

Floral display influences male and female reproductive success of the deceptive orchid *Phaius delavayi*

P. Li · B. Q. Huang · R. W. Pemberton ·
Y. B. Luo · J. Cheng

Received: 1 November 2010 / Accepted: 10 May 2011 / Published online: 4 June 2011
© Springer-Verlag 2011

Abstract The influence of floral display on male and female reproductive success is variable without consistent patterns. Few studies concentrate on the integrated influence of the different components of floral display on reproductive fitness at population level. We studied the impact of different components of floral display on reproductive success in the Chinese orchid *Phaius delavayi*. This deceptive orchid has flowers in which male and female success can be readily assessed in the field by observing rates of pollinarium removal and fruit initiation. The results showed that mean pollinarium removal ($52.05 \pm 2.08\%$) was higher than fruit set ($36.78 \pm 1.89\%$), and both male and female reproductive success decreased with increasing clump size in *Phaius delavayi*. Nevertheless, floral display

expressed by clump size and flower position impacted both female and male reproductive success, whereas flowering initiation and duration, and inflorescence size had no effect.

Keywords Clump size · Inflorescence size · Flower position · Flowering initiation · Rewardless orchid

Introduction

In animal-pollinated plants, reproductive success is expected to increase with larger floral display as a result of increased attractiveness to pollinators (Peakall 1989; Aragón and Ackerman 2001; Ackerman and Ackerman 2001). Several studies have shown a positive relationship between floral display and frequency of pollinator visits at individual plant level (Ohashi and Yahara 1999). However, the impact of floral display on male and female reproductive success seems variable, with no consistent results among those studies so far (Tremblay et al. 2005 and references therein). This may be due to different factors that have different effects on plant reproductive success and how these different factors interact. However, few studies concentrate on the integrated influence of the different components of floral display on reproductive fitness at population level.

In addition, most studies that measure reproductive success in plants deal solely with female fitness, whereas male fitness has been largely ignored (Pellegrino et al. 2005a). There have been a few studies that measured both female and male reproductive success (Fritz and Nilsson 1996; O'Connell and Johnston 1998; Parra-Tabla and Vargas 2004; Pellegrino et al. 2005b). As pointed out by Fritz and Nilsson (1996), orchids offer excellent opportunities to measure both female and male reproductive

P. Li (✉)
School of Life Science and Engineering, Southwest University
of Science and Technology, Mianyang, Sichuan, China
e-mail: pengleep@yahoo.com.cn

B. Q. Huang
Department of Environmental Science, Nanchang Institute
of Technology, Nanchang, Jiangxi, China

R. W. Pemberton
Florida Museum of Natural History, Gainesville, FL, USA

Y. B. Luo
State Key Laboratory of Systematic and Evolutionary Botany,
Institute of Botany, Chinese Academy of Sciences,
Beijing, China

J. Cheng
College of Biological Sciences and Biotechnology,
Beijing Forestry University, Beijing, China

success due to their countable pollinaria. However, because the frequency of pollinarium removal and fruit set of orchids are relatively low, it can be difficult to collect enough statistical data to adequately measure male and female reproductive success, particularly in rewardless orchids, which account for about one-third of the Orchidaceae (Van der Pijl and Dodson 1966; Nilsson 1992; Cozzolino and Widmer 2005; Tremblay et al. 2005).

Our study subject, *Phaius delavayi*, usually grows in clumps of 10–50 flowering individuals (Li et al. 2005). This rewardless orchid species is self-compatible, and its pollination success is strictly dependent on the pollen vectors, which are *Bombus* spp. (Li et al. 2010). This orchid has unusually high fruit set, which is probably due, in part, to the large amount of pollen carried by the bees; in most cases, both pollinaria, each with eight pollinium lobes, are removed and carried away by the bumblebee pollinator, in a single visitation (Li et al. 2010). Female and male reproductive success can be readily measured through direct counts of the capsules and close inspection of the anther to determine pollinarium presence or absence.

Phaius delavayi is thus an excellent subject in which to measure both male and female fitness under field conditions. We took advantage of these qualities to investigate intrinsic and extrinsic factors that may influence this orchid's fitness. The aims of this study are to examine how male and female reproductive success are influenced by the varied components of floral display: clump size, inflorescence size, flower position within an inflorescence, and flowering initiation and duration of individuals in the nectarless orchid *P. delavayi*. We addressed the following questions: (1) Are male and female reproductive success impacted, and if so differently, by floral display? (2) Which components of floral display influence reproductive success? (3) Do inflorescence size and flower position within the inflorescence affect pollinarium removal and fruit set differently in different clump sizes?

Materials and methods

Study species and site

Phaius delavayi is a terrestrial orchid species native to China (Perner and Cribb 2002). This terrestrial plant is up to 30 cm tall and bears a raceme with up to seven but usually three to five flowers. The flowers are yellow with red markings on the labellum. No floral nectar or other form of reward is produced. Each flower has two pollinaria, each containing eight pollinia. Flowering period extends from late June to late July in the study population. The experiment was conducted in Huanglong Valley,

Huanglong Nature Reserve (32°41'–32°54'N, 103°44'–104°3'E; altitude 3,100–3,570 m), Sichuan, China.

Experimental design

We chose three sites with similar habitats in Huanglong Valley. Within each site, three different sized clumps, containing 20, 30, and 40 flowering individual plants, respectively, were chosen. The clumps within each site were separated by at least 10 m in order to decrease the interaction among clumps in attracting insects. We randomly chose clumps that approximated the sizes of the experimental design, which mimicked the most typically occurring clump sizes, and removed excess flowering individuals to make the number of flowering individuals in each clump type exactly 20, 30 or 40. All flowering individuals were tagged with small plastic labels inserted into soil at the base of each plant.

Each flower was checked every 3 days at similar time of day to record the flowering process and presence or absence of pollinaria. Two weeks later, after all flowers had withered, the ovaries of the flowers were examined to identify those that were swollen enough to be distinguished as developing capsules. In this paper, male reproductive success is defined as the ratio of flowers with pollinaria removed to the number of flowers on the individual plants. Female reproductive success is the ratio of number of capsules produced to the number of flowers on the individual plants (Broyles and Wyatt 1990; Fritz and Nilsson 1996).

Data analysis

The relationship between male and female reproductive success of individuals was evaluated with the Pearson correlation coefficient, and the relationship between overall flowering numbers and those with pollinaria removed and capsules formed in all clumps and sites at any given moment was analyzed using simple regression.

There was no difference in male and female reproductive success among the three sites (nonparametric test: male reproductive success, $P = 0.262$, $P = 0.170$, and $P = 0.141$ and female reproductive success, $P = 0.638$, $P = 0.925$, and $P = 0.273$, for clumps with 20, 30, and 40 flowering individuals, respectively). For this reason, clump data from each of the three sites were pooled together, and the pooled data were then tested for the effect of clump size on male and female reproductive success using nonparametric tests [Kruskal–Wallis analysis of variance (ANOVA)], because the assumptions for distribution normality could not be met (Vallius and Salonen 2000).

Since clump size had significant effects on male and female reproductive success (see below), the effects of

inflorescence size and flower position on male and female reproductive success were analyzed separately in each clump size. The effects of inflorescence size on male and female reproductive success were tested using ANOVA. The effects of flower position on male and female reproductive success were tested using chi-square test.

Based on the measurements of flowering initiation and duration in individual plants, we sorted individuals into those with earlier or later (than the average) flowering initiation time, and those with shorter or longer (than the average) flowering duration. We then compared pollinarium removal and fruit set using ANOVA to estimate the effects of flowering initiation and duration on male and female reproductive success, respectively. Variables of pollinarium removal and fruit set per flower were subject to arcsine transformation prior to analyses. SPSS (SPSS, USA) for Windows was used for all tests.

Results

Correlation between male and female reproductive success

Average pollinarium removal of individual plants was $52.05 \pm 2.08\%$ (mean \pm SE, $n = 270$), and average fruit set of individual plants was $36.78 \pm 1.89\%$ (mean \pm SE, $n = 270$). Male and female reproductive success of individual plant were highly correlated (Pearson correlation coefficient, all data pooled, $n = 270$, $r = 0.666$, $P < 0.01$). The relationship between overall flower numbers and those with pollinaria removed in all clumps and all sites at any given time showed high correlation (regression analysis, $r = 0.9657$, $t = 11.7582$, $n = 12$; Fig. 1) also.

Clump size

There were no differences in inflorescence size among clumps of different size (ANOVA, $F = 0.083$, $P = 0.773$).

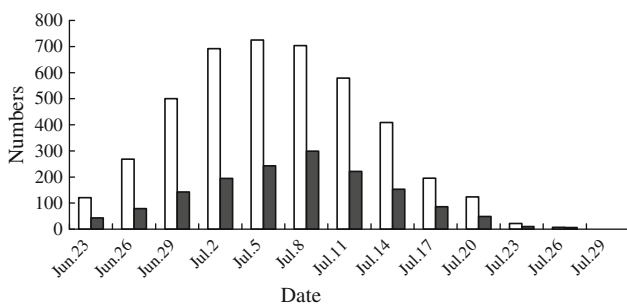


Fig. 1 Relationship between flower number and pollinarium removal in *Phaius delavayi*. White column, flower numbers, black column, number of flowers with pollinaria removed

Average male reproductive success of individual plants was $65.20 \pm 4.40\%$ (mean \pm SE, $n = 60$), $51.53 \pm 3.65\%$ (mean \pm SE, $n = 90$), and $45.86 \pm 2.95\%$ (mean \pm SE, $n = 120$) for clumps with 20, 30, and 40 flowering individuals, respectively. Average female reproductive success of individual plants was $49.94 \pm 3.97\%$ (mean \pm SE, $n = 60$), $35.33 \pm 3.48\%$ (mean \pm SE, $n = 90$), and $31.29 \pm 1.89\%$ (mean \pm SE, $n = 120$) for clumps with 20, 30, and 40 flowering individuals, respectively. Clump size had significant impact on both male and female reproductive success ($F = 14.831$, $P = 0.001$ and $F = 15.219$, $P < 0.001$ for male and female reproductive success, respectively) (Fig. 2). There was a tendency for both male and female reproductive success to decrease with increasing clump size (Fig. 2). Male reproductive success in clumps with 20 flowering individuals was higher than that in clumps with 30 and 40 flowering individuals ($P = 0.02$ and $P < 0.001$, respectively), but there was no difference between clumps with 30 flowering individuals and those with 40 flowering individuals ($P = 0.171$). Similarly, female reproductive success in clumps with 20 flowering individuals was higher than that in clumps with 30 and 40 flowering individuals ($P = 0.013$ and $P < 0.001$, respectively), but there was no difference between clumps with 30 and 40 flowering individuals ($P = 0.194$).

Inflorescence size

Inflorescence size had no effect on either pollinarium removal or fruit set in all three clump size levels (all $P > 0.113$ for both male and female reproductive success) (Table 1; Fig. 3).

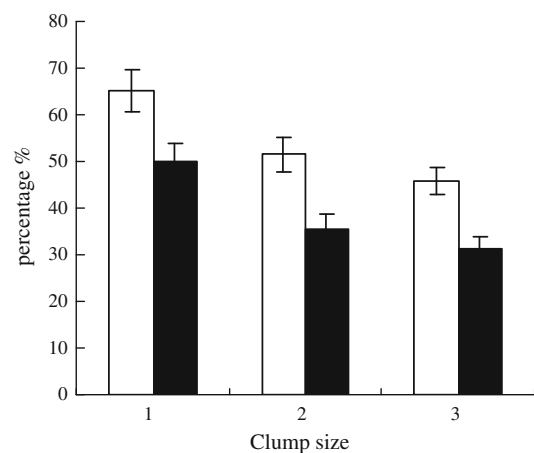


Fig. 2 Pollinarium removal and fruit set in different clump sizes in *Phaius delavayi*. White column, pollinarium removal; black column, fruit set; 1, clumps with 20 plants; 2, clumps with 30 plants; 3, clumps with 40 plants

Table 1 Nonparametric test of effect of inflorescence size on pollinarium removal and fruit set in different clump sizes in *Phaius delavayi*

Clump size	Pollinarium removal			Fruit set		
	df	F	P	df	F	P
20	4	0.214	0.771 ^{NS}	4	0.129	0.776 ^{NS}
30	5	0.676	0.643 ^{NS}	5	0.542	0.744 ^{NS}
40	4	0.113	0.978 ^{NS}	4	1.050	0.385 ^{NS}

NS not significant

Flower position

Pollinarium removal and fruit set decreased from the basal to distal positions within inflorescences in clumps with 20 flowering individuals (Table 2; Fig. 4), but only fruit set, not pollinarium removal, was significantly different in clumps with 30 flowering individuals (Table 2; Fig. 4). There were no differences in pollinarium removal and fruit set in clumps with 40 flowering individuals (Table 2; Fig. 4).

Initiation and duration of flowering

The average initiation date for flowering in individual plants was 23 ± 3 (mean \pm SE) June, and the average individual plant flowering duration was 22 ± 4 (mean \pm SE) days. Plants that flowered earlier in the season had no difference in pollinarium removal or fruit set compared with those that flowered later (ANOVA, pollinarium removal, $P = 0.671$; fruit set, $P = 0.474$). There was no significant difference between male and female reproductive success with regard to flowering duration (ANOVA, pollinarium removal, $P = 0.758$; fruit set, $P = 0.474$).

Discussion

The relationship between male and female reproductive success in *Phaius delavayi* was statistically significant

($r = 0.666$, $P < 0.01$), which indicates that male and female function are highly correlated and function simultaneously. In deceptive orchids, similar results have been observed in many cases (Schemske 1980; Barrett and Helenurm 1987; Ackerman 1989; Ackerman and Montalvo 1990; Proctor and Harder 1995). Nevertheless, the components of floral display showed different effects on male and female reproductive success in *P. delavayi*. Inflorescence size and flowering time had almost no effect on reproductive success, while clump size and flower position impacted variably.

Inflorescence size is an important trait that may affect the reproductive success of animal-pollinated plants, and choices made by pollinators can affect male and female reproductive success differently (Stanton et al. 1986). It has been stated that, in many orchid species, plants with larger inflorescence have higher pollinator visitation and probability of fruit set (Schemske 1980; Montalvo and Ackerman 1987; Frimage and Cole 1988; Broyles and Wyatt 1990; Calvo 1990; Robertson and Wyatt 1990; Young and Stanton 1990; Sabat and Ackerman 1996). Other, more recent studies, however, indicate that male and female reproductive success may be independent of inflorescence size, and that reproductive success seems to be more due to random pollinator movements than differences in attractiveness to pollinators (Ackerman 1989; Mattila and Kuitunen 2000; Aragón and Ackerman 2001; Lipow et al. 2002; Pellegrino et al. 2005a, b). In our study, the flower numbers in an inflorescence had no effect on either male or female reproductive success (Table 1; Fig. 3), concurring with the later body of research.

Several studies have investigated the relationship between flowering time and reproductive success (Campbell 1989; Fritz and Nilsson 1996). Evidence suggests that early flowering in nonrewarding orchids is advantageous because earlier-flowering plants will attract more naïve pollinators (Smithson and Macnair 1997; Castillo et al. 2002; Johnson et al. 2003; Parra-Tabla and Vargas 2004). In *Cypripedium acaule*, earlier-flowering plants have the greatest male and female pollination success (O'Connell and Johnston 1998). Zimmerman and Aide (1989) reported

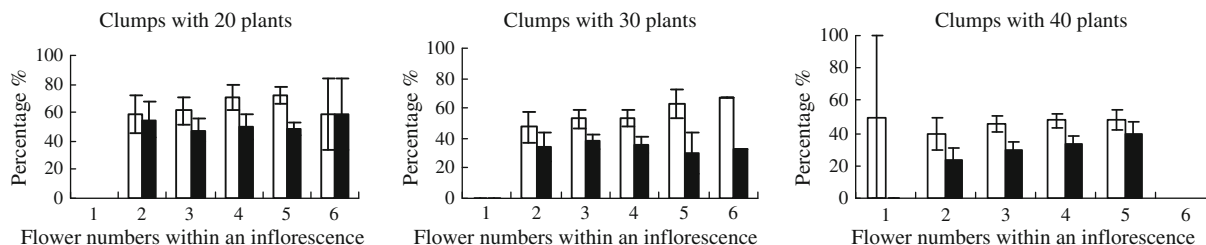


Fig. 3 Relationship between inflorescence size and pollinarium removal and fruit set in *Phaius delavayi*. White column, percentage of pollinarium removal; black column, percentage of fruit set

Table 2 Chi-square test of effects of flower position on pollinarium removal and fruit set in different clump sizes in *Phaius delavayi*

Clump size	Pollinarium removal		Fruit set	
	χ^2	<i>P</i>	χ^2	<i>P</i>
20	15.593	0.001***	14.553	0.012*
30	6.149	0.144 ^{NS}	16.291	0.001***
40	7.018	0.132 ^{NS}	3.068	0.546 ^{NS}

^{NS} not significant

* *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001

that fruit set of earlier-flowering plants was about three times higher than that of later-flowering ones in *Catasetum viridiflavum*. In contrast, Kropf and Renner (2005) found that the latest flowers in an inflorescence had higher reproductive success in *Dactylorhiza sambucina*. Parra-Tabla and Vargas (2004), however, found that individuals flowering earlier or later have higher reproductive success than population peak flowering in *Myrmecophila christinae*. However, our study showed no reproduction difference between individuals flowering early versus later, or between plants that had shorter or longer flowering duration, also indicating that pollinators may visit *P. delavayi* randomly during the whole flowering period.

In contrast, our results showed that pollinarium removal and fruit set were higher in small clumps than in large ones (Fig. 2). Although earlier studies showed that larger clumps may have higher reproductive success because they attract more pollinators (Peakall 1989; Aragón and Ackerman 2001; Ackerman and Ackerman 2001), the patterns we found in *P. delavayi* may be explained by the pollinator’s foraging behavior. Rewarded pollinators in a clump of rewarding plants tend to visit neighboring plants, whereas deceived pollinators usually immediately leave the clump (Johnson 2000). Firmage and Cole (1988) found that, in rewardless *Calopogon tuberosus*, pollinators abandon the plant clump after exploring a few unrewarding flowers, thus resulting in lower fruit set for flowers in the

whole clump. Kull (1998) found that fruit set per flower of *Cypripedium calceolus* decreased in larger clones. *Phaius delavayi* has a deceptive pollination system, and its pollinators are bumblebees (Li et al. 2010). Bumblebees can learn to discriminate flowers that offer no reward (Johnson et al. 2003; Schiestl 2005), although larger clusters would be more attractive to pollinators, receiving a greater number of approaches (Ackerman and Ackerman 2001), so they may have abandoned the clumps after a few visits, and had fewer visits per flower in larger clumps, subsequently decreasing the whole male and female reproductive success in larger clumps compared with smaller clumps.

In addition, flower position showed different effect patterns on male and female reproductive success in this study, a result clearly different from previous studies. Flower position effects on reproductive success in deceptive orchids have shown that either fruit set increases steadily from the top to the bottom of the inflorescence (Berry and Calvo 1991; Diggle 1995), that capsule production rates are highest in the middle part of the inflorescence (Vallius 2000), or that reproductive success may be independent of flower position (Vallius 2000; Pellegrino et al. 2005a, b). However, in *P. delavayi*, flower position did not produce a consistent effect on either male and female reproductive success. For male reproductive success, flower position had a significant difference in clumps with 20 flowering individuals, but not in clumps with 30 or 40 flowering individuals (Table 2; Fig. 4). However, for female reproductive success, flower position had a significant difference in clumps with 20 flowering individuals and with 30 flowering individuals, but not in clumps with 40 flowering individuals (Table 2; Fig. 4). It seems that the male function appears to be more buffered than the female function against the effect of flower position. These significant effects on male and female reproductive success may have been affected by pollinator behavior. Bumblebees may visit the lowest flowers first because of their inherent foraging behavior, and visitors may depart the inflorescence after encountering several nonrewarding

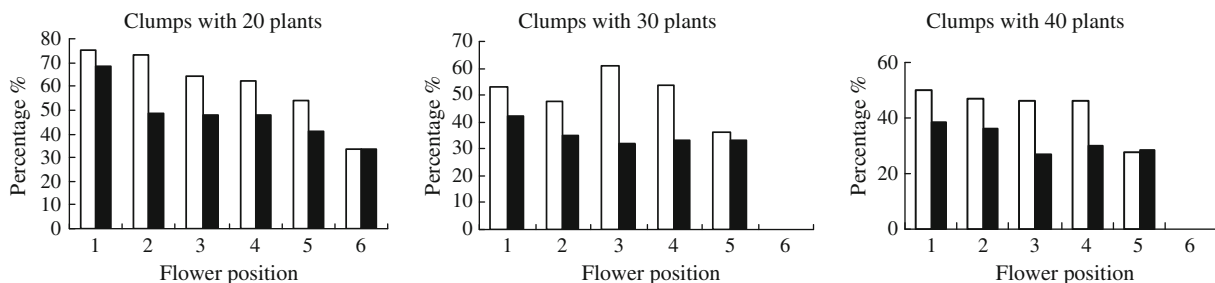


Fig. 4 Relationship between flower position and pollinarium removal and fruit set in *Phaius delavayi*. White column, percentage of pollinarium removal; black column, percentage of fruit set. The

number 1 indicates the basal flower in the raceme and 6 the distal, with 2–5 being intermediate flowers, respectively

flowers (Johnson et al. 2003; Schiestl 2005). Upper flowers will then receive less visitation compared with lower flowers, resulting in less pollinarium transfer and less pollinarium deposition. Insufficient availability of resources is probably another major reason for the reduction in capsule production from the bottom to the top of inflorescences (Light and MacConaill 1998; Vallius 2000). It is not yet clear why in our study flower position showed significant effects on male and female reproductive success in smaller clumps, but not in larger clumps. It seems that flower position may show variable effects on male and female reproductive success if clump size were taken into account. To our knowledge, this is the first study to investigate the effects of flower position on male and female reproductive success combined with clump size. Additional studies are needed to understand the relationship between flower position and male and female reproductive success with clump size.

Plants of *Phaius delavayi* grow in clusters of 10–50 individuals. However, we used only classes of 20, 30, and 40 individuals, representing the more common size classes. It is possible that the effects of fitness on display are mainly felt in the extreme classes, especially if the population is under stabilizing selection pressure, leading to disadvantage of the extremes and making the classes near the mean (20, 30, and 40) behave similarly. However, most plants of *P. delavayi* grow in clusters of 20–40 individuals, and classes of 10 or 50 individuals occur rarely without more than three in nature. Therefore, we chose the classes of 20, 30, and 40 individuals to mimic common naturally occurring groups. In addition, the number of repetitions of each class is a little low ($n = 3$), which may also influence the analysis and partly explain the results. However, we could show the patterns of floral display on reproductive fitness, and our study showed that floral display expressed by clump size and flower position impacted both female and male reproductive success in *P. delavayi*, whereas flowering initiation and duration, and inflorescence size did not.

Acknowledgments We thank two anonymous reviewers for improving the manuscript, and Drs. Qu Rongming, Shi Jun, Meng Qianwan, Yuan Xiaohong, and Yao Hong from the Institute of Botany, Chinese Academy of Sciences for their helpful advice. This paper was funded by the National Nature Science Foundation of China (30900183).

References

- Ackerman JD (1989) Limitations to sexual reproduction in *Encyclia krugii* (Orchidaceae). *Syst Bot* 14:101–109
- Ackerman EJ, Ackerman JD (2001) Density dependent variation in reproductive success in a terrestrial orchid. *Plant Syst Evol* 227:27–36
- Ackerman JD, Montalvo AM (1990) Short and long-term limitations to fruit production in a tropical orchid. *Ecology* 71:263–272
- Aragón S, Ackerman JD (2001) Density effects on the reproductive success and herbivory of *Malaxis massonii*. *Lindleyana* 16:3–12
- Barrett SCH, Helenurm K (1987) The reproductive biology of boreal forest herbs. I. Breeding system and pollination. *Can J Bot* 65:2036–2265
- Berry PE, Calvo RN (1991) Pollinator limitation and position-dependent fruit set in the high Andean orchid *Myrosmodus cochleare*. *Plant Syst Evol* 174:93–101
- Broyles SB, Wyatt R (1990) Paternity analysis in a natural population of *Asclepias exaltata*: multiple paternity, functional gender, and the “pollen-donation hypothesis”. *Evolution* 44:1454–1468
- Calvo RN (1990) Inflorescence size and fruit distribution among individuals of three orchid species. *Am J Bot* 77:1378–1381
- Campbell DR (1989) Measurements of selection in a hermaphroditic plant: variation in male and female pollination success. *Evolution* 43:318–334
- Castillo RA, Cordero C, Domínguez CA (2002) Are reward polymorphisms subject to frequency- and density-dependent selection? Evidence from a monoecious species pollinated by deceit. *J Evol Biol* 15:544–552
- Cozzolino S, Widmer A (2005) Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. *Trends Ecol Evol* 20:487–494
- Diggle PK (1995) Architectural effects and the interpretation of pattern of fruit and seed development. *Annu Rev Ecol Syst* 26:531–552
- Frimage DH, Cole FR (1988) Reproductive success and Inflorescence size in *Calopogon tuberosus* (Orchidaceae). *Am J Bot* 75:1371–1377
- Fritz AL, Nilsson LA (1996) Reproductive success and gender variation in Deceit-pollinated orchids. In: Lloyd DG, Barrett SCH (eds) *Floral biology: studies on floral evolution in animal-pollinated plants*. Chapman and Hall, New York, pp 319–338
- Johnson SD (2000) Batesian mimicry in the non-rewarding orchid *Disa pulchra*, and its consequences for pollinator behaviour. *Bot J Linn Soc* 71:119–132
- Johnson SD, Peter CI, Nilsson LA, Ågren J (2003) Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. *Ecology* 84:2919–2927
- Kropf M, Renner SS (2005) Pollination success in monochromic yellow populations of the rewardless orchid *Dactylorhiza sambucina*. *Plant Syst Evol* 254:185–197
- Kull T (1998) Fruit-set and recruitment in populations of *Cypripedium calceolus* L. in Estonia. *Bot J Linn Soc* 126:27–38
- Li P, Tang SY, Dong L, Luo YB, Kou Y, Yang YQ, Perner H (2005) Species diversity and flowering phenology of Orchidaceae in Huanglong Valley, Sichuan. *Biodiversity Sci* 13:255–261
- Li P, Zheng GL, Dafni A, Luo YB (2010) Reproductive biology of an alpine orchid *Phaius delavayi*. *Plant Syst Evol* 286:167–173
- Light MHS, MacConaill M (1998) Factors affecting germinable seed yield in *Cypripedium calceolus* var. *pubescens* (Willd) Correll and *Epipactis helleborine* (L.) Cranz (Orchidaceae). *Bot J Linn Soc* 126:3–26
- Lipow SR, Bernhardt P, Vance N (2002) Comparative rates of pollination and fruit set in widely separated populations of a rare orchid (*Cypripedium fasciculatum*). *Int J Plant Sci* 163:775–782
- Mattila E, Kuitunen MT (2000) Nutrient versus pollination limitation in *Platanthera bifolia* and *Dactylorhiza incarnata* (Orchidaceae). *Oikos* 89:360–366
- Montalvo AM, Ackerman JD (1987) Limitations to fruit production in *Ionopsis utricularioides*. *Biotropica* 19:24–31
- Nilsson LA (1992) Animal pollinators adjust plant gender in relation to floral display: evidence from *Orchis morio* (Orchidaceae). *Evol Trends Pl* 6:33–40

- O'Connell L, Johnston M (1998) Male and female pollination success in a deceptive orchid, a selection study. *Ecology* 79(4): 1246–1260
- Ohashi K, Yahara T (1999) How long to stay on, and how often to visit a flowering plant? A model for foraging strategy when floral displays vary in size. *Oikos* 86(2):386–392
- Parra-Tabla V, Vargas C (2004) Phenology and phenotypic natural selection on the flowering time of a deceit-pollinated tropical orchid, *Myrmecophila christinae*. *Ann Bot* 94:243–250
- Peakall R (1989) The unique pollination of *Leporella fimbriata* (Orchidaceae): pollination by pseudocopulating male ants (*Myrmecia urens*, Formicidae). *Plant Syst Evol* 167:137–148
- Pellegrino G, Caimi D, Noce ME, Musacchio A (2005a) Effects of local density and flower color polymorphism on pollination and reproduction in the rewardless orchid *Dactylorhiza sambucina* (L.) Soo. *Plant Syst Evol* 251:119–129
- Pellegrino G, Domenico D, Noce ME, Musacchio A (2005b) Reproductive biology and pollinator limitation in a deceptive orchid, *Serapias vomeracea* (Orchidaceae). *Plant Species Biol* 20:33–39
- Perner H, Cribb P (2002) Orchid wealth. *The Alpine Gardener* 70:285–294
- Proctor HC, Harder LD (1995) Effect of pollination on floral longevity in the orchid *Calypso bulbosa* (Orchidaceae). *Am J Bot* 82:1131–1136
- Robertson JL, Wyatt R (1990) Reproductive biology of the yellow-fringed orchid *Platanthera ciliaris*. *Am J Bot* 77:388–398
- Sabat AM, Ackerman JD (1996) Fruit set in a deceptive orchid: effect of flowering, display size, and local floral abundance. *Am J Bot* 83:1181–1186
- Schemske DW (1980) Evolution of floral display in the orchid *Brassavola nodosa*. *Evolution* 34:489–493
- Schiestl FP (2005) On the success of a swindle: pollination by deception in orchids. *Naturwissenschaften* 92:255–264
- Smithson A, Macnair MR (1997) Negative frequency-dependent selection by pollinators on artificial flowers without rewards. *Evolution* 51:715–723
- Stanton ML, Snow AA, Handel SN (1986) Floral evolution: attractiveness to pollinators increases male fitness. *Science* 232:1625–1627
- Tremblay RL, Ackerman JD, Zimmerman JK, Calvo RN (2005) Variation in sexual reproduction in orchids and its evolutionary consequences: a spasmodic journey to diversification. *Biol J Linn Soc* 84:1–54
- Vallius E (2000) Position-dependent reproductive success of flowers in *Dactylorhiza maculata* (Orchidaceae). *Functional Ecol* 14:573–579
- Vallius E, Salonen V (2000) Effects of male and female reproductive traits of a perennial orchid, *Dactylorhiza maculata*. *Functional Ecol* 14:668–674
- Van der Pijl L, Dodson CH (1966) *Orchid flowers: their pollination and evolution*. University of Miami Press, Coral Gables
- Young HJ, Stanton MC (1990) Influences of floral variation on pollen removal and seed production in wild radish. *Ecology* 71:536–547
- Zimmerman JK, Aide TM (1989) Patterns of fruit production in a neotropical orchid: pollinator versus resource limitation. *Am J Bot* 76:67–73