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The effects of inflorescence size and flower position on female reproductive success in three deceptive orchids

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ABSTRACT. Most Mediterranean orchids are deceptive, offering no reward to insect pollinators. In the absence of a reward, inflorescence size and flower position within inflorescence may be associated with the timing and the numbers of pollinators attracted, thus influencing the final reproductive success. Pollination biology and breeding system were investigated in three deceptive orchids, *Orchis italica*, *O. anthropophora*, and *Anacamptis papilionacea*. Although all examined orchids were self-compatible, bagged inflorescences produced no fruits. Artificial pollination resulted in a 76-79% fruit set by induced autogamy, a 70-76% one by geitonogamous pollination, and a 79-87% one by allogamous pollination. The natural fruit set in the open-pollinated control was 14-16%. Fruit production was neither related to the inflorescence size, nor to the number and position of flowers within the flowering spike, suggesting that variation in these floral traits does not influence pollinator attraction or female reproductive success.

Keywords: *Anacamptis*; Breeding system; Deceptive orchid; Hand-pollination; *Orchis*; Reproductive success.

INTRODUCTION

The Orchidaceae is one of the largest families of flowering plants (up to 35,000 species), making up nearly 10% of all flowering plant species in the world (Dressler, 1993). The orchids' floral structure is generally specialized to avoid spontaneous self-fertilization and promote insect-mediated outcrossing (Arditti, 1992; Dressler, 1993). In the Orchidaceae, sexual reproduction is predominantly pollinator-dependent even though it may sometimes be successfully prevented by asexual seed production (agamospermy) or, more frequently, by spontaneous or insect-mediated self-pollination. The seed set of animal-pollinated plants is limited by pollinators and/or resources (Bierzychudek, 1981; Stephenson, 1981). Levels of fruit production are frequently reported in orchid species, and fruit set production is the most widely used estimate of female reproductive success (Proctor and Harder, 1994).

It has been generally accepted that the evolutionary diversification of orchids is closely related to their complex pollination systems (Stebbins, 1984; Nilsson, 1992). The precision of pollinaria transfer in most Orchidaceae requires tighter morphological correspondence between the flower and pollinator. Orchids offer their visitors (insects and birds) a variety of rewards such as oil, floral fragrances, and, most frequently, floral nectar. It has been estimated, however, that one-third of the Orchidaceae are deceptive, offering no reward to their pollinators (Van der Cingel, 1995; Jersakova et al., 2006).

Pollinator abundance and resource limitation are factors which may limit reproductive success in orchids (Zimmerman and Aide, 1989). Inflorescence size in such cases should represent a trade off between the need to attract scarce pollinators and the quantity of resources available for the production of the attraction unit. Orchid species which rely on pollination by deceit (Jersakova et al., 2006) allocate resources differently than those that provide rewards to pollinators. The lack of pollinator reward might enable a plant to allocate limited resources for other purposes but at the same time may reduce the attractiveness of the inflorescence to pollinators, lowering annual reproductive success. For deceptive orchids the inflorescence size may be associated with the numbers of pollinators attracted, and thus the proportion of flowers that develop fruit is expected to be related to the plant size.

The probability of fruit maturation in plants has often been found to decrease from proximal to distal positions within an inflorescence (Diggle, 1995). This decrease may be caused by competition among developing fruits for resources, quantity and/or quality of pollen received, or pollinator behaviour (Wolfe, 1992; Diggle, 1995). Pollination success may also vary among flowers in different positions, since flowers opening sequentially in an inflorescence may be most attractive to pollinators at a certain phase of flowering, such as when many flowers are open at the same time (Berry and Calvo, 1991). In plants whose flowers open sequentially, pollen from flowers in different positions may have different opportunities for siring offspring (Berry and Calvo, 1991; Brunet, 1996). The orchids usually develop capsules from all pollinated flowers and thus the amount of seeds is limited by the number

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of available ovules, which decreases towards the top of inflorescence, and by pollen deposition (Diggle, 1995). Later in the season, when resources available for seed production decrease as a result of earlier fruit production, parent-offspring conflict may be decided in favour of the parent plant's interest (Obeso, 1993). Thus, for deceptive orchids the position of flowers in the inflorescence that develop fruit may be positively associated with the timing and numbers of pollinators attracted and how pollinators forage on an inflorescence.

The purpose of this study was to investigate the effects of several floral traits on the reproductive success of three deceptive orchids, *Orchis italica*, *O. anthropophora*, and *Anacamptis papilionacea*. Our research had the following specific objectives: i) to investigate the breeding system, and ii) to examine female reproductive success in relation to inflorescence size and flower position.

MATERIALS AND METHODS

Study site and model species

The observations were conducted during the flowering period of *Orchis italica* Poir., *O. anthropophora* (L.) All., and *Anacamptis papilionacea* (L.) in May-June 2007 in a natural population located at "Monte di Cassano" (39° 47' N 16°18' E, 512 m a.s.l.), Calabria region, Southern Italy. The whole area covers roughly 1,500 m^2 (25 m wide and 60 m long) of a calcareous soil and is bounded on the west by a road and on the other sides by deep gorges. In the study site the generalized food deceptive orchids (Jersakova et al., 2006), *O. italica*, *O. anthropophora* and *A. papilionacea*, overlapped extensively in their spatial distribution and grew together with sexually deceptive orchid species *Ophrys fusca* Link, *O. lutea* Cav., *O. bombyliflora* Link, *O. tenthredinifera* Will., *O. sphegodes* Miller, *O. incubacea* Bianca, *O. bertolonii* Moretti, *O. exaltata* subsp. *archipelagi* Gölz and Reinhard.

Orchis italica and *O. anthropophora* are considered to be closely related phylogenetically (Bateman et al., 2003), have an identical chromosome number ($2n$=42) (Queiros, 1985, Bianco et al., 1987; Constantinidis et al., 1997), and have been included in the *O. militaris* (Delforge, 2005) or "anthropomorphic" group (Bateman et al., 2003).

Orchis anthropophora (the Man orchid) has a Mediterranean-Atlantic distribution area. It is widespread and rather common in the centre and west, rare in the east and north. The species prefers moderately sunny meadows on dry or well-drained soils up to 1,400 m a.s.l. The flower spike, 20-40 cm tall, blooms from April to June, producing an inflorescence with up to fifty small yellow-green flowers with purple labellum borders. Unlike other members of the genus *Orchis*, flowers of *O. anthropophora* lack a labellum spur.

Orchis italica (the Italian orchid) is typical of the Mediterranean region although it extends north to Dalmatia and west to northern Portugal. The species blooms between March and June, grows in poor grassland, open garrigue and shrubby habitats up to 1,300 m a.s.l. Plants of the Italian orchid are robust, 20-60 cm tall, showing a dense inflorescence with many (up to fifty) flowers with colours ranging from pinkish-white to reddish-purple. The lip is pendent, deeply tri-lobed with a cylindrical spur, 4-8 mm long and curved downwards.

Anacamptis papilionacea is only found in the south of Europe around the Mediterranean basin. The species prefers full sunny meadows on dry or well-drained soils up to 1,700 m a.s.l. The flower spike, 20-40 cm tall, blooms from February to May producing an inflorescence with up to fifteen flowers of pink, crimson-red or purple colour with lip pendent, entire with lines, streaks and dots (Delforge, 2005).

Little information is available on the pollinators of these species. *O. anthropophora* has been reported to be pollinated by two species of sawflies (Hymenoptera) and three species of beetles (Coleoptera) (Reinhard et al., 1991; Schatz, 2006). No direct information has been reported for *O. italica*; however, its pollinators might belong to the insect assemblage (i.e. Hymenoptera, *Bombus* ssp.; solitary bees, *Osmia* ssp. *Eucera* ssp.), that visits plants of the *Orchis militaris* group (Van der Cingel, 1995). *A. papilionacea* has been reported to be pollinated by bees (*Eucera* sp.) and bumblebees (Vogel, 1972; Cozzolino et al., 2005). Recently, it has been shown that *Orchis italica* and *O. papilionacea* shared at least two pollinators. Indeed, four individuals of *Eucera nigriscens* and three of *Bombus humilis* carried hemipollinaria belonging to both *Orchis* species (Pellegrino et al., 2010).

Breeding systems

To elucidate the breeding systems of the taxa studied we performed hand-pollination experiments during spring 2007 based on Dafni's protocol (1992) and estimation of natural fruit production. To this end, we bagged with a fine meshed cloth approx. 400 unopened flowers of 100 plants of each orchid species to exclude pollinators. For hand-pollination, the cover was removed, flowers were pollinated, marked with cotton thread, and the cover replaced. Each flower was randomly assigned to one of four hand-pollination treatments: no manipulation (test of spontaneous autogamy), emasculation (test of agamospermy), artificial self-pollination (test of induced self-pollination), and cross-pollination (test of induced xenogamy). For self-pollination, the pollinia were transferred using a toothpick from the same flower (induced autogamy) or from a different flower on the same plant (induced geitonogamy). For cross-pollination, we transferred pollinia with a toothpick from a flower to the stigma of another flower, previously emasculated and located at a distance of at least 10 m. Natural fruit production was screened on 50 plants of each species.

In June, the number of capsules was counted and the proportion of flowers which had developed capsule was determined for each hand-pollination treatment and compared with natural fruit production.

Effects of inflorescence size and flower position on natural fruit production

To test the effect of inflorescence size on fruit set, 100 plants were selected for each species, the number of flowers per inflorescence was counted, and the size of inflorescences was measured as a distance from lowermost to uppermost flower. For each species, plants were divided into "tall" and "short" plants, taller or shorter than the mean height, respectively. To compare female reproductive success at the different positions within an inflorescence, individual flowers of each plant were divided into three even-size sections according to their position within an inflorescence (i.e. lower, middle, and upper). Between 35 and 40 smaller than average plants and the same number of larger plants were left open (unbagged) to pollinators as unmanipulated open-pollinator controls. At the end of the flowering period (June), the flowers that produced fruits and their position within the inflorescence were recorded and capsule production was calculated as a ratio between the number of fruits produced and the number of available flowers.

The effects of inflorescence size and position of flowers on reproductive success were examined with two sample t-tests using the statistical program package SPSS (Version 10, SPSS Inc. Chicago, USA).

RESULTS

Breeding systems

Our results exclude the occurrence of spontaneous autogamy and agamospermy since no fruit was produced by the bagged unmanipulated and emasculated flowers. Conversely, a high proportion (70-86%) of hand-pollinated parental flowers yielded fruits, and no significant differences ($F_{2,197} = 0.90$; $p = 0.43$) between autogamic, geitonogamic, and allogamic treatments were apparent (Table 1). Fruit sets in naturally pollinated plants (pollinator-mediated allogamy) and manually outcrossed plants (induced allogamy) varied significantly in *O. italica* (t-test = 2.27, $P<0.005$), *O. anthropophora* (t-test = 3.13, $P<0.005$) and *A. papilionacea* (t-test = 2.87, $P<0.005$), suggesting that pollinator visits are indispensable for seed production whether or not they are self-compatible. All examined orchid species showed a small natural fruit set in open-pollinated populations: 16% in *O. italica* and 14% in both *O. anthropophora* and *A. papilionacea* (Table 1).

Effects of inflorescence size and flower position on natural fruit production

In the open-pollinated populations of three orchids there was no difference in capsule production among the different parts of the inflorescence (Table 2). The percentage of fruit set along the inflorescence was not homogeneous. Differences between the three flower positions were not more than 3% and not statistically significant. In addition there was no evidence of a decrease in fruit production from proximal to distal positions within an inflorescence in all of the three species. On the contrary, *O. italica* showed a fruit set decrease from the distal to proximal positions (Table 2). There was no statistically significant correlation between inflorescence size and capsule production in any of the orchid species. Moreover, the species showed different patterns of reproductive success between shorter and taller plants. Though the difference was not significant, taller plants had a higher fruit set than short ones in *O italica* and vice versa in *O. anthropophora* (Table 2).

DISCUSSION

Breeding system

Pollination treatments revealed the absence of agamospermy (asexual seed production), confirming that this reproduction system is not favored in the Orchidaceae (Neiland and Wilcock, 1998). Likewise, spontaneous autogamy was not observed in examined orchids (Table 1). The herkogamous structure of the gynostemium in these species prevents autogamous pollination and promotes outcrossing (Dressler, 1993).

Fruit production in open-pollinated flowers in nature was significantly lower than for hand-pollinated flowers. The high level of fruit set obtained via artificial autogamy and geitonogamy showed that the examined orchids are highly self-compatible. Therefore, the low levels of

Table 1. Breeding system in three deceptive orchids *Orchis italica*, *O. anthropophora*, and *Anacamptis papilionacea*.

	O. italica			*O. anthropophora*			*A. papilionacea*		
	NF	FP	%F	NF	FP	%F	NF	FP	%F
Agamospermy	75	0	0.00	74	0	0.00	72	0	0.00
Spontaneous autogamy	74	0	0.00	75	0	0.00	74	0	0.00
Induced autogamy	75	57	76.00	75	59	78.67	73	55	75.34
Induced geitonogamy	72	55	76.39	74	52	70.27	74	52	71.62
Induced allogamy	74	64	86.49	72	60	83.33	73	58	79.45
Natural fruit set	82	13	15.80	79	11	13.92	72	10	13.88

*NF= number of flowers observed; FP= number of fruits produced; %F=percentage of fruit produced.

Table 2. Effects of flower position within the inflorescence (i. e. lower, middle and upper flowers) and inflorescence size (taller and shorter than mean height) on capsule production (%) of individual flowers in three deceptive orchids *Orchis italica*, *O. anthropophora*, and *Anacamptis papilionacea*.

	n	Lower	Middle	Upper	χ^2	P
Position in inflorescence						
Orchis italica	75	14.5 (± 1.2)	15.9 (± 1.1)	17.5 (± 1.2)	0.98	0.26
Orchis anthropophora	77	13.6 (± 1.3)	11.7 (± 0.9)	15.0 (± 1.4)	0.88	0.36
Anacamptis papilionacea	76	12.2 (± 1.1)	16.1 (± 1.4)	14.2 (± 1.3)	0.58	0.31
	n	Tall	Short		χ^2	P
Inflorescence size						
Orchis italica	75	17.4 (± 1.5)	14.6 (± 1.3)		0.67	0.30
Orchis anthropophora	77	12.5 (± 1.3)	14.3 (± 1.2)		0.52	0.25
Anacamptis papilionacea	76	14.0 (± 1.4)	14.3 (± 1.2)		0.93	0.11

fruit set observed under natural conditions suggest that pollination success of these deceptive orchids is limited by pollinator visitation, as has been frequently reported in other deceptive orchids (Matsui et al., 2001; Pellegrino et al., 2005).

The value recorded for the natural fruit set (14-16%) supports the theory that nectarless orchids are less successful in setting fruits than nectariferous species. For nectarless and nectariferous orchids, fruit set was 27.7% and 63.1% in Europe, and 19.5% and 49.3% in North America, respectively (Neiland and Wilcock, 1998).

Inflorescence size and flower position

Numerous studies have addressed the role between- and within-plant variation plays in reproductive success. Such variation has generally been attributed to resource limitations, pollen limitations, and/or variability in pollen source (Navarro, 1998). The physical location of a flower within an inflorescence affects its chances of maturing into a fruit both because of its vascular connection to the parent plant's pool of resources and because of its occurrence in time with respect to other developing fruits competing for a share of limited resources (Stebbins, 1984).

When resources for reproduction are limited, two factors that may influence fruit production are the location of the flower within the inflorescence or on the plant and the time of fruit initiation. Flowers in proximal positions in the inflorescence or on the plant often have higher fruit sets or produce heavier seeds than flowers in distal positions, presumably because they are closer to the main stem (Lee, 1988; Solomon, 1988). In our case, the examined orchids showed no clear relationship between fruit formation and inflorescence length or flower position along the inflorescences. Empirical evidence for these considerations is sometimes contradictory. Larger displays often attract more pollinators (Klinkhamer et al., 1989; Ohara and Higashi, 1994), but sometimes do and sometimes do not affect the proportion of flowers that develop fruit (Montalvo and Ackerman, 1987; Calvo, 1990). For example, the proportion of flowers that develop fruit in deceptive orchids *Calopogon tuberosus* (Firmage and Cole, 1988), *Orchis ustulata* (Kindlmann and Jersakova, 2006)*, Dactylorhiza* sp. (Mattila and Kuitunen, 2000; Vallius, 2000), *Orchis purpurea* (Jacquemyn et al., 2002), and *Searapias vomeracea* (Pellegrino et al., 2005) is independent of the number of flowers in the inflorescence. In other cases (*Orchis morio* and *Dactylorhiza sambucina*)*,* a negative relationship between reproductive success and the number of flowers has been found in just one of study populations (Kindlmann and Jersakova, 2006).

In deceptive plants the relationship between the inflorescence size and percentage of flowers that develop fruit is somewhat puzzling. A short plant with a low number of flowers in the inflorescence might be suboptimal, as then the plant is not attractive enough for pollinators, but a tall plant with a large number of flowers may also be suboptimal, as their production is costly (Kindlmann and Jersakova, 2006). If this is true, then for a species under given conditions there should exist some optimal number of flowers in the inflorescence.

In conclusion, the absence of differences in fruit set among flower positions and between taller and shorter under natural condition cannot be attributed to resource limitation. Indeed, our data do not support the hypothesis that within the season resources (the ability to move resources along the inflorescence) constrain fruit set, as upper and lower flower positions within the inflorescence had equal fruit sets. The absence of differences in fruit set among flowers positions suggests either that pollinators visit flowers during the whole flowering season or that the flowers are pollinated by insects with irregular visiting patterns within a spike, e.g. not bees, which always work from the bottom towards the top.

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花序大小及花之位置對三種隱瞞性蘭花雌性生殖器官成功之影響

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大部分的地中海蘭花吸引授粉昆蟲，但它們無得到報酬。這些蘭花，它們的大小和在花序上的位置可能與時間和授粉昆蟲被吸引的數目有聯結，這可能影響生殖的成功。在這方面，經研究了三種 deceptive 蘭花的授粉生物和生殖系統。這三種蘭花是：*Orchis italica*, *O. anthropophora* 和 *Anacamptis papilionacea* 。這些蘭花是自身相容的，雖然被保護的花序勿讓授粉昆蟲傳花粉，但這些花也沒有結果實。在人工授粉下得到了 76% 到 79% 的誘導自花授粉結果實，從 70% 到 76% 是同株授粉結果實，從 79% 到 87% 是異花授粉結果實。在自然環境裡，結果實百分之幾的變化是由 14% 到 16%。結果實與蘭花的大小、數目或在花序上的位置無關，花的特點 (大小，形狀) 變化不影響授粉昆蟲被吸引，所以也不影響生殖的成功。

關鍵詞：*Anacamptis*；生殖系統；隱瞞性蘭花；人工授粉；*Orchis*；生殖成功。