evidence and it is difficult to assess the contribution of either (reviewed in Andersson, 1994, but see Grafen, 1990).

The study of sexual selection has for a long time been focused on selection on males. In the run-away process proposed by Fisher (1958), the fundamental mechanism is that alleles for female preference become genetically coupled with alleles for the male trait. For the genetic coupling to take place, females initially have a benefit (e.g. offspring of higher quality) from choosing males possessing the selected trait. Offspring produced by choosy females and males with the particular trait will thereby tend to possess genes for both the ornament and the female preference. In a population where female preference is common, males possessing the ornament will have a mating advantage. In this way choosy females produce sons with above-average mating advantage. Due to this indirect benefit, female preference can be selected as long as there are no costs involved in female choice (e.g. Lande, 1981; but see Pomian-

kowski, Iwasa & Nee, 1991). The male trait will continue to be selected even when it does not increase survival of the offspring.

The run-away theory is the product of a time when females were thought to evolve (if at all) only in relation to factors affecting their role as mothers. During the late 1970s scientists started to recognize that females were evolving not only as a result of factors influencing fecundity and maternal care, but also as a result of interactions with other individuals of both sexes (Hrdy, 1981). The evolution of the ability to choose is only possible if it confers a benefit since female choice in itself is costly (reviewed in Reynolds & Gross, 1990). These benefits can be either direct, such as acquisition of an increased amount of resources, or indirect, such as increased vitality in the offspring. This realization led to the development of the 'good genes' hypothesis of sexual selection: male secondary traits indicate male genetic quality and can thus function as cues for female choice (Iwasa, Pomiankowski & Nee, 1991). Models of the 'good genes' mechanism have shown that the process is most likely to work when the male trait is condition dependent (Andersson, 1986; Iwasa *et al.*, 1991). This means that the trait is a signal of condition, which in turn reflects heritable quality of an individual. In other words, the phenotypic expression of the trait is a result of both genes coding for the trait and genes coding for other characteristics.

In summary, there are two major schools of thought as regards the evolution of female choice and male advertisement traits. The 'run-away selection' theory suggests that genes for female preference and male trait expression become coupled, so that extreme traits are selected even if they confer a high survival cost to the bearer. The 'good genes' theory predicts that the male traits are an indication of a heritable quality of the bearer, so that females benefit from mating with the highest ranked males even if the choice is costly for the female.

(a) Heritability in sexual evolution

There is an ongoing debate on the expected degree of heritability of sexually selected traits (Price & Schluter, 1991; Pomiankowski & Møller, 1995; Turner, 1995; Rowe & Houle, 1996; Ritchie, 1996; Alatalo, Mappes & Elgar, 1997). The reason for this is that all theories depend on there being heritable variation, while the magnitude varies depending on the other assumptions in the theories. However, if there is heritability of the selected trait, the additive

genetic variance will gradually become lower and the engine driving the evolution of the male trait will stop (Fisher, 1958).

The theory behind run-away selection predicts heritability of both the male trait and female preference (Fisher, 1958; Lande, 1981). Indeed, it is the linkage between genes coding for these traits that gives rise to the run-away process. The additive genetic variance will gradually get lower as the expression of the male trait comes closer to the limit where the cost of survival equals any sexual benefit of possessing the trait. Close to this limit, where the run-away process has stopped, it will be impossible to measure heritability since the genes coding for female choice and the male trait have become fixed in the population (Dominey, 1983). In the case of lekking birds, selection on modifier genes has been suggested to increase variation and allow for a high heritability of male traits (Pomiankowski & Møller, 1995). In these species the highest ranked males get most of the matings (reviewed in Balmford, 1991; but see Lank *et al.*, 1995), which leads to a skewed distribution of mating success as a function of male trait. Under such circumstances it pays to produce offspring that show a high variance in phenotypic expression: the cost of producing some offspring with small traits is compensated by the relatively bigger advantage of producing offspring with large traits. It is interesting to note that after Pomiankowski and Møller (1995) appeared the number of published studies showing a high heritability of male traits increased (Alatalo *et al.*, 1997). This was the case even in species where the mating success as a function of male trait did not show an extremely skewed distribution, one of the prerequisites in the Pomiankowski–Møller model.

The ‘good genes’ theory also predicts heritability, although in this instance it is heritability of fitness-related genes possessed by the father (Zahavi, 1975). This heritability must be high enough to compensate for the cost of exerting a choice, i.e. a ‘choosy’ female should produce offspring with a higher quality than an non-discriminating female, even if the former spends resources on making a choice that otherwise could have been invested in the offspring. The heritability should not be too high, though, since according to Fisher’s fundamental theorem genes having a large effect on fitness rapidly go to fixation within a population (Fisher, 1958; Maynard Smith, 1978; Dominey, 1983; Charlesworth, 1987). Males would then not differ in genetic quality, female choice would not increase female fitness, and since choice is costly, there would be selection against

females exerting choice. Mutations alone can in some instances be sufficient to keep the variation high, even if there is selection of fitness-enhancing genes (Lande, 1976; Rice, 1988). Hamilton and Zuk (1982) suggested that the traits used as a cue for mate choice indicate parasite load and indirectly the effectiveness of the bearer’s immune defence system (e.g. a bright plumage that only can be produced when the bearer has a low number of parasites). Females choosing males with low parasite load will produce offspring with a higher resistance. Due to the difference in evolutionary rate between host and parasite, there will always be a selection on the more uncommon host (= uncommon immunodefence system) (Hamilton, 1980). The optimal defence system and thus the ‘good genes’ will then vary with time. The cue, however, stays the same. Heterogeneity in space could also maintain heritable variation (Partridge, 1983; Houle, 1992; Stearns, 1992).

It is important to remember that Fisher’s theorem is based on the assumption that the population evolves in a constant environment. This is a common supposition in population genetic models. Indeed, Falconer & Mackay (1996) states that ‘environmental variance is a source of error that reduces precision in genetic studies’ in a book on quantitative genetics. In nature, of course, environmental variation is always present. The effect of this variation is that different traits will be selected over time. It also imposes stochastic factors affecting vigour and hence trait expression. Even within a population at a specific time there might be several different traits that are selected as a result of micro-environmental variation (Stearns, 1992). Thus, even if fitness-related traits rapidly go to fixation in a population under constant circumstances, this probably seldom happens in nature.

Heritability (in the narrow sense) is usually defined as the proportion of the phenotypic variance that is attributed to additive genetic variance (Falconer & Mackay, 1996). As a result, a low heritability can be the effect of both a low additive genetic variance and/or a high environmental (or non-additive genetic) effect on phenotypic expression. Houle (1992) shows that most fitness-related traits (as a result of the high number of loci usually affecting life-history traits) should have a high additive genetic variance. In heritability measurements, this variance can be masked by a high environmental variance. Houle (1992) suggests that it is more appropriate to find the evolvability of a trait, i.e. the variance to mean ratio, than heritability in the narrow sense. To come closer to estimating

true additive variance, heritability should further be measured under 'constant' environmental conditions. These theoretical suggestions were confirmed in a natural population of the pied flycatcher, *Ficedula hypoleuca*, studied by Merilä and Sheldon (2000).

In summary, there are several mechanisms that could maintain variation in fitness-related genes even if there is selection on 'good genes' through female choice. We expect heritability of both general vigour and male traits, even if the latter are only a side effect of the bearer's current fitness. However, due to the same factors that keep the variation high, measurements will most often show a low heritability and large sample sizes are needed to detect heritability.

(b) *Sexual selection in hermaphroditic plants*

Some authors argue that sexual selection should not be important in hermaphrodites due to the fact that an investment into one reproductive function will limit the investment in the other (Charlesworth *et al.*, 1987; Grant, 1995). There has also been some confusion regarding what is actually meant by secondary sexual traits in hermaphroditic plants (Grant, 1995; Richards, 1997). The main controversy seems to originate from the view that sexually selected traits should not give any benefit that can be selected through natural selection. Examples that supposedly adhere to this prerequisite are superior size, weapons, song and display behaviour of male animals (Grant, 1995). Kodric-Brown and Brown (1984) on the other hand, argue convincingly that several of these and other sexually selected traits in animals are also under natural selection, i.e. they give the bearer an additional benefit. It is undeniable that flower morphology in animal-pollinated species has been selected to attract pollinators, since pollination is essential for fertilization to take place at all; flower morphology is of course always affected by natural selection to some extent. This situation is not, however, unique to plants. Take, for example, songs in birds; in many species the song capacity is used by females to assess male quality (e.g. Bensch & Hasselquist, 1991; Searcy, 1992). However, bird song is also important for communication between all individuals (both males and females have the ability to sing) (Beletsky, 1983). In fact, only the capacity to sing in the preferred way can be said to be sexually selected. Even so, no one seems to have a conceptual problem with regarding bird song as a sexually selected character. In much the same way,

it should be possible to regard flower morphology in a hermaphroditic plant as a result of several selection pressures (Armbruster, 1996). What is of interest when studying sexual selection is whether flower size is larger than what is optimal for ensuring fertilization of all available ovules. It is difficult to separate the effects of selection pressures. This in itself does not rule out that selection for increased mating success (in competition with other individuals) can have substantial effects on the evolution of plant traits.

Morgan (1992, 1994) uses a quantitative genetic model to evaluate the possibility of sexual selection in hermaphrodites. He shows that the key characteristics are as relevant to hermaphroditic species as they are to species with separate sexes. There is a constraint however, as regards the possibility of Fisherian run-away processes. A run-away process starts out with viability selection, during which covariance between male and female reproduction evolves (Morgan, 1994). In a hermaphrodite, this covariance will decrease when the cost of producing a trait increases. In species with two sexes on the other hand, the female can carry genes for a trait without expressing them. Then only the male carries the cost of the trait. The optimal value for the trait can then differ between the sexes since the females express the trait to a degree that depends on natural selection alone, while the males have a further effect of sexual selection. In hermaphrodites, extreme males will carry genes with negative effects on survival. These are, by definition, expressed in all individuals, which in turn will lower selection on female preference. As a result, covariance between the male trait and female preference will occur only rarely. Consequently, the run-away process itself will be unusual.

Another way of studying the evolution of plant reproductive traits is through the use of evolutionary stable strategy (ESS) models describing phenotypic sex allocation in relation to the frequency of individuals using different strategies in a population (Morgan, 1992). This approach leads to the same general conclusions as the quantitative genetic model developed by Morgan (1992), but allows ecological aspects to be included at the cost of genetic precision. This can be a difficulty since genetic covariation between male trait and female preference, when it exists, will not be included (Morgan, 1992).

In *Leucadendron xanthoconus*, male plants with many flowers had increased mortality, while receiving a lot of pollinator visits. Female reproductive success, however, did not increase with floral display (Bond

& Maze, 1999). The authors interpreted this result as an effect of sexual selection, resulting in a vegetative dimorphism between the sexes with males having larger displays. It should be noted though, that this is not an example of run-away selection (no genetic coupling between genes for preference and male display), neither can it be explained by the handicap principle (males with many flowers do not have increased vitality). The result is rather an effect of the competition for pollinators being more intense between males than between females.

In conclusion, theory supports the idea that mate choice and competition for mates can affect evolution of hermaphroditic organisms. Even if run-away processes are expected to be rare in hermaphroditic organisms there are several examples of exaggerated sexual traits. A zoological example is the enormous penis of the sessile barnacles *Balanus* spp., which probes neighbouring individuals in search of mates that accept fertilization (Barnes, Barnes & Klepal, 1977). A striking example from the plant kingdom is the long pistils in *Hibiscus* spp.

III. POSSIBLE CANDIDATES FOR SEXUAL SELECTION IN PLANTS

(1) Traits affecting competition for pollinators

Floral display was the first plant trait that was suggested to evolve through sexual selection in plants (Charnov, 1979; Willson, 1979; Queller, 1983; Stanton, Snow & Handel, 1986). A constraint is, however, that mating is dependent on an intermediary. At this level we will thus usually not expect to find female choice (Stanton, 1994). Competition between pollen donors (and receivers) can take place, however. It should be noted that an increase in pollen deposition could be expected to influence female choice at a later stage. Evolution of traits that enhance ability in competition for access to mates can happen irrespective of who makes the choice (e.g. pollinators). Investment in floral traits further benefits both male and female reproductive functions, which thus could be selected through natural selection (Charlesworth *et al.*, 1987). There is a lack of studies that measure the effect of inflorescence size on the total fitness of an individual: even though many studies measure both seed production and some kind of pollen export/fertilization variable, we do not know of any that have included offspring quality. Since this is the most probable benefit to the

female of increasing inflorescence size it will be hard to reach a general conclusion regarding which function is more important in the selection of inflorescence size.

(2) Fleur-du-mâle

In line with Bateman's principle (Bateman, 1948), several authors have suggested that the male reproductive function of a hermaphroditic plant is dependent on the availability of pollinators to a higher degree than is the female function (e.g. Queller, 1983; Willson & Burley, 1983; Stanton *et al.*, 1986). Pollen supplementation experiments suggest that female reproductive success tends to be limited by resources more often than by pollination (Pleasants & Stephen, 1983; Snow, 1986; Stephenson, 1992; but see Wilson *et al.*, 1994). Selection on the male function might thus explain why many plants produce an excess number of flowers ('fleurs-du-mâle'), i.e. more flowers than are needed to produce the number of seeds the plant can afford to mature. Cruzan, Neal & Willson (1988) showed that the retention of older flowers (lacking nectar production) increased visitation rates and pollen removal in *Phyla incisa*. Pollen deposition, however, was not affected. In *Agave mckelveyana*, some flowers are aborted before fruit initiation regardless of pollen availability and thus do not contribute to female fitness (Sutherland, 1987). These 'functionally male flowers' also show a higher nectar production than the fruit-producing flowers on the same individuals.

Diocious *Wurmbea dioica* males produced more and larger flowers than females (Vaughton & Ramsey, 1998). Flower size, but not flower number, affected pollen removal. Flower size was further negatively related to per cent seed set indicating a trade-off between allocation to attraction and reproductive success. In gynodioceous *Phacelia linearis*, however, corolla size of hermaphrodites did not have any effect on seed set (Eckhart, 1993). In *Asclepias tuberosa*, separation of selection on total flower number and the size of inflorescence units (by manipulation) showed that intermediate umbel sizes were optimal for the male function which also was predicted by an ESS model (Fishbein & Venable, 1996). Even so, this optimum was higher for male than for female reproductive function. Pollinator visitation rates were correlated with male, but not female function. Siring success increased with corolla size in *Campanula punctata* (Kobayashi, Inoue & Kato, 1997). Kobayashi *et al.* (1997) could not find any effect on the quantity of pollen dispersal; hence

they suggest that corolla size is a result of natural selection on an unmeasured factor affecting 'pollen transfer efficiency'.

It should be noted that floral display could benefit the female function as well. A floriferous plant might have a competitive advantage over less conspicuous females. By attracting a higher number of pollinators the number of donors will also increase which, in turn, could lead to offspring of superior quality. We do not know of any studies that have measured the quality of offspring in this context, however. Another effect could be that the possibility of female choice through selective abortion increases if a high number of fruits are initiated. Producing a high number of flowers could also represent a bet-hedging strategy when resources are unpredictable (e.g. Stephenson, 1980).

(3) Inflorescence size versus visitation rates

It has been known for a long time that several floristic features affect pollinator attraction. Increased nectar and pollen production, as well as size of individual flowers or inflorescences, can increase the number of pollinator visits (e.g. Pleasants, 1981; Pleasants & Stephen, 1983; Stanton *et al.*, 1986; Mitchell, Shaw & Waser, 1988; Thomson, 1988; Zimmerman, 1988; Eckhart, 1993; Queller, 1997; Philipp & Hansen, 2000). Still, this is not unequivocally true: several studies have failed to show this relationship (Meager, 1991; De Jong & Klinkhamer, 1994; Niovi Jones & Reithel, 2001). Thomson (1988) found that visitation rates increased with umbel size and number in *Aralia hispida*. The visitation rate *per flower*, however, declined with inflorescence size. A linear or even decreasing function of visitation rate per flower has been found in several other species (Devlin, Clegg & Ellstrand, 1992; Harder & Barrett, 1995). As Thomson (1988) points out, visitation rates as a function of inflorescence size depend on pollinator availability, so that when pollinators are limited, the relative benefit will increase compared to circumstances of high pollinator availability. In the study on *Aralia hispida*, there was an abundance of pollinators. Even so, he found an indication that individuals compete for pollinations, although not to such an extent that visitation rates increased on a per-flower basis (Thomson, 1998).

When applying theoretical knowledge to nature we must allow for environmental variability, which in essence usually means that selection will be less precise. Selection will probably not act at the level

of individual flowers within an inflorescence, but rather will distinguish between large or small inflorescences. We would therefore argue that though the information on visitation rates per flower is informative, selection acts at the individual level and in most cases this is the more interesting unit.

To complicate the issue of pollen dispersal and inflorescence features further, there is the effect of within-individual movement of pollen that results from a pollinator visiting several flowers within an individual (Harder & Barrett, 1995; Rademaker & De Jong, 1998). Pollinators often visit a higher number of flowers in a large inflorescence. As a consequence a lot of self pollen will be deposited within the individual. When the plant is partially or fully self-incompatible this leads to wastage of pollen. Harder and Thomson (1989) suggest that plants should evolve to present pollen gradually. They surmise that a given proportion of the pollen will be lost between visits (due to grooming, for example). When the exchange of pollen per visit is kept low the loss of pollen decreases. This will also lower the cost of having flowers visited repeatedly.

So how does visitation rate affect male function? The conflicting evidence led Wilson *et al.* (1994) to suggest a scenario where the evolution of floral traits depends on the variation in pollen availability. They point out that the steps from pollinator visitation to reproduction are fewer with regard to female function (pollen insertion) than for the male function (pollen removal). This ought to mean that the relationship between female reproduction and floral traits is less stochastic, allowing for a more continuous selection of these traits. When pollinator availability is low, competition for pollinators should initially act most effectively on female function. However, pollinator availability will vary over time in most species. When pollinators are abundant there will be selection on male function to present pollen gradually. After this change has occurred, pollinators are more likely to become limiting for the male function at times of pollinator scarcity. The net result will then be that floral advertisement traits will respond more to selection on the male than the female function when pollinators are few (Wilson *et al.*, 1994).

(4) Floral display and male reproductive output

The difficulty in determining exactly how floral traits relate to the reproductive function of either sex

can be illustrated by the investigations on *Asclepias* ssp. Queller (1983) showed, in *Asclepias exaltata*, that inflorescence size was positively correlated to pollinium removal (male function) while seed set (female function) was unaffected. Broyles & Wyatt (1990, 1995), however, found that both male and female function were positively affected in the same species. They measured male gain by paternity analysis of seeds produced in recipient plants. They maintain that the high flower to seed ratio found in *Asclepias exaltata* cannot be explained through the fleur-du-mâle hypothesis. In response to this, Queller (1997) argues that the positive effect of inflorescence size on female fitness is an artefact of plant size: larger plants have more resources to produce both more flowers and more fruit. Further, when plant size was controlled for (in the Broyles & Wyatt, 1995 study), male reproductive function gained close to three times as much as did female function from the increase in flower number. These studies focused on pollen deposition and removal and did not investigate offspring quality.

It is expected from population genetic models on hermaphroditic plants that the selection gradient through one gender is equal in magnitude but opposite in sign to the selection gradient of the other gender (Morgan, 1994). Within an individual there is thus expected to be a negative trade-off between reproductive functions. Among individuals however, it is possible to find positive relationships between both sexes and some other trait related to plant fitness (Queller, 1997). Both Morgan (1994) and Queller (1997) further stress the importance of using relative measures of sex-specific fertility, and/or of controlling for plant size. In a study of *Asclepias syriaca*, Morgan and Schoen (1997) found that several traits of floral morphology showed statistically significant selection gradients. In four of these traits, there was opposed selection through male and female reproductive function. They suggest that current evolution is occurring through the female rather than the male reproductive function and is not an effect of sexual selection. It should be noted that offspring quality was not measured in these studies.

To circumvent the problems associated with measuring pollen export and deposition, several studies have instead used genetic markers to determine male reproductive success. Devlin *et al.* (1992) showed in wild radish, *Raphanus sativus*, that male success, measured as the number of seeds sired, increased with inflorescence size. Although there was some effect on female reproductive success

as well, the overall effect was stronger for the male function. Galen (1992) used isozyme markers in *Polemonium viscosum* and found that inflorescence size had a positive effect on siring ability. In this species, however, seed production decelerates with stigma pollen load, which means that the relationship between pollen export and paternal success shows diminishing returns. Emms, Stratton & Snow (1997) combined the use of genetic markers with experimental manipulation of inflorescence size on *Zigadenus paniculatus*. Pollen donors with large inflorescences sired more seeds than donors with small inflorescences. They did not, however, find a correlation between relative inflorescence size and relative paternity. They further found large stochastic effects on male performance. The experimental design allowed them to control for inbreeding effects but they did not account for differences in pollen competitive ability. As we shall discuss in further sections, this trait can have a genetic basis and there can be large individual differences between donors. If this is the case in *Zigadenus paniculatus*, then male performance will depend on the composition of pollen grains competing for fertilizations. The stochastic behaviour in donor performance could, at least in part, be explained by such circumstances.

In *Raphanus raphanistrum*, pollinators preferentially visited one of two different petal-colour morphs (Stanton *et al.*, 1986). In this study the colour was used as a genetic marker to assess paternity. The increased visitation rates had a pronounced effect on pollen donation but not on fruit and seed production. Seed quality, however, was not recorded. Charlesworth *et al.* (1987) point out the importance of considering pollinator behaviour in relation to this kind of result. If pollinators develop search images for common morphs, this might weaken selection of the preferred colour-morph, when this occurs at a lower frequency. In other words: a mutant with a new 'more attractive' colour might not be able to invade a population of another colour.

Although estimates of heritability of flower morphology are scarce, it is known that several traits such as flower size and colour, as well as nectar production are genetically controlled (Willson, 1994). Eckhart (1993), however, showed that corolla diameter was heritable in gynodioecious *Phacelia linearis*. Campbell (1989) found that selection on male and female functions affected floral morphology in *Ipomopsis aggregata*. Plants that had exerted stigmas and narrow corollas achieved a greater pollination success as females, while the opposite was true for male success.

(5) Pollen traits affecting competitive ability

Pollen grains display traits that affect their siring ability. Individuals are variable with regard to the expression of these traits. In many circumstances pollen from different individuals will be deposited in amounts that result in pollen competition. As a result non-random mating occurs. There are stochastic factors affecting the outcome of pollen competition. Even so it has been shown that individuals with the highest inherent siring ability fertilize most ovules in a recipient plant. Selection should thus favour individuals with a high competitive ability.

(a) Pollen grain characters

When pollen grains are deposited on a stigma they germinate, penetrate the cuticle and then produce pollen tubes that grow towards the ovules where fertilization takes place (Herrero & Hormaza, 1996). The female organs can affect pollen performance at all these stages (see Section III.6). If the number of pollen grains deposited exceeds the number of ovules in the flower, traits that enhance the chance that pollen coming from a given donor fertilizes the ovules can be selected (Mulcahy, Sari-Gorla & Mulcahy, 1996). There are several traits that can have this function, such as general viability, germination ability and rate, pollen tube growth rate and size of pollen grains (Bertin, 1988). Snow and Spira (1991a) have shown that differences in pollen tube growth rates are more important than differences in pollen germination rate for pollen competitive ability in *Hibiscus moscheutos*. The same is true for violets where pollen tube growth rate explains 46 per cent of the variation in siring ability between individuals (Skogsmyr & Lankinen, 1999). In *Echium vulgare*, however, pollen tube growth rate was not related to siring ability, although this study only included three genotypes (Melser, Rademaker & Klinkhammer, 1997). Larger pollen grains can store more resources which have an effect on siring ability (Cruzan, 1990b). In a study on *Erythronium grandiflorum* Cruzan (1990b) found pollen size to be negatively correlated with fertilization ability and positively correlated with post-fertilization siring ability. Post-fertilization processes in this case appear to be influenced by paternal differences that are expressed through competition among developing seeds for maternal resources.

The given examples show that pollen grains have traits that affect their ability to fertilize ovules. For sexual selection to take place there must be differ-

ences at the individual level; some individuals should produce a higher proportion of pollen grains that possess these traits, which ultimately gives these individuals a higher number of progeny. Individual plants have been shown to differ with respect to these pollen traits (e.g. Schemske & Fenster, 1983; Walsh & Charlesworth, 1992; Pfahler, Pereira & Barnett, 1997; Skogsmyr & Lankinen, 1999). Pollen viability, germination rate and pollen tube growth rate have been found to be influenced by the number of apertures in *Viola diversifolia* (Dajoz, Till-Bottraud & Gouyon, 1991). The proportion of pollen grains with few apertures differs between individuals. Pollen grains with a high number of apertures are fast growers but have a higher mortality. The trade-off between survival and growth rate allows for the co-existence of high and low numbers of apertures. In *Petunia hybrida*, different pollen genotypes varied in their ability to tolerate pollen storage (Mulcahy, Mulcahy & Pfahler, 1982).

(b) Non-random mating

Studies of at least eight cultivated and 11 wild species have found non-random mating after controlled pollination experiments (reviewed in Marshall & Folsom, 1991; Namai & Ohsawa, 1992; Björkman, Samimy & Pearson, 1995; Pasonen *et al.*, 1999; Skogsmyr & Lankinen, 1999). The occurrence of non-random mating, however, does not tell us whether it is pollen donors, maternal plants or embryos that influence the outcome of mating (Lyons *et al.*, 1989). Marshall and Diggle (2001) made an attempt to sort out these effects in wild radish *Raphanus sativus*. Even if they could show that pollen donors varied in siring ability, they could not make any conclusions as to which developmental mechanisms were most important.

Differential fertilization ability among pollen donors has been shown in several studies (e.g. Bookman, 1984; Marshall & Ellstrand, 1986; Snow & Mazer, 1988; Bertin, 1990; Snow & Spira, 1991b; Björkman *et al.*, 1995; Havens & Delph, 1996; Pasonen *et al.*, 1999) while in other studies no differences were detected (e.g. Mazer, 1987b; Fenster & Sork, 1988; Cruzan, 1990a). Most of these studies involved only a small number of individuals but a high number of pollinations and offspring to ensure that the differences found were consistent (but see Snow & Spira, 1996). Differences in pollen tube growth rates can result from incompatibility effects. It can therefore be advantageous to study pollen tube growth rate *in vitro* to avoid the female

influences. In such a study on *Viola tricolor* we found individual differences in pollen tube growth rate *in vitro* to be common (Skogsmyr & Lankinen, 1999).

(c) *Male performance versus recipient plants*

In some cases siring ability depends on the recipient plant, so that a pollen donor is a better competitor in some pistils than others (Pfahler, 1967; Sarr, Fraleigh & Sandmeier, 1983; Fenster & Sork, 1988; Cruzan, 1990*b*; Johnston, 1993; Leach, Renfrey & Mayo, 1993; Herrero & Hormaza, 1996). In *Hibiscus moscheutos*, however, Snow and Spira (1996) found consistent differences in siring ability of three pollen donors after mixed-donor pollinations involving many recipient plants. The three pollen donors were allowed to compete in pairs with a number of donors and each combination was repeated on 11–15 recipient plants. The authors conclude that the existence of ‘supermales’ allows for selection on pollen competitive ability. In *Raphanus sativus* four pollen donors had the same rank order regarding seed siring on 16 recipient plants following mixed pollinations (Marshall, 1998). In *Betula pendula*, six donors had consistent *in vivo* pollen tube growth rates as well as seed siring ability on 11 recipient plants (Pasonen *et al.*, 1999).

(d) *The potential for pollen competition in natural populations*

As mentioned above seed set is not pollen limited in many cases (Pleasants & Stephen, 1983; Snow, 1986; Stephenson, 1992). In fact, pollen loads deposited by pollinators on the stigma are in many instances large enough to allow pollen competition to take place (Snow, 1986; Spira *et al.*, 1992; Quesada, Winsor & Stephenson, 1996; Winsor, Peretz & Stephenson, 2000). For sexual selection to occur, however, pollen from more than one donor must be deposited on stigmas. This seems to be commonly occurring (reviewed in Snow, 1994). In a wild population of *Cucurbita foetidissima* Winsor *et al.* (2000) found that not only did most flowers receive enough pollen for competition to take place but also that the progeny produced from the flowers with the highest number of pollinator visits was more vigorous. Even when pollen limitation takes place, competition between different pollen donors should not always be excluded (Snow, 1986; Walsh & Charlesworth, 1992; Stanton, 1994). For example, in populations where plants are pollen-limited some individuals may receive excess pollen. Also, in

some species there is differential probability of seed maturation of differently placed ovules. Even if there is pollen limitation, there might thus be competition for fertilization of the ovules that are most likely to be matured. In these circumstances, faster pollen tubes fertilizing ovules at more preferable positions in the ovary should have an advantage (Walsh & Charlesworth, 1992).

In nature, pollinator behaviour affects the proportion and composition of the pollen deposited. Marshall *et al.* (2000) found that the relative performance was consistent among four donors across pollen load sizes. The donors were allowed to compete in pairs and pollen quantity was regulated by the number of flowers used from each donor. In some males, however, siring ability depended on pollen grain productivity rather than pollen performance *per se*. In *Viola tricolor* pollen performance was consistent for a given donor when the proportion of two donors was varied while pollen load size was held constant (Lankinen & Skogsmyr, *in press*). An exception was found at very low proportions (1:10) where siring ability was lower than expected from performance *in vitro*. This study included 22 pollen donors.

When investigating the potential for selection of pollen donors in a natural population it is important to include many male genotypes. This is especially important when no differences are found in a small sample (Willson, 1994). To balance the cost of producing a trait, the situation where a benefit is gained (through possessing the trait) must occur frequently. We should expect a high incidence of non-random mating in species where there is selection for increased siring ability in competition with other pollen donors. In a study involving 38 individual pollen donors, non-random mating occurred in 23 out of 34 randomly selected donor comparisons in *Viola tricolor*. This indicates that differences in siring ability are a common occurrence in this species (Skogsmyr & Lankinen, 1999).

Some detailed investigations of the potential for selection under natural conditions have been carried out (Mulcahy, Curtis & Snow, 1983; Snow, 1986; Spira *et al.*, 1992; Spira, Snow & Puterbaugh, 1996; Mitchell & Marshall, 1998; Winsor *et al.*, 2000), but clearly more studies involving more species are needed before any general conclusions can be drawn. Under natural conditions pollen competition is more affected by stochastic factors than it is in hand-pollination experiments (Spira *et al.*, 1996). Mitchell and Marshall (1998), however, found rank ordering of pollen donors to be consistent following hand

pollinations and field pollinations in *Lesquerella fendleri*. By performing hand pollinations, Spira *et al.* (1996) concluded that it is still possible for late-arriving pollen (given that they have a higher pollen tube growth rate) to sire ovules when pollen arrives 1–2 h after other pollen in *Hibiscus moscheutos*. A theoretical comparison between pistil length and variance in pollen tube growth rate *in vitro* in a population of *Viola tricolor*, showed that this time lag could be up to 14.8 h (Skogsmyr & Lankinen, 1999).

(e) *Pollen grain interactions*

Pollen competitive ability is also affected by interactions with other pollen grains. The size of pollen grains has been shown to be influenced by the genotypes of the other grains developing in the same anther (Gambier & Mulcahy, 1996). More pollen lumped together can increase the proportion of germinated pollen grains and pollen tube growth rate (Brewbaker & Majunder, 1961; Schemske & Fenster, 1983). This may be caused by an increased release of Ca^{2+} from the pollen grains (Bertin, 1988). Calcium ion release is necessary for pollen germination in many cases (Marshall & Folsom, 1991).

Growing pollen has been suggested to interfere with pollen performance of other donors (Aizen, Searcy & Mulcahy, 1990; Cruzan, 1990a; Marshall *et al.*, 1996; Mulcahy *et al.*, 1996; Niesenbaum, 1999). Travers and Holtsford (2000) found that the siring success of donors with different *Pgi* genotypes in *Clarkia unguiculata* varied depending on the pollen load, so that the B-allele donor was superior at low deposition levels while this advantage disappeared when the stigma was saturated with pollen. Pollen tubes from a single pollen donor have been shown to be more stimulated by each other than by pollen from other donors (Landi & Frascaroli, 1988; Cruzan, 1990a). In *Erythronium* (Cruzan, 1990a), when local pollen grains were allowed to germinate with self pollen from the recipient plant, the pollen experienced more attrition (stylar inhibition) than when coupled with more distant pollen. Cruzan (1990a) regards this as an incompatibility effect. Marshall *et al.* (1996) found interference competition between pollen donors that was not a result of incompatibility. They compared the percentage seeds sired by two donors when pollen loads were mixed by applying pollen loads to opposite sides of the stigma. Only when pollen tubes from the two different donors were in contact in the style did the percentage seeds sired decrease compared to single-donor pollinations. This might indicate that com-

petition between pollen from different donors has a chemical basis (Snow, 1986; Spira *et al.*, 1992, 1996; Mitchell & Marshall, 1998; Furlow, 1999).

(f) *Heritability and environmental effects*

There is a genetic component of pollen performance (Ottaviano, Sari-Gorla & Arenari, 1983; Ottaviano, Sari-Gorla & Villa, 1988; Schlichting *et al.*, 1990; Quesada *et al.*, 1996). In an inbred maize *Zea mays* population, pollen tube growth rate and germination ability showed a high heritability (Sari-Gorla *et al.*, 1992). In *Viola tricolor*, a narrow-sense heritability of 0.49 for pollen tube growth rate was found (Skogsmyr & Lankinen, 2000). This result was further supported in another investigation on this species where clonal repeatability of pollen tube growth rate was over 0.8 (Lankinen, 2000).

Broad-sense heritability measurements in 16 clones of *Oeothera organensis*, however, showed that only approximately 9 per cent of the variation in pollen tube growth rate could be explained by a genetic component (Havens, 1994). Furthermore, Snow and Mazer (1988) reported a selection experiment that failed to enhance siring ability in wild radish. In the intense-competition line, pollen from three donors was applied to maternal plants *versus* only one in the control. The F_2 progeny were produced by applying three new donors to maternal plants derived from the F_1 generation. Thus, the selected generation might be the best out of six donors, while the control was unselected. Only one maternal plant was used to produce the F_1 generation. The lack of any effect of the selection experiment might result from the relatively low number of individuals included, if this limited the range of variation in siring ability. In *Viola tricolor*, where 21 individuals were included, siring ability increased while variation in pollen tube growth rate decreased after one generation of selection on siring ability (Skogsmyr & Lankinen, 1999).

Most studies on heritability have been carried out under constant conditions. In nature, however, the impact of environmental effects on pollen performance should result in low heritability in the narrow sense, i.e. additive genetic variance is often hidden by environmental factors (Houle, 1992; reviewed in Delph, Johannsson & Stephenson, 1997).

Environmental conditions often affect pollen performance e.g. ageing (Thomson *et al.*, 1994), herbivory (e.g. Quesada, Bollman & Stephenson, 1995; Mutikainen & Delph, 1995), soil fertility (e.g. Young & Stanton, 1990; Lau & Stephenson, 1993, 1994;

but see Snow & Spira, 1996), and temperature (e.g. Delph *et al.*, 1997; Johannsson & Stephenson, 1998). Young and Stanton (1990) showed that pollen of *Raphanus raphanistrum* produced under low-nutrient conditions sired less seed in competition with pollen produced under better conditions. In *Hibiscus moscheutos*, however, environmental stress did not have an effect on the relative siring ability of pollen donors when compared to a standard donor (Snow & Spira, 1996).

Lankinen (2001) found a gene–environment effect of temperature on pollen performance in *Viola tricolor*. Such interactions have also been detected in tree species (Travers, 1999; Pasonen, K  pyl   & Pulkkinen, 2000). This kind of interaction in combination with spatial variation and gene flow between patches, can account for the maintenance of variation in pollen traits (Lankinen & Skogsmyr, 2001*b*; Delph *et al.*, 1997). In fact, selection on competitive ability of pollen can maintain variation better than natural selection alone (Lankinen & Skogsmyr, 2001*b*). Other suggestions of how heritable variation in pollen performance can be maintained in situations of strong selection include mutations and recombination, genotype by environment interactions (Delph *et al.*, 1997) and limitations for certain pollen genotypes within the style (Mulcahy *et al.*, 1996; Delph *et al.*, 1997).

(6) Pollen–pistillate interactions

It has been generally assumed that female reproductive function in plants is often limited by the availability of nutrients. The question we ask here, however, is whether it is also a function of the quality of the pollen donor. Although we have been unable to find a study that measures the exact cost of producing pistils and stigmas, it is reasonable to assume that there is a cost involved (Charlesworth *et al.*, 1987). When pollen is not limited, why should a plant invest in this production? One reason for investment in pistillate tissue is to optimize pollen transfer between pollinators and plants (Armbruster *et al.*, 1995; Armbruster, 1996). Another reason could be that individuals that increase the chance that their ovules are fertilized by certain pollen produce more vigorous offspring. Many plants have post-pollination mechanisms that sort among mates (Marshall & Folsom, 1991).

Non-random mating may result from inbreeding/outbreeding depression, physiological self-incompatibility as well as differences in pollen donor quality (Charlesworth *et al.*, 1987; Cruzan & Barrett, 1993;

Marshall, 1998). It is thus important to design experiments so that these effects can be ruled out in studies of sexual selection (Charlesworth *et al.*, 1987; Marshall, 1998). In experiments where material from several populations is used, in- or outbreeding effects are not substantial if siring ability and offspring vigour are the same in intra- and inter-population crosses. By only comparing compatible pollen donors in experiments there will be no effects of incompatibility. Likewise, we suggest that when only the degree of compatibility is important, there should be no inherent differences in pollen performance between individuals. This can be studied by growing pollen grains *in vitro* or testing all donors over a large range of recipient plants. In a study on wild radish, Marshall (1998) used 16 recipient plants known to have different compatibility (4×4) for mixed pollinations with four pollen donors of different compatibility. Since pollen donors had similar rank ordering across maternal plants and maternal lineages this indicates that in this species there is some additional post-pollination sorting mechanism apart from self-incompatibility.

Female choice and male competition can often be difficult to separate, but this is particularly complex at stages after pollination/mating (Arnold, 1994). When maternal plants sort among mates by intensifying pollen competition, selection of female choice can never be independent of selection on pollen competitive ability. The benefit of a given pistil length depends on the difference between pollen tube growth rates and *vice versa* (Lankinen & Skogsmyr, 2001*a*). Co-evolution between the male and female reproductive functions can thus, depending on circumstances, result in situations when the two traits are selected either in the same or opposite directions. In general, though, it is not crucial to separate the effects of the different functions unless the exact contribution is to be quantified. While interpreting data it is important to keep in mind that selection acts on both reproductive functions.

(a) How female morphology affects pollen competition

A longer pistil may increase competition by allowing more pollen grains to be included in the race as well as extending the length of the race (Mulcahy, 1979). In *Ipomopsis aggregata* flowers with more exerting stigmas, i.e. longer pistils, and a higher proportion of time spent in the pistillate phase, received more pollen (Campbell, 1989). Neither of these traits affected pollen export. Most species of *Dalechampia* have expanded stigmatic surfaces that extend from

the stylar tip and down the sides of the styles (Armbruster *et al.*, 1995; Armbruster, 1996). Pollen landing on the edges of the stigma has to grow to the tip of the stigma in order to reach the style. Thus, the distance the pollen tubes have to grow is increased without affecting pistil length. This could be an advantage when the length of the pistil is an adaptation to a specific pollinator. This structure will add a note of stochasticity though, since pollen deposited on the tip will have an advantage over that deposited on the sides. The structure can thus be regarded as a compromise between increasing pollen competition and adaptation to a specific pollinator.

For pollen grains on the stigma to be able to germinate they need to take up water, become metabolically active and produce a pollen tube (Marshall & Folsom, 1991). The germination process is also pH dependent. Lumps of pollen grains have been found to increase the stigmatic pH more effectively and thus increase the germination rate (Ganeshiah & Uma Shaanker, 1988). This ensures a high number of pollen grains on the stigma before germination starts, which can be beneficial for the recipient plant since the intensity of pollen competition increases with pollen grain number. To produce fewer ovules per ovary is another trait that potentially can be selected to increase the intensity of pollen competition (Snow & Mazer, 1988).

In some insect- and wind-pollinated species delayed pistil receptivity occurs (Herrero, 1983; Douglas & Cruden, 1994; Dahl & Fredrikson, 1996). This mechanism allows a maximum number of grains from different pollen donors to accumulate on the stigma before the start of the race. In essence, this synchronizes the growth of the pollen tubes and thus increases the opportunity for the recipient plant to make a choice.

(b) Direct effects on pollen performance

Choi and Friedman (1991) have shown that during pollen tube development in the primitive *Zamia furfuracea*, outgrowths are formed which penetrate cells of the female tissue. These pollen tubes are not involved in transmission of the male gametophyte. Choi and Friedman (1991) suggest that pollen tubes originally had the function of acquiring resources from the maternal tissue. Possibly the germination of pollen grains in primitive species elicited typical host–pathogen responses in the recipient plant. Only in more advanced groups (such as flowering plants) does the recipient tissue assist in pollen tube growth and development. This has laid the ground for a

more specified selection on resource allocation from the pistillate tissue.

Results from *Petunia hybrida* as well as from wild radish show that immature pistils are less discriminating, indicating that male mating success is indeed influenced by the pistillate environment (Cruzan, 1993; Marshall, 1998). When the pollen grains germinate they are dependent on their own nutrients. As the pollen tubes continue to grow, however, they become dependent on the resources available in the style (Herrero & Hormaza, 1996). The recipient plant thus has the potential to interact with growing pollen tubes. The transmitting tissue may also direct the growth of pollen tubes to the ovules. Although controversial, observations suggesting mechanical, electrical, chemical and pollination-induced signals for pollen tube guidance have been reported (Cheung, 1995). Tiny latex beads applied to the stylar transmitting tissue in three different species moved at the same rate and in the same direction as pollen tubes (Sanders & Lord, 1989). This suggests maternal control of pollen growth in the style. In incompatibility systems, the pistil is known actively to constrain pollen tube growth of certain pollen (see also Richards, 1997). Even when there is no incompatibility, the pistil affects pollen tube growth by varying the timing and amount of nutritional support (Herrero & Hormaza, 1996). In peach *Prunus persica*, for example, the transmitting tissue at the base of the style is reduced (Herrero & Hormaza, 1996; Hormaza & Herrero, 1996a). This provides the pollen tubes with less resources and space and thus leads to increased pollen competition. The fastest growing pollen tubes will deplete the resources available.

A transmitting tissue-specific (TTS) glycoprotein has been found that influences nutrition of pollen tubes in *Nicotiana tabacum* (Cheung, Wang & Wu, 1995). The amount produced is genetically determined. Differences between individuals can then explain certain observations where pollen performance is a result of maternal genotype (Herrero & Hormaza, 1996). High TTS production could increase the relative pollen tube growth rate and thus augment the difference between pollen. This trait could then respond to selection on the recipient plant's ability to sort between donors.

Another way the pistil can affect pollen competition is through the timing of maturation of the pistil (Herrero & Hormaza, 1996). In some species, the stigma matures after the flower has opened. Even when pollen is deposited over a period of time, the pollen tube 'race' will then be synchronized. A

similar effect occurs when there is a threshold number of pollen grains needed for germination to begin.

The ovary has also been proposed to play a role in pollen-style interactions (Mulcahy & Mulcahy, 1985). Nutritional support for pollen tube growth is provided inside the ovary (Herrero & Hormaza, 1996). It is not always the first ovule in the ovary that gets fertilized. In wild radish *Raphanus raphanistrum* there is evidence of mechanisms that non-randomly sort pollen tubes to different ovule positions (Hill & Lord, 1986). In this species, the pollen tubes sometimes fail to achieve fertilisation because they grow past all available ovules (Marshall & Folsom, 1991; Herrero & Hormaza, 1996).

(7) The four requirements for evolution of female preference

(a) Assessment of genetic quality

Genetic quality must be advertized in a way that the recipient plant can assess. In other words: the pollen trait that increases siring ability should mirror the genetic quality of the pollen grains. Note that female choice, whether in animals or plants, does not imply a cognitive process (Kirkpatrick & Ryan, 1991). An overlap in the genetic expression between the gametophytic and sporophytic phases of the plant life cycle is generally found (Mulcahy, Mulcahy & Searcy, 1992; Walsh & Charlesworth, 1992; Hormaza & Herrero, 1994; Hormaza & Herrero, 1996*b*). Both phases exhibit a similar behaviour in response to external agents (Hormaza & Herrero, 1994). *Lolium rigidum* pollen expresses the same herbicide resistance in both phases in two out of three cases (Richter & Powels, 1993). Selection on pollen in inbred lines of maize during four generations improved pollen performance *in vivo* (Ottaviano *et al.*, 1988). If the same genes regulate growth in the two life phases, pollen grains that are fast growing not only come from vigorous donors but could also produce offspring with a high sporophytic growth rate (Mulcahy, 1971). Pollen tube growth rate increased with the quality of the donor (measured as seed production) in hermaphroditic violets (Skogsmyr & Lankinen, 2000).

(b) Advantage of developing a preference

Pistillate flowers that increase the chance that the ovules are fertilized by competitive pollen should, as a result, also increase the quality of their seeds. The stigma and pistil provide the arena for pollen

competition making it possible for a recipient plant to affect the intensity of competition. This intensity depends on the distance the pollen tubes have to grow, the number of pollen grains in relation to the number of ovules and when the pollen grains get deposited on the stigma in relation to one another (Mulcahy & Mulcahy, 1987). When pollen competition is intense only superior pollen grains have a chance to fertilize the ovules.

Offspring quality often increases with intensity of pollen competition (McKenna & Mulcahy, 1983; Winsor, Davis & Stephenson, 1987; Winsor *et al.*, 2000; Bertin, 1990; Quesada, Winsor & Stephenson, 1993; Palmer & Zimmerman, 1994; Björkman, 1995; Mitchell, 1997; Johannsson & Stephenson, 1997; but see Snow, 1990, 1991). There can be several reasons for this, that are unrelated to individual competitive ability of the pollen donors. For example, the increased number of pollen grains/donors could lead to the avoidance of incompatibility effects and inferior pollen.

A few of these studies have also found a positive correlation between pollen performance and offspring vigour. To study the effect at an individual level it is important to use the average pollen performance (of a given individual) since this is the selected unit (Snow & Spira, 1996). Mulcahy (1971) found that more vigorous pollen donors in maize produced offspring of a higher quality. Paternal effects on seed weight have been found in *Raphanus sativus* (Marshall & Whittaker, 1989) and *Betula pendula* (Pasonen, Pulkkinen & Käpylä, 2001), although the exact relation to lifetime fitness of the offspring in these species remains unclear. In *Viola tricolor* (Skogsmyr & Lankinen, 2000), however, there was a direct correlation between competitive siring ability (and pollen tube growth rate) and offspring seed production.

When studying selection of pollen donor quality it is important to separate effects of pollen load size from paternal gamete effects in studies on offspring quality, i.e. pollen load size should be held constant (Charlesworth *et al.*, 1987; Walsh & Charlesworth, 1992). Other factors requiring control are differential abortion, negative trade-offs between seed numbers and seed size and the condition (e.g. age) of pollen from different donors (Walsh & Charlesworth, 1992). Lyons *et al.* (1989) suggest that complete factorials and diallele crosses are desirable when studying plant fertilization characteristics. This design makes it possible to distinguish between maternal and paternal effects and gives a very precise estimate of the various mechanisms involved.

These benefits, however, come at the cost of the number of individuals that can be included. A complete factorial cross including two donors and recipient plants of two types (genotypes, phenotypes or lines) necessitates 25 crosses (Lyons *et al.*, 1989). The number of crosses increases rapidly with the number of individuals included. This approach is thus not suitable when the aim is to get a general picture of relationships between specific traits and, e.g., pollen donor vigour, in a population. In these cases, more information will be gained by using randomized crosses and including as many individuals as possible (Darwinian crossing design, Charlesworth *et al.*, 1987). To study this kind of relationship it is important to include the whole range of variation of both traits. By choosing mates randomly for each cross (and using many different individuals) the chance is high that much of the variation is represented. For the same number of crosses, the factorial crossing design only investigates a limited part of the range (i.e. only a few individuals) since each individual must be included in many crosses. Although the Darwinian approach tells us little about the exact relationship between two given individuals in a population, the randomized crosses should cancel out any bias introduced by specific interactions between certain mate combinations (Snow, 1994).

It has further been suggested that the increased vigour of offspring can be a result of the maternal plant allocating more resources to the first sired ovules (Delph, Weinig & Sullivan, 1998). In *Silene vulgaris*, Delph *et al.* (1998) defoliated plants to produce pollen donors with slow-growing pollen tube growth rates. They applied pollen from a 'slow' pollen donor some time before a 'fast' donor to allow the slow donor to fertilize the first ovules. In this case, there was a significant effect of fertilization time on seedling biomass. Delph *et al.* (1998) thus argue that differences in vigour resulting from differences in pollen tube growth rate are a result of how the maternal plant allocates resources.

(c) Heritability of genetic quality

Pollen performance should be heritable or indicate heritable sporophytic quality (Marshall & Whittaker, 1989; Snow & Spira, 1991*b*). Pollen performance could, in a more general sense, mirror the genetic quality of the pollen donor, i.e. be condition dependent (for definition see Section II.2). In animals, many sexually selected traits have been found to be condition dependent (Kodric-Brown &

Brown, 1984; Johnstone, 1995). The offspring can then inherit the general vigour of the pollen donor, rather than a specific trait. The expression of the trait used as a cue for mate choice depends on both the genetic make-up of the pollen donor and environmental circumstances (both past and present). A fast-growing pollen tube can thus indicate e.g. drought tolerance in dry conditions or the ability to withstand lower temperatures in a shady habitat. In this case, it is not a question of direct overlap between the traits expressed at the haploid and diploid level. Instead, pollen tube growth rate is an indication of how well a genetic individual fares in its current environment (compare to Hamilton & Zuk, 1982). This would mean that the cue for mate choice (pollen tube growth rate) stays the same even when the 'good genes' vary depending on environmental variation in time or space. A similar mechanism has been proposed for certain ornaments in animals (see Section II.2*a*). Selection for the pistillate function to sort between pollen donors with different pollen tube growth rates will then be continuous even if the genes that are beneficial vary with time and/or space. This mechanism will override the problems caused by genetic fixation of 'good genes' (Mulcahy *et al.*, 1996; Delph *et al.*, 1997).

(d) Variation in preference

The ability to sort among mates should vary between individuals (Richards, 1997). So far very few studies have addressed this question. In silver birch *Betula pendula*, however, differences in pollen tube growth rates between donors depended on recipient plants in compatible crosses (Pasonen *et al.*, 1999). The ranking between donors, however, stayed the same. If fast-growing pollen tubes reflect quality, the recipient plants that produce the largest differences should have a greater chance to be fertilized by the superior pollen. Variability in pistil length or size ought to lead to differences in the ability to segregate between pollen with different tube growth rates. Although we have not found a study on the variation in pistil length or size, in *Asclepias syriaca*, Morgan and Schoen (1997) found enough variation in stigmatic traits to have a significant effect on pollinia insertion.

(8) Selective abortion

In many instances plants produce more ovules than they can afford to mature (Lee, 1984). An example

is *Phaseolus coccineus*, where potentially viable seeds are regularly aborted (Rocha & Stephenson, 1991). Since this production is costly it should infer a benefit for the plant. One benefit could be that plants are unable to judge resource availability later in the season. Plants that have a reserve of initiated fruits could then produce a higher number of offspring than plants that only initiate fruit in relation to the amount of resources available at the beginning of the season (Stephenson, 1992). Most abortion, however, is known to occur very early during seed development (Stephenson, 1992). Another reason for initiating more fruits could be that competition between zygotes might lead to selection of the most fit offspring (Marshall & Folsom, 1991). There is considerable evidence indicating that plants abort seeds or fruits selectively (Bookman, 1984; Lee, 1984; Casper, 1988; Rocha & Stephenson, 1991; Niesenbaum, 1999). Some studies have also found increased progeny vigour through selective abortion of seeds or fruits (Stephenson & Winsor, 1986; Marshall, 1988; Casper, 1988; Rocha & Stephenson, 1991). Stephenson and Winsor (1986) for example, compared natural and experimental (random) abortion on inflorescences of *Lotus corniculatus*. The naturally aborting inflorescences not only contained significantly more seeds per fruit but also produced offspring of higher viability. Progeny fitness in *Erythronium grandiflorum* was enhanced after pollinations with more pollen donors (Cruzan & Thomson, 1997). Observations of pollen tube growth rate indicate that this was probably a result of seed abortion. Abortion can also occur when the embryo is defective, e.g. resulting from self-incompatibility (Wiens *et al.*, 1987). This raises the question of whether abortion is simply a way to eliminate defective embryos or is, in fact, a more delicate form of sorting among paternal genomes.

The maternal plant can again provide an arena for contest competition to take place (as in the case of female choice on pollen competitive ability). This time, however, it is not solely the genes originating from the donors that are compared but rather their interactions with genes from the maternal plant. To separate these phenomena from effects of different kinds of incompatibility it is important to use compatible individuals and avoid self-pollinations.

In self-fertile *Chamaecrista fasciculata* variation in resource allocation to embryos was determined by the seed parent without any effect of the pollen donor (Fenster, 1991). Pollen donors only differed in resource allocation due to self *versus* non-self pollinations. In *Raphanus sativus*, on the other hand,

pollinations with mixed-donor pollen loads resulted in less fruit abortion and also higher seed mass compared to single-donor pollen loads (Marshall, 1988). There was further an increased allocation of resources to branches with higher offspring diversity (Marshall & Oliveras, 1990). Havens and Delph (1996) demonstrated that siring success was affected by selective abortion in the gametophytic incompatible *Oenothera organensis*. The proportion of ovules fertilized by a certain donor in two-donor crosses differed significantly from the proportion of seeds sired by the same donor. In other words, the plant allocated proportionally more resources to the progeny from one donor. All individuals in this study were half-compatible. Non-random seed and fruit abortion due to preference for certain mates has also been shown in *Asclepias speciosa* and *Erythronium grandiflorum* (Bookman, 1984; Cruzan, 1990*b*), both species with incomplete self-fertilization. In the study on *Asclepias speciosa*, individuals from seven populations were used (Bookman, 1984). Although the results suggest no genetic relatedness between donors and recipients, this does not exclude heterosis effects between populations. Cruzan (1990*b*) showed that pollen grain size of donors affected abortion rates following two-donor pollinations in *Erythronium grandiflorum*. When donors differed in pollen size the abortion rate for seeds sired by the donor with smaller pollen grains was increased. Seed production was further decreased when both donors had large pollen. This indicates that seed abortion is influenced by paternal differences expressed through competition for maternal resources among the developing seeds.

In wild radish, plant condition affected mating patterns (Marshall & Fuller, 1994). Water-stressed maternal plants appeared to be less discriminating (Marshall & Fuller, 1994; Marshall & Diggle, 2001). Thus, maternal effects on the outcome of male competition might increase when resources are limiting.

In naturally pollinated *Lindera benzoin* plants, pollen tube number in the pistil was positively correlated to the probability of fruit maturation (Niesenbaum & Casper, 1994). In this study, fruit abortion was not a result of unfertilized ovules or incompatibility reactions, which indicates selective maturation of fruits produced under more intense pollen competition. Stressing the plants led to increased abortion rate, even though it did not increase selectivity based on pollen tube number (Niesenbaum, 1996). Instead the fruit's position on the branch seemed more important for the abortion

probability. Fruit position also influenced abortion in the deciduous tree *Sophora japonica* (O'Donnell & Bawa, 1993). The pattern of seed abortion followed the sequence of fertilization. Those seeds that were sired by the fastest microgametophytes also had the highest probability to be matured.

In summary, resources are often allocated to seeds in relation to the quality of the zygotes. This quality is not only a result of the accuracy of the meiotic processes, but can also, at least in some instances, be interpreted as a result of the genetic quality of the pollen donor. It is therefore feasible that seed parents having structures that increase the competition between the offspring will produce more fit offspring than seed parents that allocate resources irrespective of offspring competitive ability. This ability, however, remains to be closely studied.

IV. BORDERLINE ISSUES

(1) Sexual selection or parent–offspring conflict?

Even when plants develop seeds fertilized by certain individuals, the choice will most often be based on endosperms or embryos (Queller, 1994). In this sense, the interaction can also be viewed as a conflict between a parent and its offspring (Mazer, 1987a; Shaanker & Ganeshiah, 1997). Friedman (1995) has studied the development of the endosperm and 'double fertilization' in ancestors of the angiosperms. He suggests that the endosperm developed as an outcome of kin selection on the two embryos resulting from a primitive form of 'double fertilization'. The 'altruistic' embryo allocates all its resources to the sibling embryo. As a result the receiving embryo will have a low risk of being aborted relative to 'selfish' embryos. For this resource allocation to be selected, the risk of being aborted must be at least twice as high for the 'selfish' embryos. Friedman (1995) further shows that the triploid condition of the endosperm is a later development. These phenomena can also be regarded in the light of conflicts between the sexes: the female is selected to increase the number of egg cells in a gametophyte that will only mature one embryo. As a result the competition between zygotes increase. The pollen donor can then be selected to produce multiple sperm to ensure that 'his' offspring are not aborted. The resource allocation by the 'altruistic' endosperm can initially be regarded as further selection on the male to distort competition. The addition of a second female nucleus to the endosperm could then be selected to

increase female control over nutrition of the embryo (see also Härdling & Nilsson, 2001).

Seed abortion has been suggested to result from sibling rivalry, i.e. competition among the fertilized zygotes for development and survival (Wiens *et al.*, 1987; Arathi *et al.*, 1996; Shaanker & Ganeshiah, 1997). Sibling rivalry could be manifested by the developing embryos producing harmful chemicals or hormones (Arathi *et al.*, 1996). It could also occur by fertilized ovules altering the sink capacity in order to get a higher amount of resources and thus leaving the other ovules to starve (Wiens *et al.*, 1987). The occurrence of sibling rivalry does not necessarily imply that there is a conflict between parent and offspring (Willson & Burley, 1983). When this competition reveals the relative offspring quality it may in fact be advantageous to the parent.

Male–female conflict and parent–offspring conflict can in many cases be difficult to separate (Queller, 1994). Both processes have similar underlying causes and very often exhibit identical results. An interesting aspect in this context refers to genomic imprinting, i.e. when the expression of alleles differs depending on if they are inherited from the mother or from the father. In *Arabidopsis thaliana*, for example, genes that are imprinted by the pollen donors (and silenced in the maternal genome) increase the size of the seeds (Scott *et al.*, 1998; Adams *et al.*, 2000). Genes that are maternally imprinted, on the other hand, reduce this size. This difference could evolve through divergent selection on paternal and maternal genomes in the embryo (Moore & Haig, 1991). In the presence of such imprinting, parent–offspring conflicts will often turn out to be a special case of male–female conflicts (Queller, 1994).

(2) Incompatibility and 'good genes'

In the wake of the run-away hypotheses there seems to be a tacit supposition that sexual selection is always directional (e.g. Charlesworth *et al.*, 1987; Willson, 1994). In situations where (groups of) females differ in their preferences, donors can have on average equal siring ability and there will be no directional selection. These circumstances will then often be regarded as a case of incompatibility rather than sexual selection. The mechanisms involved are then selected by natural selection where inbreeding avoidance is the primary force.

Mating in plant species with incompatibility shows a marked similarity with mate choice based on the major histo-compatibility complex (MHC) in

animals (Potts & Wakeland, 1993). There are also genetic similarities between the MHC in animals and the genetic construction of incompatibility in plants. MHC is a part of the DNA in animals that is closely related to the immunity system (Wedekind, 1994).

In many reviews on sexual selection there seems to be an implicit assumption that good genes are uniformly beneficial whatever the (genetic) environment. This can be true in some circumstances, for example for certain simple resistance genes (as long as the occurrence of the disease is high enough to compensate for the cost associated with expressing the gene). In most circumstances, however, life-history traits are governed by complicated gene complexes where the expression is dependent on the alleles in both loci of a diploid organism (Price & Schluter, 1991; Rowe & Houle, 1996). A female should then choose a gene donor depending on her own genome. In other words, the 'good genes' and hence female preference, differ between individuals (Tregenza & Wedell, 2000). Further, 'good genes' might also be taken to mean 'not bad genes', i.e. females are selected to avoid certain males. In this case, there will be no difference between inbreeding avoidance and selection for good genes. Males will then compete with others in the subgroup of males that are 'suitable' for a given female. The selection on males to avoid inbreeding should furthermore be less intense than for the female function: when deposited on a stigma the pollen cannot gain anything by not fertilizing an ovule. Even so, in these cases the intensity of competition, and hence that of sexual selection, will be comparatively low. Through this reasoning we suggest that incompatibility systems can also provide interesting information about the mechanisms involved in female choice, provided that there is a focus on the individual level.

V. CONCLUSIONS

(1) We review the theory of sexual selection and its potential application to plants with special reference to empirical studies of reproductive traits.

(2) We suggest that sexual selection should be defined as a subset of natural selection distinguished only in that it concerns the interaction between members of one sex with regard to their relationship with the opposite sex. This includes all traits that evolve as the result of competition over quantity or quality of mates. As soon as there exists a difference in the ability either to attract mates or to choose a

suitable mate, this ability will be selected until the benefit is counteracted by a cost that acts on another trait important for reproductive output. The usefulness of this definition is that it is close to what the biological community at large infer from the term and allows for an interchange of ideas between scientists studying different aspects and intensities of sexual selection. The focus has then shifted from an explanation of exaggerated traits to that of understanding the interactions and conflicts arising from the production of individuals with two sets of genetic origin. The division will not primarily be between natural and sexual selection but between the study of sexual selection and that of sexual and parent-offspring conflicts.

(3) The fundamental aspects of sexual selection such as competition over mates, matings and fertilizations are clearly present in plants. It can be argued though, that female choice in plants is not a result of sexual selection. At the diploid level, females do not choose their mates (but they can compete for pollinators) and at the haploid level they do not compete. Even if the ability to sort out superior pollen can be selected, this ability does not hinder other females from making the same choice. Even so, many of the underlying mechanisms for the evolution of female choice are the same for plants and animals. In both kingdoms, female choice *per se* drives the sexual selection of males.

(4) One objection to the idea of sexual selection in plants has been that the theory of sexual selection is inapplicable to hermaphrodites (Willson, 1990). As Charnov (1979) and Morgan (1994) point out, however, the basic processes of sexual selection are the same, even if the evolution of secondary sexual characters in hermaphrodites is limited to some extent.

(5) Another objection concerns the fact that outcrossing plants are dependent on external pollen vectors for their reproductive success. Thus, plants have to rely on pollinator choice for the evolution of secondary sexual characters before pollination. Although this imposes limits as regards a run-away response in flower morphology, since the preference genes and the male trait can not get coupled, it does not hinder individuals from competing for acquisition of matings through floral traits.

(6) That mating occurs through an intermediary does not affect what takes place after pollination. This is also where most opportunities for mate choice in plants occur (Queller, 1987; Marshall & Folsom, 1991). In general, it is more difficult to distinguish sexual selection from natural selection in processes

occurring after insemination/pollination or fertilization, than before (Stephenson & Bertin, 1983; Eberhard, 1996). Separating male competition and female choice is also more difficult at this stage (Arnold, 1994). These complications clearly do not eliminate the potential for competition over mates, either in plants or in animals. Another problem is that not enough is known about the level of information available to maternal plants (Marshall & Folsom, 1991). To understand the possibilities for choice, detailed information about patterns and variation in fertilization and embryo development is needed. Nevertheless, this seems to be more of a practical problem than a conceptual one.

(7) Much can be gained through a dialogue between botanists and zoologists. There are several similarities between sperm competition/cryptic female choice in animals and pollen competition/female choice in plants. Many of these mechanisms can only be studied by killing the experimental organism (or a part of it). These phenomena are thus more readily studied in plants. Given the modular organization of plants it is easier both to do experiments on only part of an individual (which makes it possible to separate genetical and environmental effects) and to clone individuals. The latter is of special interest when gene–environment effects are studied. It would be a pity if semantic conflicts hindered us from using these advantages in our endeavours to understand how sexual selection acts at all ploidy levels.

(8) When considering the number of previous review articles summarizing the research on sexual selection in plants (e.g. Willson, 1979, 1990, 1994; Stephenson & Bertin, 1983; Queller, 1987; Charlesworth *et al.*, 1987; Lovett Doust & Lovett Doust, 1988; Lyons *et al.*, 1989; Lovett Doust, 1990; Snow, 1994; Furlow, 1999) it is amazing that the subject remains controversial (e.g. Grant, 1995; Richards, 1997). Even though there is, at present, a large amount of empirical evidence that sexual selection can act on plants, many scientists are against this interpretation. From a mechanistic perspective, which seems to be the view taken by many botanists, the focus lies on populations or groups within populations. An evolutionary outlook needs to redirect the interest to the individual level. If the debate is going to be solved, we need to at least tentatively accept the idea that sexual selection may act on plants. This will give rise to a different set of questions and experiments, without which we will never know the answer to the question of whether the theory of sexual selection is applicable to plants.

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