

## THE EVOLUTION AND MAINTENANCE OF ANDROMONOECY

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**ABSTRACT:** The advantages and disadvantages of andromonoecy relative to hermaphroditism, monoecy and androdioecy were considered in light of data from red buckeye and other species. The advantage of andromonoecy over hermaphroditism seems to lie in more efficient resource allocation, with energy diverted from pistil growth and early fruit development to production of male flowers. This does not lower female fitness because fruit production is not limited by the number of functional pistils, and it may increase male fitness through donation of pollen to other plants. Monoecy may replace andromonoecy if male and female functions in bisexual flowers interfere with each other, as, for example, in some wind-pollinated species. Androdioecy is very unlikely to replace andromonoecy because the amount of resources that it is advantageous to invest in the female function is strongly affected by environmental conditions. Factors expected to be associated with andromonoecy include large fruits, many flowers per plant, and male and female functions compatible in bisexual flowers. Factors that could be associated with andromonoecy under specific conditions include visual attraction of pollinators, few stamens per flower, pollen vectors that feed on pollen, self-compatibility, and unpredictability of pollination.

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### Introduction

Among the several hundred thousand species of seed plants, perhaps 70% consistently bear bisexual flowers. Roughly 10-20% are monoecious (including andromonoecy and gynomoecy), about the same number are dioecious, and the remainder are of mixed or variable breeding systems (Yampolsky and Yampolsky 1922; Bawa 1974; 1979; Bawa and Opler 1975; Croat 1978). These figures are approximate because many species of seed plants have yet to be described, and because the breeding systems of some species are variable and difficult to categorize.

The relative advantages of dioecy and hermaphroditism have received considerable attention (Bawa and Opler 1975, 1977; Charnov et al. 1976; Ross and Weir 1976; Charlesworth and Charlesworth 1978a), but monoecious systems (including andro- and gynomoecy) have received less attention, despite their equal or greater frequency of occurrence. Many discussions of the evolution of monoecy (Grant 1975; Maynard Smith 1978) suggest that avoidance of inbreeding is of predominant importance. While the need for outbreeding may help in explaining the evolution of some breeding systems, it seems less useful in interpreting the evolution of monoecious systems (Lloyd 1979; Willson 1979; Primack and Lloyd 1980).

In this paper I evaluate several hypotheses concerning the evolution of andromonoecy (the presence of male and bisexual flowers on individuals of a species). I also demonstrate a possible means by which monoecy may have evolved in some species via andromonoecy.

### Evolution and Maintenance of Andromonoecy

Unisexual flowers are usually thought to be derived (evolutionarily) from bisexual flowers, and monoecy from hermaphroditism (Bessey 1915; Hutchinson 1926; Stebbins 1950; Lawrence 1951; Grant 1975). The presence of vestigial pistils in functionally male flowers of many andromonoecious species (Mukherjee 1953; Hardin 1956; Carr et al. 1971; Nevling and Elias 1971; Styles 1972; Tomlinson 1974; Nambiar 1977; Primack and Lloyd 1980) supports this view. I assume, therefore, that andromonoecy evolved

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from hermaphroditism. Hypotheses for the evolutionary origin of andromonoecy must, therefore, account for either the production of excess male flowers or the suppression of functional pistils in some flowers.

Potential evolutionary options for andromonoecious species include 1) return to the original hermaphroditic condition, 2) evolution of monoecy through suppression of stamens in bisexual flowers, and 3) evolution of androdioecy by genetically fixing male flower production in some plants and bisexual flower production in others. Hypotheses explaining the maintenance of andromonoecy must thus account for 1) the value of male flowers, 2) the absence of stamen reduction in bisexual flowers, and 3) the absence of male and bisexual functions genetically fixed on separate plants. I examine these three options in turn, with the first being essentially the same as considering the evolutionary origin of andromonoecy.

### Andromonoecy vs Hermaphroditism

#### Hypothesis I Inbreeding is Reduced

Heithaus et al. (1974:418) state that inbreeding in andromonoecious species is reduced because "functionally male flowers cannot be self-pollinated". This statement is true but does not explain the evolution or maintenance of andromonoecy. All functional pistils on an andromonoecious plant still occur in flowers that produce pollen, and self-fertilization is still possible unless other floral mechanisms have evolved to prevent it. This hypothesis addresses neither why male flowers increased in number nor why functional ovaries decreased. Charlesworth and Charlesworth (1978b), Lloyd (1979, 1980), Primack and Lloyd (1980) and Dulberger et al. (1981) similarly reject this argument.

#### Hypothesis II Pollen Deposition per Stigma is Increased

Heithaus et al. (1974), Benseler (1975) and Dulberger et al. (1981) suggest that increased pollen deposition will result from an increased ratio of pollen to ovules on a plant. They suggest that this may be important if vectors carry pollen on a large area of the body relative to the size of the stigma surface. Presumably the increased pollen/ovule ratio results in a greater buildup of pollen on the body of the pollinator, and greater deposition on each stigma. This idea can actually apply to any situation in which pollen deposited on stigmas of a plant is inadequate to allow maximum seed set.

These arguments seem to have limited applicability unless group (interdemic) selection is involved. Inadequate pollen deposition per stigma cannot directly select for increased pollen production on other individuals by individual selection, although it could select for increased pollen production within the same individual if increased geitonogamous (same plant) pollinations were advantageous. The fact that some andromonoecious species are self-incompatible (Ruiz-Zapata and Kalin Arroyo 1978; Symon 1979), and that various evolutionary options for ensuring self pollination of bisexual flowers are available renders this interpretation doubtful.

If the original arguments are framed in a slightly different way they may, however, be consistent with individual selection. The modified argument is that pollen production is increased because it enhances male reproductive success (because fruit set on other plants is pollen-limited). This option is considered under hypothesis 4.

#### Hypothesis III Predation of Ovaries and Fruits is Reduced

If some predators specialized on functional ovaries and/or developing fruit, plants bearing relatively few functional ovaries, in flowers scattered among male flowers, would probably attract fewer predators than those with a functional ovary in every flower.

This hypothesis predicts that bisexual flowers on inflorescences and/or plants with a greater percentage of bisexual flowers should suffer more predation than those

on inflorescences and/or plants with fewer bisexual flowers. Data from red buckeye (*Aesculus pavia*) do not support this prediction. In one population examined (Bertin 1980) bisexual flowers comprised 6-30% of all flowers on different plants and 7-47% of these flowers were eaten (on different plants), but no significant correlation existed between percent predation and percent bisexual flowers ( $r = 0.23$ ).

If this hypothesis is correct we might also predict that selection would very closely adjust bisexual flower production to fruit production. We would not expect to see the drop of many undamaged young fruits because selection would favor production of male flowers instead of bisexual flowers when fruit production is resource limited, to reduce the risk of attracting predators to the remaining bisexual flowers. In fact, several andromonoecious species consistently drop many healthy young fruits (Mukherjee 1953; Cobley 1956; Mallik 1957; Bigger 1960; Bertin 1980).

A final objection is that such simple "hiding" of bisexual flowers among male flowers seems unlikely to outstrip the evolution of detection mechanisms by insects.

#### Hypothesis IV Allocation of Resources is Optimized

Aspects of this hypothesis have been suggested by Ruiz-Zapata and Kalin Arroyo (1978) and by Primack and Lloyd (1980). The former authors state (p. 229) that andromonoecy involves "more efficient use of reproductive energy" because "female sterility... prevents unnecessary outlay of energy for initial fruit development, a large part of which cannot be matured". The cost differential between functional and vestigial pistils can also be included here. Primack and Lloyd (1980) suggest that andromonoecy might "be due to different spatial and temporal strategies for removing and depositing pollen". The problem can also be viewed in terms of sexual selection (Willson 1979), with competition between males (or male functions on different individuals) being much keener than female/female competition. The common theme in these arguments is that resources that would have been allocated to functional pistils (and preliminary fruit development) in hermaphroditic individuals will contribute more to reproductive success if they are placed elsewhere.

This hypothesis has two requirements. 1) A flower without a functional pistil must be cheaper to produce than a flower with a functional pistil. This will always be true because a reduced, nonfunctional pistil will always be less costly than a functional one. 2a) The reduced number of functional pistils should not reduce fruit production, or more strictly, any reduction in female fitness accompanying pistil loss should be compensated by the savings in resources that would have been put into functional pistils. 2b) A fitness increase should accompany production of male flowers that more than compensates for the resources invested into their production (and hence unavailable for other activities, such as maturing fruits). Because male and female functions in a hermaphroditic organism share a common energy budget, 2a and 2b are likely to be linked.

A decline in female fitness would accompany pistil loss if fruit production were limited by the number of bisexual flowers. Fruit production is not limited by pistil number in red buckeye, cashew (*Anacardium occidentale*) and mango (*Mangifera indica*) (Mukherjee 1953; Cobley 1956; Mallik 1957; Bigger 1960; Bertin 1980), apparently the only andromonoecious species examined in this regard. All abort many sound young fruits.

Fitness increases might accompany addition of male flowers if 1) they attract pollinators that would otherwise not visit the plants to pollinate the bisexual flowers (Lloyd 1979; Primack and Lloyd 1980; Dulberger et al. 1981) or 2) they enhance male fitness through pollen donation (Willson and Rathke 1974; Lloyd, 1979).

The former is amenable to test, and was examined in red buckeye by comparing pollinator visitation rates in inflorescences with their normal complement of male flowers to those in inflorescences from which all male flowers were removed (Bertin 1980). In 104 flower-hours of observation (one flower-hour = observation of one pair of bisexual flowers for one hour) there was no significant difference in pollinator visitation rates (0.16 vs 0.15 visits per hour). This does not demonstrate unequivocally, however, that male flowers are unimportant for pollinator attraction. The

conspicuous, red, flower buds were not removed from the inflorescences, and these may well serve in pollinator attraction. Most were male, though this cannot be determined by external observation. Additionally, the entire plant may be an important unit of pollinator attraction, in which case male flowers should have been removed from entire plants.

Primack and Lloyd (1980) consider an attractive function of male manuka (*Leptospermum scoparium*) flowers to be unlikely because pollinator activity does not limit fruit production. This argument is valid so long as the plant does not selectively abort fruit so as to produce only the best offspring (e.g. Janzen 1977). If plants do exercise much selectivity, as demonstrated by Bertin (ms) and Bookman (ms), it may be advantageous to attract more pollinators to allow greater selectivity in fruit abortion, even though the number of fruit matured may not increase.

If male flowers do function primarily in pollinator attraction, olfactory cues should be relatively unimportant in attraction of pollinators to andromonoecious plants, because a large olfactory stimulus would not require a large number of flowers. Red buckeye apparently does not use scent to attract pollinators, as no odor is detectable by humans, and hummingbirds, the primary pollinators of this species, apparently do not use olfactory cues (Proctor and Yeo 1972). Floral scents have, however, been reported in the cashew (Bigger 1960).

If attraction of pollinators rather than provision of more pollen *per se* is the primary function of male flowers, we would expect each flower to have relatively little pollen, perhaps having few stamens. Some andromonoecious species have relatively few stamens: buckeyes: 5-8 (Hardin 1957; Bertin 1980), mangos: 1-8 (Mukherjee 1953; Mallik 1957), cashews: 1-9 (Nambiar 1977), many umbellifers: 5, but at present we lack meaningful comparative data.

The importance of male flowers in pollinator attraction is not, therefore, presently clear. More information is needed on 1) effects of experimental removal of male flowers and 2) the importance of "extra" pollinations in determining offspring quality by allowing selective abortion.

The degree to which male flowers enhance the male fitness of a plant is difficult to demonstrate directly because of problems in tracing pollen flow from flowers in natural populations (but see Schlising and Turpin 1971; Linhart 1973; Handel 1976; Reinke and Bloom 1979 for possible methods). In red buckeye, however, consider that an average mature fruit weights about 15 g (dry wt). Furthermore, an average of about 20 bisexual flowers never produce a mature fruit for every one that does. Most of these drop with slightly swollen ovaries. Based on dry weights of developing ovaries of known sizes and knowledge of fruit abortion patterns (Bertin 1980), I conservatively estimated the dry weight of an average aborted fruit at 0.2 g. Twenty of these combined with one mature fruit would weight 19 g, or as much as about 500 male flowers. This admittedly crude estimate indicates that if seeds in more than one fruit on another plant could be fathered with the pollen of each 500 flowers on a given plant, then a greater genetic representation in the next generation would be obtained than if the plant nurtured one cross-pollinated ovary to maturity. The existence of self-fertilization would complicate this relationship, but the point is made that the production of even large numbers of male flowers could be a cost efficient way of increasing reproductive output.

Similar arguments could apply to several other andromonoecious species, which bear fruit that are large relative to flower size (other buckeyes, Mooney and Bartholomew 1974; Benseler 1975; cashew, Bigger 1960; manuka, Primack and Lloyd 1980; mango, Mukherjee 1953; *Solanum* spp., Symon 1979, Dulberger et al. 1981 and Umbelliferae, Lovett Doust 1980, Primack and Lloyd 1980). Data are presently inadequate, however, to make useful comparisons of fruit weights in andromonoecious species with those in species having other breeding systems.

In summary, while the requirements of the resource allocation hypothesis have not all been demonstrated, none is refuted by available data. Importantly, all points could be refuted by appropriate data if it were available. For the best-studied species (all woody, including buckeyes, manuka, cashew and mango), the fourth hypothesis seems the most reasonable of the four presented here. The other hypotheses are either logically unsound or are unsupported by circumstantial evidence from

the few species studied to date. Andromonoecy may have arisen for different reasons in different species, and studies of andromonoecious grasses, sedges, and umbellifers are badly needed.

#### Andromonoecy vs Monoecy

Retention of functional stamens in pistillate flowers could have at least four causes. First, self fertilization may be possible, if pollen vectors are inadequate. In red buckeye self pollen can be deposited on stigmas without the aid of vectors, and individuals are self compatible. However, no clear cases of effective fertilization were found in 97 bagged flowers that were allowed to self (Bertin 1980), suggesting that selfing may be unimportant. Bisexual mango flowers (Mukherjee 1953; Mallik 1957) and those of many andromonoecious umbellifers (Muller 1883; Cruden and Hermann-Parker 1977) also apparently do not self. These data and the occurrence of andromonoecy in some self-incompatible species (Ruiz-Zapata and Kalin Arroyo 1978) suggest that the need for self pollination is not often a factor selecting for retention of male function in pistillate flowers of andromonoecious species. Second, stamens may act as pollinator attractants (Lloyd 1979), though this has not been examined in andromonoecious species. Third, pollen may be needed in bisexual flowers if it is a reward for pollinators. Pollen is not a reward for hummingbirds, the most frequent visitors to red buckeye, but it is for bumblebees and anthophorid bees, the next most common visitor groups (Bertin 1980). A logical test of the importance of this function of pollen would be to compare frequency of visits to bisexual flowers with anthers removed with those to unmanipulated control flowers. Finally, a plant may simply be making more efficient use of fixed costs (e.g. perianth, nectar production; Charnov et al. 1976; Lloyd 1979) if both male and female functions are combined in some flowers rather than always separated.

Because of the savings of investment in fixed costs in bisexual flowers, an actual disadvantage to either male or female function would have to be demonstrated to account for the replacement of bisexual flowers by male and female flowers. Some wind-pollinated plants could fall into this category, because wind-blown anthers in small flowers would coat the stigmas with self pollen and reduce the likelihood of cross-pollination. Among the large-fruited, many-flowered trees of eastern North America (e.g. *Carya*, *Castanea*, *Fagus*, *Juglans*, *Quercus*) monoecy is in fact the predominant breeding system. Clearly monoecy is not the only option for avoiding such interference of male and female functions, however, as dichogamy or dioecy would also prevent interference. Further, many wind-pollinated grasses and sedges are andromonoecious (Yampolsky and Yampolsky 1922; Connor 1979), so wind pollination does not preclude this breeding system.

#### Andromonoecy vs Androdioecy

Androdioecy is the condition wherein some individuals in a population are male and some are bisexual, with gender genetically fixed. In several andromonoecious species some individuals bear only male flowers in one season (Benseler 1975; Primack and Lloyd 1980; Bertin 1980), but this is not androdioecy because individuals that do not bear bisexual flowers in one year may do so in another year (Bertin 1980).

Charnov and Bull (1977:828) suggest that labile sex determination (e.g. andromonoecy) is favored when "an individual's fitness (as a male or female) is strongly influenced by environmental conditions and where the individual has little control over which environment it will experience". Seed plants certainly have little control over their environment, having to grow wherever a seed is deposited. Female reproductive output of red buckeye is strongly influenced by the environment, especially light intensity (Bertin 1982). Female reproductive success is also influenced by the environment in other andromonoecious species, including manuka (Primack and Lloyd 1980), mango (Cobley 1956; Mukherjee 1953) and cashew (Nambiar 1977). Environmental effects on male fitness are unknown. Given these constraints it is difficult to see how androdioecy would be advantageous for any species of seed plant, a

conclusion similar to that reached by Lloyd (1975) and Charlesworth and Charlesworth (1978a,b, 1979), using different approaches. In fact, Yampolsky and Yampolsky (1922) found only 10 androdioecious species out of over 120,000 species examined, and conceivably even these might show some year to year variability in sex expression.

### Correlates of Andromonoecy

The discussion above can be summarized into a series of factors favoring either andromonoecy or other breeding systems.

1) Fruit that are large relative to flower size will favor andromonoecy or monoecy over hermaphroditism. Plants with large fruit are less likely to be able to mature one from every flower than plants with smaller fruit (and the same number of flowers), and therefore could reduce investment in functional pistils without lowering female reproductive success. Lloyd (1979) and Charlesworth and Charlesworth (1981) also suggested that andromonoecious plants are likely to have large fruit or seeds.

2) Large numbers of flowers per plant will favor andromonoecy or monoecy over hermaphroditism. Plants with many flowers are less likely to be able to mature a fruit from each flower than are plants with fewer flowers, and therefore could reduce investment in functional pistils without lowering female reproductive output. This and correlate 1 together can be restated that fruit production is limited by factors other than the number of bisexual flowers.

3) Incompatibility of male and female functions within a flower will favor monoecy over andromonoecy or hermaphroditism, e.g. Charnov et al. (1976).

If male flowers are important in pollinator attraction:

4) Autogamous species would bear all bisexual flowers.

5) Andromonoecy would not be expected in species that attract pollinators through non-visual cues (e.g. olfactory cues).

6) Andromonoecious species should have relatively few stamens per flower, because adding extra flowers with few stamens provides a bigger visual display than increasing the number of stamens in existing flowers, unless pollinators are preferentially attracted to flowers with many stamens.

If pollen in bisexual flowers functions in attracting pollinators to those flowers:

7) Andromonoecy should not occur in wind-pollinated species. The occurrence of andromonoecy in grasses and sedges indicates that pollen in bisexual flowers is often not important in pollinator attraction.

8) Pollinators of andromonoecious species should feed at least in part on pollen (as opposed to nectar). That some do not is evidence that pollinator attraction does not always explain the occurrence of bisexual flowers on andromonoecious species.

If pollen in bisexual flowers serves as a backup self-pollination system:

9) Andromonoecy would not occur in self-incompatible species.

10) Plants having a low probability of adequate pollination except by autogamy would be andromonoecious or bisexual, but not monoecious.

Two problems arise in this sort of attempt to predict the circumstances in which a particular breeding system will occur. First, there are often several ways in which a given end may be achieved, e.g. outcrossing may be enforced by physiological self-incompatibility, dioecy, or extreme dichogamy. Second, phylogenetic and/or historical peculiarities may affect the evolutionary options available to a species in ways that are not clear to us. Given these limitations, we can at best expect statistical, rather than absolute, relationships between breeding systems and particular morphological or ecological conditions. Of the conditions listed above, the first six are most likely to occur in andromonoecious species, with the last four conditional on certain features that we know for some species not to be true.

Andromonoecy thus appears to be one evolutionary response to fruits that are large relative to the size of flowers, and whose production is limited by factors other than the number of bisexual flowers per plant. High male flower production appears necessary either for pollinator attraction or to increase the likelihood of

fertilizing ovules on other plants. Most the data available on the reproductive biology of andromonoecious species comes from woody plants, and more data are needed to determine whether andromonoecy in herbaceous and wind-pollinated plants can be explained by similar reasoning.

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