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## SPATIAL SEGREGATION OF THE SEXES OF DIOECIOUS PLANTS

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Several studies have demonstrated the existence of ecological differences between males and females in populations of dioecious plants, especially the spatial segregation of the sexes along some environmental gradient (Dodson 1962; Grant and Mitton 1979; Wade et al. 1981; Lovett Doust and Cavers 1982). Some of these studies concluded that such differences are evolved responses to competition between males and females (Freeman et al. 1976; Cox 1981; for studies that did not, see Fox and Harrison 1981; Waser 1984), and these differences are often referred to as "niche partitioning" or "niche differentiation" (Onyekwelu and Harper 1979; Vernet and Harper 1980; Cox 1981; Melampy 1981; Vitale and Freeman 1986; Lovett Doust et al. 1987). Some studies have suggested that the spatial segregation of males and females is evidence that the reduction of competition between the sexes can be important in the evolution of dioecy (Freeman et al. 1976; Willson 1979; Cox 1981; Lovett Doust et al. 1987).

In this paper, we address the following questions.

1. What proximate mechanisms are capable of causing spatial segregation of the sexes (SSS)?
2. What selective factors might favor the evolution of SSS through one of these proximate mechanisms? Is competition between males and females one of them?
3. What evidence is there that any observed cases of SSS are adaptive?
4. What information is necessary to determine whether an observed instance of SSS represents an evolved response or a nonadaptive one? In particular, what is needed to demonstrate that the existence of SSS in any particular case is an example of niche partitioning?

## PROXIMATE MECHANISMS AND SPATIAL SEGREGATION

Differential mortality of males and females in different environmental patches can cause spatial segregation of the sexes, and differences in the reproductive biology of the two sexes can be the source of such mortality. Successful reproduc-

tion can be more costly for one sex than for the other; apparently, this is a common phenomenon (Putwain and Harper 1972; Lloyd and Webb 1977; Wallace and Rundel 1979; Hancock and Bringham 1980; Conn and Blum 1981; Gross and Soule 1981; Bullock 1984; Vitale and Freeman 1986). The reproductive allocation of one sex can occur at a more stressful time, making reproduction *effectively* more costly for that sex (Freeman et al. 1980*b*). In either case, individuals of the sex incurring the higher cost may suffer higher mortality in relatively stressful microhabitats; that is, we would observe some degree of SSS (Lloyd and Webb 1977; Meagher 1980). Individuals of some species may be able to avoid this higher mortality by adjusting their reproductive output to the amount of resources available; others may not. There have been numerous reports of sex-differential mortality (see references in Lloyd and Webb 1977).

A second mechanism capable of generating SSS is sex choice, the ability of individuals to vary their sex according to their physiological condition or environment (Charnov 1982). Dioecious plant species with this ability are thus either truly dioecious (if sex expression, once "decided," remains fixed) or only apparently so (sequentially hermaphroditic, if the "decision" to perform as one sex or the other is reversible). To produce SSS, sex choice must depend on site quality, either directly or through the effects of site quality on plant vigor or size. Sex expression has been found to depend on site quality in some orchid species (Dodson 1962; Gregg 1975; J. Zimmerman, unpubl. data) and in cultivated spinach (Freeman and Vitale 1985), but in the few other species for which sex choice has been carefully documented, sex is determined by plant vigor, size, or age, not site quality (Bierzychudek 1982, 1984*a,b*). Although sex choice according to environmental conditions has been posited for numerous other plant species (Freeman et al. 1980*a*), most of these reports are anecdotal; the real frequency of sex choice in plants is still unknown.

SSS could also be produced if females at different sites can skew the sex ratio of their progeny in opposite directions. Maternal adjustment of the sex ratio is well documented for some haplodiploid arthropod species (Charnov 1982) and may occur in vertebrates (Clutton-Brock 1985), but it has not been reported for plants.

A fourth mechanism by which plants might achieve SSS is through active habitat selection. Habitat choice by male and female plants could occur through male and female propagules with different dispersal properties or through directed vegetative growth. We know of no examples of the former. Preferential colonization of certain microsites has been demonstrated for one clonal plant species (Salzman 1985), but the generality of this phenomenon is unexplored. Even if habitat selection were common among plants, this mechanism could explain SSS only on an extremely local scale (the size of an individual genotype) and only for species capable of vegetative spread.

Finally, SSS could be generated if male and female seeds have different germination requirements. This mechanism would require differential mortality by sex across environments at the time of seed germination. We are aware of no reports of different germination requirements of male and female seeds. Of course, it would be extremely difficult to gather evidence for such a phenomenon, since *seeds* cannot ordinarily be sexed, certainly not nondestructively.

## SELECTIVE FORCES FAVORING SPATIAL SEGREGATION

Consider a dioecious population in a spatially heterogeneous environment. If male fitness and female fitness do not respond in the same way over the set of environmental patches, then selection favors the occupation of a given patch by individuals of the sex that is relatively more fit in that patch, or, in other words, SSS (Charnov and Bull 1977; Charnov 1982). If individuals have control over which type of patch they enter (or if parents have control over the patch type their offspring enter), then selection favors habitat selection by sex; if there is no such control, then selection favors sex choice (Charnov and Bull 1977; Charnov 1982). Since, as mentioned above, the ability of plants to exercise habitat choice is limited, sex choice should be favored in populations in which these conditions apply. This suggests one pathway by which dioecy might evolve, accompanied by SSS. For a population in a heterogeneous environment, if the gender (relative allocation to male and female functions) with the highest relative fitness is 100% male in some patches and 100% female in others, the evolution of dioecy is predicted, with individuals choosing sex expression according to the environment to which they are dispersed (Freeman et al. 1980*a*). For a species in nature that exhibits SSS by sex choice, however, it may still not be possible to determine whether SSS accompanied or followed the evolution of dioecy.

We have already discussed how different environmental patches could confer differential mortality on males and females. Different patches could also differentially affect the fecundity of males and females. The kinds of stresses (drought, nutrient scarcity, low light levels) that can cause sex-differential mortality could also result in sex-differential reproductive success (Vitale and Freeman 1986), especially if reproduction for one sex involves high fixed costs. Male and female reproductive success could co-vary inversely across habitats for other reasons as well. It has been suggested, for example, that in some wind-pollinated dioecious species, male success may be higher on windy slopes than in valleys (because of more-effective pollen dispersal), whereas female success may be relatively higher on lower-lying sites (where pollen may accumulate, or where soil is relatively moister during seed and fruit maturation) (Freeman et al. 1976). The average fitness of males and females in these situations could be increased by SSS. In this way, differences in reproductive biology between males and females could cause sex-differential mortality and/or fecundity across environments, selecting for SSS via some proximate mechanism.

In contrast to the effects of environmental heterogeneity on male and female fitness, intraspecific competition between the sexes has often been cited, explicitly or implicitly, as the selective force responsible for SSS (Freeman et al. 1976, 1980*b*; Cox 1981). Can such competition favor spatial segregation?

On the average, in the absence of SSS, one-half of an individual's conspecific competitors are of the opposite sex. Conceivably, natural selection could favor traits that decrease the extent to which males and females compete with one another, such as a means of spatial segregation. However, spatial segregation (or any other ecological difference between the sexes) does not reduce competition between individuals of the same sex (Ghiselin 1974). Therefore, SSS would be

avored only if the deleterious effects of competition between males and females are more severe than those of competition between individuals of the same sex. This seems unlikely, given the ecological similarity between individuals of the same sex. Indeed, Putwain and Harper (1972) and Wade (1981) have demonstrated greater interference between plants of the same sex than between plants of opposite sex. Competition between the sexes seems a priori an unlikely ultimate cause of SSS.

Sex-differential mortality by habitat can clearly cause nonadaptive SSS and select for proximate mechanisms that achieve adaptive SSS (thus avoiding such mortality), but it is difficult to imagine how differential mortality per se could be favored by natural selection. Nevertheless, this has been proposed. Traditionally, arguments for the role of competition in the evolution of SSS have pointed to the benefit to survivors of the "voluntary death" of individuals dispersed to the wrong habitat, in this way invoking group selection (this flaw in the traditional argument was pointed out by Fox and Harrison 1981; Lovett Doust and Lovett Doust 1983). It follows from the limited ability of plants to choose what patch they enter that mortality levels in this situation would be substantial; any group advantage of the voluntary death of individuals would thus be strongly opposed by selection on individuals.

There is yet another constraint on the evolution of SSS by niche partitioning. To the extent that increasing the distance between individuals of the opposite sex reduces the likelihood that pollen reaches ovules, SSS can reduce the average reproductive success of both males and females (Bawa and Opler 1977; Meagher 1980, 1984; Cox 1981). Any benefit of reduced competition would have to be large enough to repay this cost.

#### INTERPRETING OBSERVED CASES OF SPATIAL SEGREGATION

Table 1 lists published and unpublished studies that have looked for SSS. The studies include temperate, tropical, and arctic species representing a variety of families and life histories. We have evaluated each of these studies in order to determine (1) whether SSS was actually observed, (2) the nature of the observed segregation, and (3) whether any evidence was provided that the observed pattern was the result of something other than differential mortality.

Of the 32 species for which quantitative evidence of SSS has been sought, spatial segregation was significant in 21, or 66%. This may indicate that patterns of SSS (from whatever cause, adaptive or not) are common among dioecious species. This high percentage, however, may result from an inclination on the part of biologists to study those species that appear to display interesting patterns or from a bias on the part of authors and editors to give publishing priority to positive results.

Of the 21 observed cases of SSS reported here, only 3 (14%) involved species known to possess a mechanism for generating habitat assortment by sex: *Arisaema triphyllum*, *Catsetum viridiflavum*, and *Spinacia oleracea*, all of which exhibit sex choice. Only a few studies sought evidence of the evolved nature of SSS (Fox and Harrison 1981; Waser 1984; Vitale and Freeman 1986); the data

TABLE 1  
SPATIAL SEGREGATION OF THE SEXES IN DIOECIOUS SPECIES

Species (Family)	SSS Observed: Pattern	Evidence of Evolved SSS	Source
<i>Acer negundo</i> (Aceraceae)	yes: more females at moister sites	no	Freeman et al. 1976
<i>Anisotome flexuosa</i> (Apiaceae)	yes: fewer females at "exposed" sites	no	Lloyd & Webb 1977
<i>Antennaria parvifolia</i> (Asteraceae)	no		Bierzychudek, Eckhart, and R. Smith, MS
<i>Arisaema triphyllum</i> (Araceae)	yes: more females at brighter sites	yes: sex choice	Lovett Doust & Cavers 1982
<i>Atriplex confertifolia</i> (Chenopodiaceae)	yes: more females at moister sites	no	Freeman et al. 1976
<i>Catasetum viridiflavum</i> (Orchidaceae)	yes: more females in open areas (brighter sites)	yes: sex choice	J. Zimmerman, un- publ. data
<i>Chamaelirium luteum</i> (Liliaceae)	yes: no obvious gra- dient (nearest-neigh- bor analysis)	no	Meagher 1980
<i>Compsonura sprucei</i> (Myristicaceae)	no		Bullock 1982
<i>Distichlis spicata</i> (Poaceae)	yes: more females at less saline sites	no	Freeman et al. 1976
<i>Ephedra viridis</i> (Ephedraceae)	yes: more females at moister sites	no	Freeman et al. 1976
<i>Fragaria chiloensis</i> (Rosaceae)	no		Hancock & Bringhurst 1980
<i>Fucus serratus</i> (Fucaceae)	no		Vernet & Harper 1980
<i>F. vesiculosus</i>	sometimes: more fe- males in "lower shore"	no	Vernet & Harper 1980
<i>Guarea luxii</i> (Meliaceae)	no		Bawa & Opler 1977
<i>Hesperochloa kingii</i> (Poaceae)	yes: more females at wetter sites	no	Fox & Harrison 1981
<i>Laretia acaulis</i> (Hydrocotylaceae)	yes: more males at higher elevations	no	Hoffmann & Allende 1984
<i>Mercurialis perennis</i> (Euphorbiaceae)	yes: more females at low-pH sites	no	Cox 1981
<i>M. perennis</i>	yes: more females at low-light sites	no	Wade et al. 1981
<i>Osyris quadripartita</i> (Santalaceae)	no		Herrera 1984
<i>Peumus boldus</i> (Monimiaceae)	yes: more males at drier sites	no	Hoffmann & Allende 1984
<i>Populus tremuloides</i> (Salicaceae)	yes: females decrease with elevation	no	Grant & Mitton 1979
<i>Randia spinosa</i> (Rubiaceae)	no		Bawa & Opler 1977
<i>Salix arctica</i> (Salicaceae)	yes: more females at mesic sites	no	T. Dawson, pers. comm.
<i>S. polaris</i> , <i>S. herbacea</i>	no		Crawford & Balfour 1983
<i>Silene alba</i> (Caryophyllaceae)	no		Lovett Doust et al. 1987

TABLE 1 (Continued)

Species (Family)	SSS Observed: Pattern	Evidence of Evolved SSS	Source
<i>Simmondsia chinensis</i> (Buxaceae)	no		Wallace & Rundel 1979
<i>S. chinensis</i>	yes: more females at wetter sites	no	Waser 1984
<i>Spinacia oleracea</i> (Chenopodiaceae)	yes: more males at higher densities	no	Onyekwelu & Harper 1979
<i>S. oleracea</i>	yes: more males in drier conditions	yes: sex choice	Freeman & Vitale 1985
<i>S. oleracea</i>	yes: more males in more-saline condi- tions	yes: sex choice	Vitale & Freeman 1986
<i>Thalictrum dioicum</i> (Ranunculaceae)	yes: no obvious gra- dient (nearest-neigh- bor analysis)	no	Melampy 1981
<i>T. fendleri</i>	yes: more females at wetter sites	no	Freeman et al. 1976
<i>T. polygamum</i>	yes: no obvious gra- dient (nearest-neigh- bor analysis)	no	Melampy 1981
<i>Triplaris americana</i> (Polygonaceae)	no		Bawa & Opler 1977
<i>T. americana</i>	no		Melampy & Howe 1977
<i>Trophis involucrata</i> (Moraceae)	yes: more females at high-phosphorus sites	no	Cox 1981
<i>Zanthoxylum setulosum</i> (Rutaceae)	no		Bawa & Opler 1977

collected by the majority of studies do not exclude nonadaptive differential mortality as a possible cause of SSS. Thus, it is unclear how frequently SSS in nature connotes adaptation. No study to date provides evidence that competition between the sexes is ultimately responsible for the patterns observed.

#### DEMONSTRATING NICHE PARTITIONING

The observation of ecological (or niche) differences between males and females in a dioecious population is not sufficient evidence of niche partitioning; this term implies that competition between individuals of the two sexes has favored the evolution of the observed ecological differences. Ecological differences between males and females exist whenever maleness and femaleness have different fitness consequences across habitats, independent of the effects of intraspecific competition. Ecological differences are expected to reduce the effects of competition, but this does not mean that competition explains why the differences exist.

Before the concept of niche partitioning (or resource partitioning, etc.) can validly be applied to cases of SSS in plants, three things need to be established. First, the observed SSS must be shown to be something other than simply habitat-dependent differential mortality by sex. If the amount of differential mortality is

insufficient to explain the observed pattern, the next step is to demonstrate the existence of a mechanism for adaptive SSS, such as habitat selection or sex choice, and to show that the fitness of males and females is enhanced by their segregation in space. But even if one were successful in demonstrating that a particular case of SSS was indeed the result of evolution, how could one be sure that it was actually an example of niche partitioning, that is, that it was an adaptive response to competition between the sexes? This can only be done experimentally. Males and females would have to be reciprocally transplanted to one another's preferred habitat. For each sex, three treatments are necessary: transplants with male competitors only; transplants with female competitors only (at approximately natural densities); and transplants without competitors (and thus at very low density). To rule out the possibility that the observed spatial segregation resulted from physiological differences between the sexes, one would need to observe that the fitness of transplants without competitors was no higher at their home site than at the opposite sex's site. To implicate competition between males and females as a selective force favoring SSS, the presence of competitors would have to depress fitness, and the presence of competitors of the opposite sex would have to depress fitness more than the presence of competitors of the same sex.

Such an experiment has never been done, and it would be more difficult than it appears. Ideally, one would want to observe the effect of competition on seedlings as well as on adults; however, most plants cannot be sexed until they flower. Thus, the sex of transplanted individuals that died before flowering could never be determined. A reciprocal-transplant experiment could also demonstrate whether sex choice occurs in the population under study. If sex choice is present, then assessing the effects of competition between the sexes may be impossible, because it might not be feasible to grow males and females in the same location: plants would develop into one sex in one location and into the opposite sex in the other.

We believe that most reported cases of SSS (whether adaptive or not) reflect differences in reproductive biology between the sexes rather than competition between them. Support for this belief can be found in the table, which summarizes the relative distributions of males and females with respect to particular environmental factors. In 17 of 18 instances, females are more common under what might be considered less stressful conditions: sites that are moister, less exposed, sunnier, less saline, lower in elevation, at lower conspecific densities, or at higher nutrient concentrations. This observation is consistent with the hypothesis that the most important cause of SSS is differences in reproductive biology; successful female reproduction is often more costly than male reproductive effort, which may lead to greater mortality under stressful conditions and to relatively greater gains in reproductive success in more-favorable environments (Freeman et al. 1980a; Charnov 1982). Both of these conditions select for habitat choice or sex choice; differential mortality can generate nonadaptive SSS. If the avoidance of competition between the sexes were the only force producing SSS, we could expect males and females to be equally likely to acquire the "better" niche.

Our conclusion is that competition between the sexes, if it plays any role at all in evolved cases of SSS, rarely operates alone; instead, it is likely to be accompanied by the more potent selective forces created by differences in reproductive biology. Indeed, to the extent that differences in reproductive biology indicate differences in the fundamental niches of males and females, competition should be less severe between the sexes than within a sex; this would select against SSS and thus oppose selection created by differences in reproductive biology. We urge that future studies of the spatial distributions of male and female plants (and of any other ecological features regarding the sexes) avoid inferring that SSS is adaptive or represents an evolved response to competition between the sexes, until confirmatory evidence is obtained.

#### SUMMARY

Several recent studies have shown that males and females in some populations of dioecious plants are spatially segregated with respect to an environmental gradient. The inference is often made that such spatial segregation of the sexes (SSS) is favored by selection because it reduces competition between individuals of opposite sex (sexual "niche partitioning"). This paper was written to clarify the evolutionary interpretation of cases of SSS. We describe the possible proximate mechanisms capable of producing SSS and evaluate their plausibility. Then, we identify the selective factors that could favor the evolution of SSS. We argue that SSS can be favored if male fitness and female fitness respond differently across environments (because of differences in reproductive biology), that a reduction in competition between males and females is unlikely to be an evolutionary cause of SSS, and that differential mortality is unlikely to evolve as a proximate mechanism for achieving adaptive SSS. Such a pattern is reported in 21 of 32 species studied, but this may overestimate its true natural frequency. Few studies have sought evidence that an observed pattern of SSS evolved in response to selection, and few have ruled out nonadaptive differential mortality as the cause of the pattern observed. No study to date has demonstrated that competition between males and females is ultimately responsible for SSS. We outline the design of the critical experiments that need to be done to implicate niche partitioning as an ultimate cause of SSS. The evidence currently available indicates that most reported cases of SSS (whether due to adaptation or differential mortality) are caused by differences in the reproductive biology of male and female plants.

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