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Original article

Flowering synchrony and floral display size affect pollination success in a deceit-pollinated tropical orchid

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ABSTRACT

Due to frequency-dependent negative selection, a strong relationship between reproductive phenology traits and pollination success is expected in deceit-pollinated species. This paper assesses the effects of floral display size on both female (fruit production) and male (pollen removal) pollination success in a population of the deceit-pollinated tropical orchid *Myrmecophila christinae* during two consecutive years (1998–1999). Low pollen removal (~9% of total flowers) and fruit production values (~3% of total flowers) were recorded during both years. As expected, binary logistic regressions showed a significant negative effect of floral synchrony, and a positive effect of floral display size on both male and female success, although these effects varied across years. Pollination rates in the field and in hand pollinations suggest a doubling in pollinator abundance between years. Results suggest that floral display size and flowering synchrony are of adaptive value for *M. christinae*. However, between-year fluctuations might indicate that reproductive phenology traits in deceit-pollinated species undergo fluctuating selection regimes among years and are probably linked to short-term changes in environmental (abiotic and biotic) conditions.

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1. Introduction

Flowering phenology is considered a key characteristic in plant reproductive biology as it influences many mutualistic and antagonistic interactions and thereby impacts on the success of plant reproduction (Ratchke and Lacey, 1985). Furthermore, previous studies have found strong relationships between traits associated with reproductive phenology and

fruit and seed production, suggesting that these traits are of adaptive value (e.g. Augspurger, 1981; Dieringer, 1991; Widén, 1991; Ollerton and Diaz, 1995).

Nevertheless, pollinator-mediated selection on flowering phenology has been questioned for different reasons. First, doubts about the adaptive value of phenology patterns have been raised in part because of: (a) a lack of a significant relationship between phenology traits and reproductive success

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in many species (Aizen, 2003), (b) the presence of only a weak relationship between these variables (Gómez, 1993; O'Connell and Johnston, 1998), or (c) that this relationship varies spatially or temporally due to changes in both abiotic and biotic conditions (Herrera, 1992, 1996; Ollerton and Lack, 1998). Based on this, it has been suggested that the observed variation in flowering phenology has largely arisen by chance (Ollerton and Lack, 1992) and that it has a strong phylogenetic component (Kochmer and Handel, 1986; but see Lobo et al., 2002).

The importance of pollinator-mediated selection on traits associated with flowering phenology is likely to change from species to species and depends partially on the specific characteristics of a species' pollination biology. The Orchidaceae are especially suitable biological models for testing the relationships between phenology traits and pollination success because of their highly specialized pollination systems (Dafni, 1984; Ackerman, 1986; Nilsson, 1992) and because their fruit and seed production is frequently limited by pollinators (e.g. Calvo, 1993). In addition, most orchid species have specialized pollination systems, such as deception (Dafni, 1984; Ackerman, 1986), which allows testing for specific hypotheses on the relationship between phenology traits and pollination success. For instance, in plant species with deceit pollination, temporal concentration of floral resources is a predicted disadvantage because pollination success depends on the frequency with which pollinators can be deceived (negative frequency-dependent selection) (Ferdy et al., 1998; Smithson and Macnair, 1997; Gigord et al., 2001). Thus, in deceit-pollinated orchids, selection is expected to favor asynchrony in flowering events (O'Connell and Johnston, 1998).

An additional research advantage of orchids is that their pollen grains are packed into specialized structures (pollinarium). This makes it possible to estimate both female (fruit) and male (pollen removal) pollination success, and thus evaluate the importance of pollinator-mediated selection via both sex pathways (Nilsson et al., 1992; Ackerman et al., 1997; Maad and Alexandersson, 2004). Based on the hypothesis of sexual selection in plants (Wilson, 1979), it has been suggested that male pollination success will be limited by pollen dispersal, while resources will be the main factor influencing the female function. Because of this, it is expected that a greater floral display will be more tightly linked to male success than to female success. However, in orchids, fruit production is commonly limited by pollinators and resource limitation only occurs on a long term basis (Primack and Stacy, 1998). In addition, floral display is a signal that increases pollinator attraction in deceit-pollinated species (Johnson and Nilsson, 1999), and thus it is probable that in these species a greater floral display is a characteristic of adaptive value for both male and female pollination success.

Myrmecophila christinae is a food-deception pollinated orchid characterized by a low visitation rate (it only has two pollinator species) and generally low fruit-set (Rico-Gray and Thien, 1987). This species is known to experience directional and disruptive phenotypic selection on flowering onset where individuals flowering far from the population flowering peak are favored (Parra-Tabla and Vargas, 2004). However, phenotypic selection is highly variable between populations and years and it is not known if pollination success is related to other components of phenology, as well as to temporal variation in

pollinator activity and abundance (Herrera, 1996). Some authors have recently suggested that if selection shapes flowering phenology it should be acting on more than one component of phenology and not just flowering onset (Bolmgren, 1998). In deceit-pollinated species such as *M. christinae*, components of phenology such as flowering synchrony (i.e. when an individual flower, in relation to the population flowering, peaks), and total resource allocation for sexual reproduction (i.e. floral display size) could be related to pollination success.

The main goals of this study were to determine whether flowering synchrony and/or floral display size affects pollination success in a *M. christinae* population over a period of two consecutive years, and in doing so explore the adaptive value of these traits associated with flowering phenology in this deceit-pollinated species. The specific questions addressed were: (1) will a greater flowering synchrony negatively affect male and female pollination success? (2) will a greater floral display increase both male and female pollination success? and (3) will the effect of flowering synchrony and floral display on pollination success be of the same magnitude across genders and seasons?

2. Materials and methods

2.1. Study species

Myrmecophila christinae var. *christinae* (i.e. *Schomburgkia tibicinis*; (Batem), Rolfe; Carnevali et al., 2001) is an epiphytic orchid that grows on palms trunks (*Coccolobus reedii* and *Thrinax radiata* 1.0 and 2.5 m height) as well as branches of small shrubs (e.g. *Pithecolobium keyense*) in the northern coastal shrub vegetation of the Yucatan Peninsula. It normally produces from 1–2 pseudobulbs every year, though individuals with more than 40 pseudobulbs have been reported (Rico-Gray and Thien, 1987). Its flowering period extends from March to June and fruits are produced from May to July.

Myrmecophila christinae flowers are located at the end of 1.5–2.0 m long inflorescences. Each plant produces 1.8 ± 2.1 (mean \pm SD, $N = 115$) inflorescences, each of which sequentially produces between 6–15 large (8–9 cm in diameter) flowers, with colors varying from creamy yellow to purplish rose. Although *M. christinae* is completely self-compatible, it requires pollen vectors for fruit-set. Flowers last from 6–10 days and are receptive from the first day of anthesis. No floral nectar or other form of reward is produced, though flowers produce a strong vanilla scent at dawn (Rico-Gray and Thien, 1987). Each flower has a pollinarium containing eight pollinia. Pollination takes place via food deception of "naive" bees (Rico-Gray and Thien, 1987; Parra-Tabla and Vargas, 2004). The only known pollinators are *Eulaema polychroma* and *Xylocopa* sp. (Rico-Gray and Thien, 1987). During the study period (1998 and 1999) *Xylocopa* sp. was relatively abundant, but only two *E. polychroma* individuals were recorded. Pollination by *Xylocopa* sp. was observed between 05:00 and 06:30 h, with rapid (approximately 2 s) and effective (entire pollinarium usually removed) visits. During a pollination approach, *Xylocopa* sp. and *E. polychroma* never visit more than one flower

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