

Reproductive role of sterile pollen in cryptically dioecious species of flowering plants

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Flowers of females from some species of dioecious flowering plants produce dysfunctional anthers or infertile pollen. Their cryptic dioecy has frequently been mistaken for androdioecy. Earlier insights into androdioecy were drawn from sexual allocation theory. However, several cryptically dioecious taxa share a common pollination syndrome, including nectarless but showy flowers that bear yellow, often porose anthers. These flowers are visited solely by female bees seeking pollen. For these cases, cryptic dioecy is explained by pollinator foraging behavior and not sexual allocation theory. Pollen as a nutritional reward to foraging bees is largely overlooked in current studies of pollination and foraging ecology.

ANDRODIOECY is a rare form of sexual allocation among flowering plants, wherein individuals bear either all staminate flowers (males) or all bisexual, morphologically perfect flowers (hermaphrodites). The possibility of androdioecy was recognized as early as 1877 (ref. 1). However, the only compelling evidence for its existence comes from studies of two plant genera, *Datisca* and *Ricinocarpus*^{2,3}. Hence, earlier enthusiasm for androdioecy as a transitional step between hermaphroditism and dioecy has waned in recent years⁴⁻⁷.

For the sexual systems of the remaining 25 or more cases of apparent androdioecy, available information has proven inconclusive, or the species have been found to undergo temporal gender changes, or else the species that appear to be androdioecious have proven to be cryptically dioecious^{8,9}. The pollen from the perfect flowers of these cryptically dioecious species has been found to be either inviable and often malformed¹⁰⁻¹⁵, or else the anthers never dehisce^{16,17}. Hence, the species consist of male and female individuals, the latter often producing infertile pollen. Sexual allocation theory offers no satisfactory explanation for the existence of sterile pollen, but several authors have suggested that pistillate flowers of morphologically androdioecious plants may persist in producing inviable pollen for the purpose of rewarding pollinators^{5,15,18,19}. Evidence for this hypothesis lies with the foraging of floral visitors. A review of the current examples, including my own studies of pollination of *Saurauia*, lends support to this pollinator attraction hypothesis for cryptic dioecy.

The genus *Saurauia* Willd. (Actinidiaceae [= Dille-

niaceae]) consists of several hundred species of small- to medium-sized trees of tropical pan-Pacific distribution that vary in apparent sexual allocation, including androdioecy²⁰⁻²². Like species of the related genera *Hibbertia*¹⁵ and *Wormia*, species of *Saurauia* have porose anthers. Herbarium specimens of some *Saurauia* species bear only perfect flowers. The remaining species are morphologically androdioecious. However, they may be cryptically dioecious, as evidenced by anucleate or inaperturate pollen grains in anthers of their pistillate flowers²⁰⁻²². Some species of *Saurauia* thus offer the opportunity to explore the hypothesis that the pistillate flowers of morphologically androdioecious plants retain pollen-producing stamens to lure pollinators.

The undescribed species of *Saurauia* that I studied grows along the edges of clearings between the Lower Montane Wet Forest and the Lower Montane Rain Forest²³ in the highlands of Costa Rica, near Monteverde. During the three-year study, 20 large and small trees of this species consistently produced either staminate flowers or perfect flowers ($n=300$ censused), the latter bearing stamens plus visible pistils. Flowers bagged in netting do not set fruit. In 60 hand-crosses using pollen from either staminate or perfect flowers, only pollen from flowers of male trees set fruit with fully-seeded locules. Hence, the species is cryptically dioecious and not androdioecious, as the pollen from perfect flowers is incapable of siring seed, even when applied to flowers of other individuals.

Only female bees were seen to visit flowers of *Saurauia* at this location. The bees' proboscises remained retracted while visiting the *Saurauia* flowers, suggesting the absence of active nectaries. Likewise, typical nectarivores like butterflies, flies and hummingbirds, while active at nearby flowering species, did not visit this *Saurauia*. All 15 bee species, including species of *Neocorynura*, *Bombus*, *Trigona* and *Melipona*, audibly sonicated the porose anthers of both staminate and pistillate *Saurauia* flowers to gather pollen, which they frequently groomed and accumulated in their scopae. Honey bees (*Apis mellifera*), which do not sonicate flowers²⁴, were present at neighboring flowers, but never at *Saurauia*. Bumble bees (*Bombus*) were often the sole visitors to *Saurauia* flowers during the frequent cool, foggy and windy periods. Pollen appears to be the

sole reward by which this *Saurauia* attracts its pollinating bees.

Does pollinator attraction explain the evolutionary persistence of fully-formed, dehiscent stamens in the perfect flowers of female plants of *Saurauia* and some but not all other cryptically dioecious taxa? For a related form of sexual allocation, gynodioecy, stamens are typically vestigial or absent from the pistillate flowers of female plants¹, suggesting that a sterile, otherwise functionless androecium is soon lost evolutionarily. Actual androdioecy in *Datisca glomerata* appears to be an extremely rare, ephemeral transitional stage en route to hermaphroditism to dioecy². In contrast, cryptic dioecy has arisen independently in at least seven different plant families (Table 1). Several of these taxa, such as *Trochodendron*, represent odd, taxonomically depauperate lineages. Others, such as *Solanum*, *Saurauia* and *Acer*, are speciose genera whose transoceanic distributions and abundance in disturbed or successional habitats argues for their evolutionary longevity and ecological success.

Cryptically dioecious taxa whose flowers lack nectar form a distinctive subgroup whose members are pollinated exclusively by bees (Table 1). The anthers of their pistillate flowers produce misshapen pollen grains that are smaller and less numerous than those of staminate flowers. Most of the bees reported to visit flowers of these species are taxonomic generalists (*Apis*, *Bombus*, *Trigona*, *Melipona*) that forage at flowers of many different plant families. Among the common taxa of insects, birds and mammals that visit flowers, only bees rely upon pollen for their dietary proteins and most lipids. Hence, nectarless flowers might retain the pollinating services of female bees, but not other potential pollinators, so long as the flowers continued to advertise and provide adequate pollen rewards^{15, 18, 19, 22, 25}.

Pollen is a necessary and sufficient reward to engage bees as pollinators of nectarless, sexually dimorphic plants. Showy stamens are required to attract bees to nectarless flowers of andromonoecious *Solanum carolinense*. Emasculated hermaphrodite flowers set only 1/15 as many fruits as intact flowers of this self-incompatible species²⁶. Despite their disparate taxonomic affinities, only the nectarless species of cryptically dioecious plants have showy flowers with prominent yellow stamens (Table 1), indicative of their role in the visual attraction of pollinating bees.

Although some species may falsely advertise copious pollen rewards to deceitfully gain pollinator services²⁷, this strategy seems an unlikely evolutionary option for females of cryptically dioecious plants. Bees tailor their foraging efforts to maximize pollen gain, at least from flowers with poricidally-dehiscent anthers. Female *Bombus* and *Ptiloglossa* quickly curtail their pollen-foraging visits to unrewarding flowers of *S. elaeagnifolium*, either when pollen is experimentally removed or simply rendered unavailable²⁸. Curtailed visits by bumble bees to flowers of *Erythronium* leave fewer pollen grains on a flower's stigma²⁹. Consequently, plants with no nectar and deceptive indehiscent or empty anthers would be more poorly pollinated and thus at a reproductive disadvantage. For female flowers of cryptically dioecious flowers that lack nectar but rely on bees as pollen vectors, the retention of functional anthers is requisite to attract and reward pollinating bees.

Bees may not be able to assess and compare the nutritional values of pollen, however, and so the pollen of pistillate flowers could be nothing more than metabolically cheap, nutrient-poor particulate²⁷. Such a nutritional dichotomy between pollen of so-called fodder anthers and fertile anthers was not found for species of *Solanum*³⁰ or *Chamaecrista*³¹. For the *Saurauia* species studied here, I found equivalent amino

Table 1. Survey of floral and visitor characteristics for morphologically androdioecious genera of plants

Genus	Family	Petals	Anthers	Nectar	Visitors	Dehiscence	Visitor foraging
Bee pollinated							
<i>Actinidia</i>	Actinidiaceae	Showy	Bright yellow	No*	Bees (incl. <i>Apis</i>)	Porose	Buzz for pollen
<i>Decaspermum</i>	Myrtaceae	Showy	Yellow?	No	Bees (incl. <i>Apis</i>)	Not porose	Harvest pollen
<i>Saurauia</i>	Actinidiaceae	Showy	Bright yellow	No	Non- <i>Apis</i> bees	Porose	Buzz for pollen
<i>Solanum</i>	Solanaceae	Showy	Bright yellow	No	Non- <i>Apis</i> bees	Porose	Buzz for pollen
Variably pollinated							
<i>Acer rubrum</i>	Aceraceae	None	Red	Yes	Bees, other insects [†]	Indehiscent	Nectar, rarely pollen
<i>Polyscias</i>	Araliaceae	Tiny	Pale	?	?	Protandrous	?
<i>Thalictrum</i>	Ranunculaceae	None	White	No?	Diverse insects	?	?
<i>Trochodendron</i>	Trochodendraceae	Tiny	Yellow	Yes**	<i>Apis</i> and butterflies	Delayed	Nectar
<i>Vitis</i>	Vitaceae	Shed	Pale	Yes	Bees and flies [†]	Normal	Nectar, rarely pollen
<i>Xerospermum</i>	Sapindaceae	Tiny	Pale	Yes	Bees and butterflies	Indehiscent	Nectar, rarely pollen

*At least pistillate flowers are known to be nectarless. Honey bees visit flowers for nectar and are of debatable pollination value³⁴. Although anthers of *A. chinensis* appear to dehisce pollen through longitudinal slits, other members of the genus have porose anthers^{25, 35}.

**Author claimed flowers to be nectarless (with no evidence), but describes 'shining, viscid fluid that coats the external surface of the gynoeceum'³⁶.

[†]May be wind-pollinated^{33, 37}.

acid constitutions of pollen from staminate and perfect flowers using HPLC analyses of pollen digests. It would appear that such sterile fodder pollen has nutritional value for pollinating bees.

Species of three of the more speciose genera whose flowers are both nectarless and morphologically androdioecious also produce anthers which dehisce their pollen through apical pores (Table 1). To harvest pollen from these flowers, bees sonicate the anthers using trains of audible buzzes generated by the thoracic flight muscles^{24,25}. Pollen, unlike nectar, cannot be renewed once it has been depleted by a visitor, but poricidal dehiscence offers a nectarless flower a means of dispensing pollen rewards to sequential pollinators²⁵. Alternatively, *Decaspermum* packages pollen into abundant but short-lived flowers¹⁵ that sequentially open over the course of a prolonged blooming season, again ensuring revisitation from pollinating bees despite the nonrenewable nature of its pollen rewards. Efficient strategies for dispensing and packaging pollen to ensure pollinator revisitation is characteristic of plants pollinated by bees seeking pollen rewards³², and may be a preadaptation among nectarless plant taxa that give rise to morphologically androdioecious species.

The remaining morphologically androdioecious species all have inconspicuous flowers (Table 1). Several of these species are likely to be wind-pollinated: *Acer rubrum* (which nonetheless is attractive to various bees³³) and *Thalictrum polygamum* (whose list of floral visitors is largely comprised of dubious pollinators¹² despite more recent claims¹³). Both *Xerospermum* and *Trochodendron* reward their visitors with nectar (Table 1). The indehiscent nature of the anthers of *Xerospermum*, like those of *Acer*, suggest that the androecium of pistillate flowers in these species may be becoming vestigial, as is common among andromonoecious species. In all four of these remaining cases, the pollen from pistillate flowers serves no purpose in pollination, neither as a functional male gametophyte nor as a critical pollinator reward. With no selective advantage maintaining the androecium in pistillate flowers of these species, it is conceivable that their stamens will become vestigial or lost in the evolutionary future. In contrast, the pollen produced by pistillate flowers of nectarless, morphologically androdioecious species is critical to the plant's sexual reproduction, not because of any ability to sire seed, but for its role in rewarding pollinating bees that deliver stigmatic pollen.

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ACKNOWLEDGEMENTS. I am grateful to Robert Lawton for his botanical expertise and assistance with fruit collection, and to William Haber for his botanical advice. Linda Kervin, Phil Waclawski and students from the summer 1990 Monteverde Institute and Organization for Tropical Studies tropical ecology courses were invaluable during field data collection. I am indebted to David Roubik, Robert Brooks, Charles Michener and George Eickwort for assistance in bee identifications. Helpful reviews were provided by Gregory Anderson, Robert Boyd and Scott Mort. Research was partly supported by a travel grant from Auburn University and the Monteverde Institute.

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