PROCEEDINGS OF THE ROYAL SOCIETY B

Proc. R. Soc. B (2005) **272**, 2651–2657
doi:10.1098/rspb.2005.3268
Published online 4 October 2005

Adaptive plasticity of floral display size in animal-pollinated plants

Lawrence D. Harder[1,*] and Steven D. Johnson[2]

[1]*Department of Biological Sciences, University of Calgary, Calgary, Alta., Canada T2N 1N4*
[2]*School of Botany and Zoology, University of KwaZulu-Natal, Private Bag X01 Scottsville, Pietermaritzburg 3209, South Africa*

Plants need not participate passively in their own mating, despite their immobility and reliance on pollen vectors. Instead, plants may respond to their recent pollination experience by adjusting the number of flowers that they display simultaneously. Such responsiveness could arise from the dependence of floral display size on the longevity of individual flowers, which varies with pollination rate in many plant species. By hand-pollinating some inflorescences, but not others, we demonstrate plasticity in display size of the orchid *Satyrium longicauda*. Pollination induced flower wilting, but did not affect the opening of new flowers, so that within a few days pollinated inflorescences displayed fewer flowers than unpollinated inflorescences. During subsequent exposure to intensive natural pollination, pollen removal and receipt increased proportionally with increasing display size, whereas pollen-removal failure and self-pollination accelerated. Such benefit–cost relations allow plants that adjust display size in response to the prevailing pollination rate to increase their attractiveness when pollinators are rare (large displays), or to limit mating costs when pollinators are abundant (small displays). Seen from this perspective, pollination-induced flower wilting serves the entire plant by allowing it to display the number of flowers that is appropriate for the current pollination environment.

Keywords: floral longevity; geitonogamy; orchid; plant mating

1. INTRODUCTION

Uncertain environments favour plastic traits that allow organisms to capitalize on prevailing conditions. Plasticity can evolve whenever the benefits of adopting a new state minus the costs of changing states exceed the outcome that would have been realized by not changing (see DeWitt *et al.* 1998; Relyea 2002). This condition arises when environmental conditions vary on a time-scale that allows the organism both to detect environmental change and to respond profitably (Alpert & Simms 2002).

Reproduction by animal-pollinated plants should commonly involve plastic traits, because outcrossing depends on pollinators whose abundance varies within and between reproductive seasons. Such variation can create strongly different pollination environments for individual plants (e.g. Schemske & Horvitz 1984; Young 1986; Schemske & Horvitz 1989), which favours different suites of traits to promote outcrossing success (e.g. Harder & Wilson 1994). During pollinator scarcity, outcrossing plants confront the risk of insufficient pollen export and import and so they should benefit most from increased attractiveness to pollinators. In contrast, during pollinator abundance, the emphasis shifts to enhancing the quality of pollinator visits. Because of the change in the types of traits favoured by low versus high pollinator abundance, fixed reproductive phenotypes should be less successful than plastic phenotypes when abundance varies extensively. Such plasticity requires that plants detect the prevailing abundance of pollinators and adjust their reproductive characteristics accordingly.

* Author for correspondence (harder@ucalgary.ca).

Plants that produce new flowers during a protracted period have the opportunity to adjust their reproductive organs to the prevailing pollination conditions. Nevertheless, the morphology of individual flowers is remarkably constant (e.g. MacDonald *et al.* 1988; Worley & Barrett 2000; Herrera 2001), perhaps reflecting the advantages of maintaining the mechanical fit between flower and pollinator (e.g. Cresswell 2000). In contrast, the number of open flowers per inflorescence (display size) can vary extensively with growth conditions (e.g. MacDonald *et al.* 1988; Worley & Barrett 2000; Meagher & Delph 2001). Floral display size emerges from the aggregate phenology of individual flowers (Ishii & Sakai 2001*a*; Meagher & Delph 2001). For example, if flowers open at a fixed rate, r, and each flower remains open for L days, then maximal display size equals rL (figure 1*a*; also see Primack 1985), so that a change in either anthesis rate or floral longevity alters display size by the same proportion (figure 1*b*). Either of these floral characteristics could be used to adjust display size to exploit the prevailing pollination environment. However, alteration of floral longevity in response to pollination provides a simpler mechanism than changing anthesis rate, because both the detection of pollination rate and the response involve the same flower. Furthermore, maintaining already open flowers to sustain a large display may be less demanding energetically than opening more, shorter-lived flowers per day.

Many angiosperms may adjust display size dynamically, as pollen–pistil interaction induces flower closure or wilting in species from at least 25 families of flowering plants (van Doorn 1997). In such species, rapid pollination shortens floral longevity and reduces floral

Received 28 April 2005
Accepted 1 August 2005

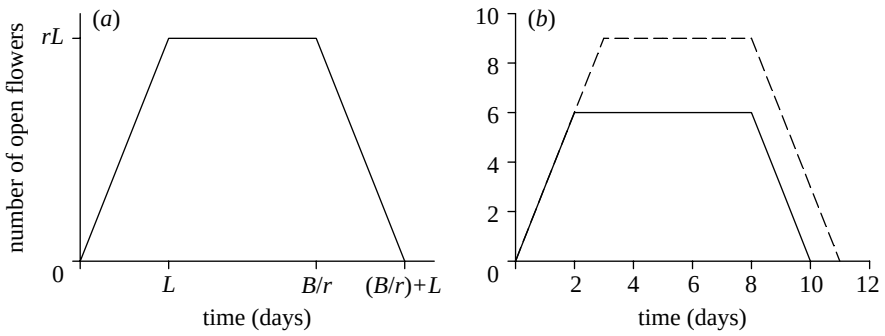

Figure 1. A simple model of the number of flowers open t days after flowering begins (D_t). The model plant produces B flower buds, which open at a constant rate, r, and each remains open for L days. Panel (*a*) illustrates the general dynamics of display size: $D_t = rt$ during the growth phase, which lasts L days; $D_t = rt - r(t-L) = rL$ during the equilibrium phase, between L and B/r days; and $D_t = B - r(t-L)$ during the senescent phase, from B/r days until flowering finishes. Panel (*b*) demonstrates that shortening floral longevity from $L = 3$ days (dashed line) to 2 days (solid line) both condenses the period of inflorescence display and reduces maximal display size. For panel (*b*), $B = 24$ buds and $r = 3$ flowers per day.

display size (figure 1*b*), although the latter response has seldom been reported (Karrenberg & Jensen 2000). We hypothesize that such adjustment of display size allows plants to benefit from contrasting advantages, depending on pollinator abundance. When pollinators visit infrequently, large displays are advantageous because they attract more pollinators (reviewed by Ohashi & Yahara 2001), which should increase a plant's likelihood of pollen import and export. In contrast, when pollinators visit often, the advantage turns to small displays, because they experience less self-pollination between flowers (geitonogamy: Harder & Barrett 1996; Snow *et al.* 1996), thereby limiting inbreeding in self-compatible species and leaving more pollen on pollinators to be exported to other plants (reviewed by Harder *et al.* 2004). Indeed, because of geitonogamy costs, an increased number of visits per flower when pollinators are abundant can counter-intuitively reduce a plant's fitness, particularly through pollen export (Iwasa *et al.* 1995; Harder *et al.* 2001). The costs of retaining older flowers may be compounded if a flower's ability to exchange pollen with pollinators declines with age, because of a decline in stigmatic receptivity (e.g. Young & Gravitz 2002) or the susceptibility of pollen to removal, thereby hampering pollen import and/or export. In general, the advantage of adjusting display size to pollination rate will depend on the extent to which the overall benefits and costs increase with the number of open flowers.

In this paper, we assess adaptive plasticity in the number of flowers displayed by the orchid *Satyrium longicauda* Lindl. We first demonstrate that pollination-sensitive floral longevity controls display size in this species. Then, we assess whether alternative display sizes realize differing benefits and costs during subsequent pollination when pollinators are abundant and small displays should be favoured. This analysis illustrates the mating advantages associated with dynamic adjustment of display size when pollinator abundance varies.

2. METHODS

(a) *Study species*

We studied *S. longicauda* at Garden Castle in Ukhahlamba-Drakensberg Park, South Africa (29°45′ S, 29°15′ E). This species is moth-pollinated and occupies grasslands from southeastern South Africa to Tanzania (Hall 1982). Flowering plants produce a single spike with greater than 20 flowers, which open gradually from the bottom upward. The entrance to each of the two nectar spurs in a *S. longicauda* flower is hidden behind the rostellum of the sexual column, so that a pollinator's proboscis is likely to contact one of the two viscidia and remove the attached pollinium (Johnson 1997). Unlike many orchids, the pollinarium of *S. longicauda* does not reorient after a latency period, so that pollen can be deposited on the stigma of any flower visited subsequently. A *S. longicauda* pollinium is segmented into many massulae (mean ± s.d. = 153 ± 21.0 massulae at our study site, $n = 15$ plants), so that pollen from a single pollinium can disperse to stigmas of many recipient flowers.

(b) *Display plasticity and pollination*

Our assessment of the plasticity of display size and its effects on pollination involved plants that had not been exposed to pollinators during the 2001 flowering season. On 1st December, we enclosed 47 individual inflorescences with swollen flower buds in mesh bags. One week later, on 8th December, we selected half of the plants randomly and pollinated all of their open flowers with pollinaria removed from plants at least 1 m away and then enclosed them again. If pollination induces flower senescence, these 'pre-pollinated' plants should have smaller inflorescences a few days later than the remaining 'unpollinated' plants.

We quantified pollen removal and deposition for non-wilted flowers on experimental inflorescences during a single night's exposure to moth pollination. During the afternoons of 12th and 13th December (i.e. 4 or 5 days after hand-pollinating pre-pollinated inflorescences), we removed the mesh bags from half of the pre-pollinated and previously unpollinated plants, selected to form clusters of four plants (two of each treatment), which were separated from other clusters by at least 5 m. To measure self-pollination on these inflorescences, we injected aqueous histochemical stain into the anther sacs of half the flowers on an inflorescence to mark the pollinia. Pollinia were stained in only half of an inflorescence's flowers to allow us to distinguish with-flower self-pollination from geitonogamy, as revealed by the presence of stained massulae on stigmas of flowers on the same inflorescence whose pollinia had not been stained. The staining procedure followed Peakall's (1989) protocol (also see Johnson *et al.* in press) and we used a different stain colour for each of the four plants in a cluster. Staining does not affect the probability of either pollinarium removal by

pollinators (Peakall 1989) or pollen deposition (Johnson *et al.* in press). After staining, we left the experimental inflorescences exposed to pollinators until the next afternoon. During the evenings of 12th and 13th December, we observed the study population for 1 h to record the behaviour of moths on inflorescences. On both nights we counted the numbers of visited and open flowers on inflorescences during visits by individual moths.

After experimental inflorescences had been exposed to pollination for one night, we collected them to assess pollination outcomes. For each inflorescence, we numbered open flowers from the top, youngest flower downward. We examined each flower under a dissecting microscope (12×) and recorded the following information: the number of pollinaria that had been removed, the number of pollinaria that had been dislodged by a pollinator, but remained in the flower, whether massulae had been deposited on the stigma and the number of stained massulae on the stigma with the same colour as was applied to the plant's own pollinaria (self-pollination).

We estimated the relative occurrence of between- versus within-flower self-pollination, following the approach of Johnson *et al.* (in press). In particular, for each plant we recognized two classes of stained self-massulae. The m_g stained massulae on stigmas of the f_g self-pollinated flowers with either unstained pollinaria or no stained pollinaria removed could have been deposited only by geitonogamy. In contrast, the m_{ag} stained massulae on stigmas of the f_{ag} self-pollinated flowers from which pollinators removed stained pollinaria could have been deposited by geitonogamy and/or facilitated autogamy. Given these massulae and flower counts, the fraction of self-massulae resulting from geitonogamy can be estimated by $g = m_g(f_g + f_{ag})/(f_g[m_g + m_{ag}])$. We conducted this calculation based on the sums of f_g, f_{ag}, m_g and m_{ag} for all plants, rather than the average g based on estimates for each plant, because simulation studies indicated that the latter approach results in a slight positive bias. We used bootstrap resampling (10 000 samples) of the 36 experimental inflorescences with at least two open flowers on which we found stained self-massulae to estimate the 95% confidence interval associated with the average geitonogamy fraction.

(c) *Statistical analyses*

Our statistical analyses considered the effects of experimental treatment (pre-pollinated versus previously unpollinated inflorescences) on pollinator behaviour, pollinarium removal and self-pollination. We also included independent variables that were not components of the experimental design (e.g. flower position, pollinarium removal) in the final analyses if they affected the dependent variable of interest significantly ($\alpha = 0.05$), as determined by backward elimination. In the analysis of display plasticity, we identified the details of a significant interaction between pollination treatment and experimental stage (at the time of hand pollination versus during open pollination) with *a posteriori* contrasts that used the Dunn–Šidák procedure to control the experiment-wise Type I error rate to $\alpha = 0.05$ (Kirk 1995).

We used general linear models (Neter *et al.* 1996) to test statistical hypotheses concerning most absolute outcomes (e.g. number of self-massulae received per flower) with F-tests. All of these analyses involved suitable transformation of the dependent variable to assure that error terms were normally distributed and had homogenous variances. We used the GLM procedure of SAS to analyse variables measured once for each inflorescence and the Mixed procedure to analyse repeated measures (version 8.2, SAS 2001).

We analysed statistical hypotheses about rare absolute outcomes (e.g. number of pollinaria dislodged, but not removed from inflorescences) and most proportional outcomes (e.g. proportion of flowers on inflorescences receiving self-massulae) with likelihood-ratio (G) tests of generalized linear models (McCullagh & Nelder 1989). Analyses of frequency counts involved ln-transformation and considered a Poisson error distribution, whereas those of proportions involved logit-transformation of the dependent variable and incorporated a binomial error distribution. These analyses used the GENMOD procedure of SAS (2001).

We assessed whether flower position within inflorescences (F: $F = 1$ for top flowers) affected the proportion of flowers receiving self-pollen (P_s) according to $\hat{P}_s = P_{max}(1 - e^{-dF})$, where P_{max} estimates the asymptotic proportion of self-pollinated flowers and d governs the rate at which the asymptote is approached as F increases. This analysis incorporated a binomial error distribution and the model was fit by maximum likelihood with the NLP procedure of SAS (2001).

3. RESULTS

The number of open flowers on a *S. longicauda* inflorescence represents a dynamic balance between the wilting of pollinated flowers at the bottom of the inflorescence and the opening of new flowers at the top. During the first week of flowering, bagged inflorescences opened flowers at a mean (±s.e.) rate of 1.2±0.05 flowers per day. No flowers wilted on bagged inflorescences during this period, so that they displayed an average of 8.2 flowers (lower s.e. = 0.42, upper s.e. = 0.43, based on square-root transformed data) at the time of hand pollination, with no significant difference between plants that we then hand-pollinated or left unpollinated (Dunn–Šidák multiple comparison, $t_{90} = 1.32$, $p > 0.25$). During the next 4 or 5 days, inflorescences in both treatment groups continued opening flowers at the same rate as before hand pollination (1.3±0.08 flowers per day, $F_{1,77} = 0.32$, $p > 0.5$), with no difference between groups (treatment effect, $F_{1,77} = 0.65$, $p > 0.4$; treatment×stage interaction, $F_{1,77} = 1.10$, $p > 0.25$). However, hand pollination induced a significant difference in flower wilting, so that a median of seven flowers wilted on pre-pollinated inflorescences (lower quartile = 5, upper quartile = 8.5 flowers), compared to a median of only two wilted flowers on unpollinated inflorescences (lower quartile = 0, upper quartile = 4 flowers: Kruskal–Wallis test, $\chi^2_1 = 23.5$, $p < 0.001$). As a result, unpollinated inflorescences displayed an average of 12.2 flowers (lower s.e. = 0.73, upper s.e. = 0.76) when they were exposed to pollinators, whereas those that had been hand-pollinated presented an average of only 6.4 open flowers (lower s.e. = 0.52, upper s.e. = 0.54: Dunn–Šidák multiple comparison, $t_{90} = 6.5$, $p < 0.001$), resulting in a significant interaction between pollination treatment and stage of the experiment ($F_{1,90} = 13.4$, $p < 0.001$). Thus, by inducing senescence of individual flowers, pollination controls the display size of entire inflorescences. Unmanipulated plants in the general population displayed a median of 6.4 flowers (lower quartile = 5 flowers, upper quartile = 7 flowers; $n = 107$) when the experimental plants were exposed to pollinators.

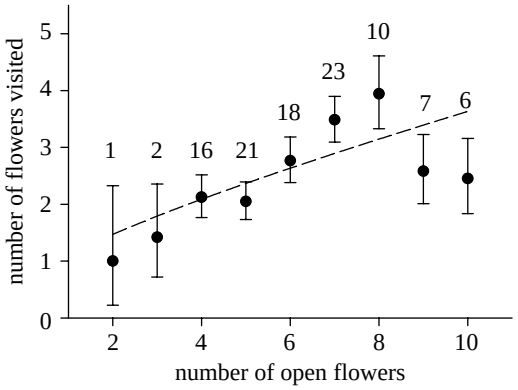

Figure 2. The tendency of moths to visit more flowers on larger *Satyrium longicauda* inflorescences ($F_{1,96}=8.39$, $p<0.005$). Data represent least-square means (±s.e.: based on square-root transformed data) from a repeated-measures analysis for 70 moths, with the number of observations per display size indicated numerically. The dashed line illustrates the regression model based on square-root transformed data for number of flowers visited (V) and floral display size (N), $\sqrt{V}=0.651+0.397\sqrt{N}$.

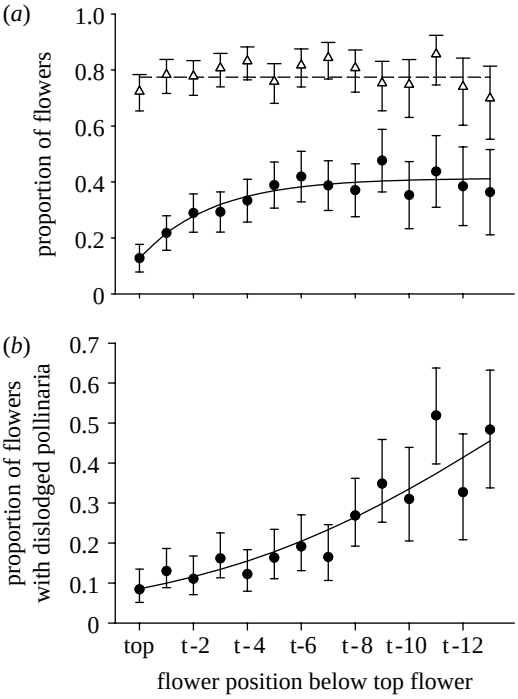

Figure 3. Relations of the mean (±s.e.) proportions of flowers with (*a*) at least one pollinarium removed (open symbols), receipt of at least one self-massula (closed symbols) and (*b*) at least one pollinarium dislodged, but not removed, to flower position within *Satyrium longicauda* inflorescences during a single night's exposure to moth pollination. Note that flower age increases from the youngest top flower down an inflorescence to the lowest, oldest flowers, because flowers open sequentially at the top of an inflorescence. Lines indicate general variation in means within inflorescences, based on regression analysis (see text for details).

At our study site, noctuid and sphingid moths visited *S. longicauda* actively after dusk, so that all experimental plants showed evidence of having been visited (pollinaria removed and/or massulae on stigmas). Seventy moths observed foraging in the general population during two evenings visited significantly more flowers on larger inflorescences (figure 2). The proportion of flowers visited

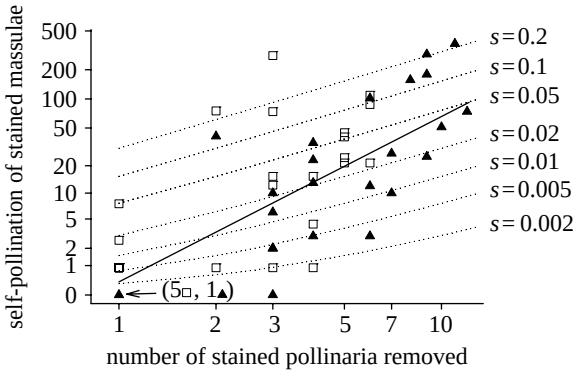

Figure 4. Dependence of self-pollination of *Satyrium longicauda* inflorescences on pollinarium removal during a single night's exposure to moth pollination. Open squares indicate pre-pollinated inflorescences, whereas closed triangles represent previously unpollinated inflorescences. The dotted isoclines illustrate fixed proportions of removed massulae that were deposited on a plant's own stigmas (s). The solid regression line ($F_{1,42}=30.28$, $p<0.001$: based on ln-transformed data) crosses these isoclines, indicating an acceleration in self-pollination with increased pollinarium removal.

per inflorescence did not vary significantly with display size (generalized linear model, $G_1=2.98$, $p>0.05$).

A single night of moth visits resulted in contrasting patterns in the incidence of pollinarium removal and self-pollination among flowers within inflorescences (figure 3*a*). On average, moths removed at least one pollinarium from 77.4% (lower s.e.=5.50%, upper s.e.=4.69%; based on logit-transformed data) of all flowers and removal did not vary significantly with flower position ($G_1=0.11$, $p>0.5$; figure 3*a*, open symbols). In contrast, the mean (±s.e.) percentage of flowers receiving at least one self-massula increased from 12.8±4.92% on top, youngest flowers to an asymptote of 41.4±1.75% on lower, old flowers (figure 3*a*, closed symbols). As pollinaria were stained in only half of the flowers on inflorescences, the preceding results underestimate the actual incidence of self-pollination.

By visiting more flowers on large displays, moths caused pollination differences between pre-pollinated and previously unpollinated inflorescences, which largely reflect their twofold difference in average display size. Overall, moths removed half as many pollinaria from pre-pollinated plants (mean±s.e.=7.5±0.9; based on square-root transformed data) as from previously unpollinated plants (13.6±1.3: $F_{1,43}=15.80$, $p<0.001$). In addition, half as many flowers on pre-pollinated plants received pollen massulae on their stigmas (mean±s.e.=5.4±0.64 flowers) as on previously unpollinated plants (10.0±0.65 flowers: $F_{1,43}=25.73$, $p<0.001$). Thus, both pollen removal and receipt during a single night's exposure to pollinators differed between the inflorescence types in direct proportion to their display size.

In contrast to this proportionality, two mating costs accelerated with increasing display size in *S. longicauda*. One cost resulted when moths dislodged pollinaria without removing them, precluding removal by subsequent visitors. The incidence of these lost opportunities for pollen export increased with floral age ($G_1=11.85$, $p<0.001$; figure 3*b*). In particular, moths dislodged pollinaria in over 30% of flowers that were old enough

that eight or more flowers had opened above them. Previously unpollinated inflorescences had large floral displays because they retain flowers of this age or older, so that moths dislodged an average of 2.8 pollinaria (lower s.e = 0.33, upper s.e. = 0.37, based on ln-transformed data) on previously unpollinated inflorescences compared to only 1.2 pollinaria (lower s.e. = 0.21, upper s.e = 0.25) on pre-pollinated inflorescences. Thus, plants with large displays experienced significantly less pollen removal overall ($G_1 = 15.31$, $p < 0.001$) than would have been possible if pollinators had visited their older flowers sooner.

The second potentially detrimental outcome of maintaining unpollinated flowers involved self-pollination. We detected self-pollination on 66.7% of pre-pollinated inflorescences and 91% of previously unpollinated inflorescences ($G_1 = 4.50$, $p < 0.05$). Furthermore, previously unpollinated plants received significantly more self-massulae than pre-pollinated plants ($F_{1,43} = 4.62$, $p < 0.05$; figure 4). These differences in the incidence and intensity of self-pollination arose because moths removed more stained massulae from the larger displays of previously unpollinated inflorescences than they removed from pre-pollinated inflorescences. As a result, differences between inflorescence types disappeared when the analyses included the number of stained massulae removed from an inflorescence as a covariate (incidence, $G_1 = 0.12$, $p > 0.7$; intensity, $F_{1,42} = 0.01$, $p > 0.9$). Overall, the intensity of self-pollination increased disproportionately with removal of stained pollinaria, rising from an average of 0.2% of removed massulae following removal of one pollinarium to 4% after removal of 10 pollinaria (figure 4). Such increased self-pollination could greatly aggravate losses of progeny to inbreeding depression in self-compatible species, such as orchids.

The greater self-pollination experienced by previously unpollinated plants probably also reduced their relative success at exporting pollen to other plants, because geitonogamy accounted for an estimated 90% of the detected self-pollination (95% confidence interval, 72.9–101.4%). Geitonogamy involves the same processes as pollen transport between plants and so diminishes opportunities for male outcrossing directly (Lloyd 1992; Harder & Barrett 1995). Of the stained massulae removed from our experimental inflorescences, 4.9% were involved in self-pollination on pre-pollinated inflorescences compared to 7.0% on previously unpollinated plants. These percentages represent sizeable fractions of the 12.7% of removed pollen massulae that reached stigmas in this population (based on pollinarium removal and massulae receipt for 32 open-pollinated plants). Therefore, plants that retain old flowers to increase display size may suffer a considerable reduction in their outcross siring potential (pollen discounting).

4. DISCUSSION

By inducing senescence of individual flowers, pollen receipt altered the number of flowers displayed by *S. longicauda* inflorescences. Such plasticity in display size is probably widespread, as floral longevity varies with pollination success in at least 25 families of angiosperms (van Doorn 1997). In particular, induction of floral senescence by pollination occurs in taxa in which floral longevity can be shortened by elevated ethylene concentrations (van Doorn 1997), which includes at least six monocot and 28 eudicot families (van Doorn 2001). Thus, pollen receipt may alter floral display size in many plant species. Notable exceptions seem to include species with protogynous flowers, species with single-day flowers and the Asteraceae, as floral longevity is insensitive to pollen receipt in these plants (van Doorn 1997). Rapid pollen removal may also affect display size, as it shortens the male phase in flowers of some species (reviewed by Ashman 2004).

The plasticity in display size exhibited by *S. longicauda* seems adaptive, providing a means of increasing pollination when pollinators are rare and limiting pollination costs when pollinators are abundant. Our results show that *S. longicauda* plants subjected to pollen limitation develop larger floral displays, which should enhance their attractiveness to pollinators (see Ohashi & Yahara 2001). This benefit was probably weak in our experiment, because moths were so common that all plants received visits during a single night's exposure. Increased attractiveness comes at the cost of both increased pollen-removal failure due to a decline in competency as flowers age (dislodged pollinaria, figure 3*b*) and increased geitonogamy (figure 4, closed symbols) caused by each pollinator visiting more flowers per visit (figure 2). Nevertheless, increased display size should be advantageous when pollinators are rare, as long as the benefits of increased attraction outweigh the costs. For example, the increased assurance of some reproductive output may mitigate the negative effects of geitonogamy in self-compatible species, such as orchids. Although geitonogamy has been characterized as unlikely to provide reproductive assurance (Herlihy & Eckert 2002), it can play this role when it is associated with more pollinator visits to a plant (Lloyd 1992), such as when pollinator-limited plants become more attractive by retaining older flowers. Thus, display-size plasticity allows plants to promote pollination quantity, despite reduced quality, during pollinator scarcity. As a consequence, declining seed production due to pollen limitation should be accompanied by more pollinator-mediated self-pollination for species with plastic display size.

Plants that displayed few flowers because they had been pollinated recently benefited during subsequent intensive pollinator visitation. Because of their small displays, these plants experienced less geitonogamous self-pollination (figure 4, open symbols). This advantage was probably smaller than possible, because younger, upper flowers of *S. longicauda* seem less able to receive pollen, even though they experience similar pollen removal, to older, lower flowers (compare closed and open symbols, respectively, in figure 3*a*). As a consequence of the lower self-pollination on plants with small displays, their seeds would be less likely to suffer inbreeding depression. In addition, the limitation of geitonogamy probably allowed plants with small displays to export a larger proportion of removed pollen than if they had displayed more flowers. Therefore, the reduction in display size in response to previous intensive pollination allowed plants to capitalize on pollinator abundance and control the quality of mating resulting from each visit.

The ability of floral longevity to influence floral display size in a manner that promotes pollination and mating success indicates that floral longevity serves both floral and

inflorescence functions for multi-flowered plants. In contrast, floral longevity is currently viewed as a trait that primarily serves individual flowers, balancing the benefits of pollen import and export per flower against the resource costs of producing and maintaining a flower (reviewed by Ashman 2004). One exception is Schoen & Ashman's (1995) consideration of the implications of floral longevity for pollinator attraction; however, their model proposed that attraction varies linearly with total flower production, rather than with display size, and it did not consider the implications for geitonogamy. For example, Ishii & Sakai (2001*b*) found that flowers of *Iris gracilipes* lived 2 days, rather than 10 days predicted by Schoen & Ashman (1995) model, which they attributed to selection for smaller floral displays to limit geitonogamy. This example and our results illustrate that understanding of the function and evolution of floral longevity would be enhanced by an expanded perspective, which considers its consequences for the effects of display size on pollination and mating.

In conclusion, plants with multiple flowers and pollination-induction of floral senescence do not participate passively in their interaction with pollinators. Instead, they can react to pollination rate to adjust the number of flowers they display. In particular, flexibility in display size enhances pollinator attraction when pollinators are rare and limits self-pollination when pollinators are common. Given that pollinator abundance governs the relative merits of different display sizes, plants that experience variable pollinator abundance, either within or between seasons, should benefit greatly from the ability to adjust display size to pollination rate. As we have demonstrated, pollination-induced senescence of individual flowers provides a simple mechanism for implementing such adjustment.

We are grateful to D. Hensley for field assistance, KwaZulu-Natal Wildlife for accommodation and permission to conduct field research in Ukhahlamba-Drakensberg Park, and S. C. H. Barrett and three anonymous reviewers for comments on the manuscript. This research was funded by the Natural Sciences and Engineering Research Council of Canada (LDH) and the National Research Foundation of South Africa (SDJ).

REFERENCES

Alpert, P. & Simms, E. L. 2002 The relative advantages of plasticity and fixity in different environments: when is it good for a plant to adjust? *Evol. Ecol.* **16**, 285–297. (doi:10.1023/A:1019684612767.)

Ashman, T. L. 2004 Flower longevity. In *Cell death in plants* (ed. L. D. Nooden), pp. 349–362. London: Elsevier.

Cresswell, J. E. 2000 Manipulation of female architecture in flowers reveals a narrow optimum for pollen deposition. *Ecology* **81**, 3244–3249.

DeWitt, T. J., Sih, A. & Wilson, D. S. 1998 Costs and limits of phenotypic plasticity. *Trends Ecol. Evol.* **13**, 77–81. (doi:10.1016/S0169-5347(97)01274-3.)

Hall, A. V. 1982 *A revision of the southern African species of Satyrium. Contributions from the Bolus Herbarium. No. 10.* Rondebosch, Republic of South Africa: University of Cape Town.

Harder, L. D. & Barrett, S. C. H. 1995 Mating cost of large floral displays in hermaphrodite plants. *Nature* **373**, 512–515. (doi:10.1038/373512a0.)

Harder, L. D. & Barrett, S. C. H. 1996 Pollen dispersal and mating patterns in animal-pollinated plants. In *Floral biology: studies on floral evolution in animal-pollinated plants* (ed. D. G. Lloyd & S. C. H. Barrett), pp. 140–190. New York: Chapman & Hall.

Harder, L. D. & Wilson, W. G. 1994 Floral evolution and male reproductive success: optimal dispensing schedules for pollen dispersal by animal-pollinated plants. *Evol. Ecol.* **8**, 542–559. (doi:10.1007/BF01238257.)

Harder, L. D., Williams, N. M., Jordan, C. Y. & Nelson, W. A. 2001 The effects of floral design and display on pollinator economics and pollen dispersal. In *Cognitive ecology of pollination* (ed. L. Chittka & J. D. Thomson), pp. 297–317. Cambridge: Cambridge University Press.

Harder, L. D., Jordan, C. Y., Gross, W. E. & Routley, M. B. 2004 Beyond floricentrism: the pollination function of inflorescences. *Plant Species Biol.* **19**, 137–148. (doi:10.1111/j.1442-1984.2004.00110.x.)

Herlihy, C. R. & Eckert, C. G. 2002 Genetic cost of reproductive assurance in a self-fertilizing plant. *Nature* **416**, 320–323. (doi:10.1038/416320a.)

Herrera, J. 2001 The variability of organs differentially involved in pollination, and correlation of traits in Genisteae (Leguminosae: Papilionoideae). *Ann. Bot.* **88**, 1027–1037. (doi:10.1006/anbo.2001.1541.)

Ishii, H. S. & Sakai, S. 2001*a* Effects of display size and position on individual floral longevity in racemes of *Narthecium asiaticum* (Liliaceae). *Funct. Ecol.* **15**, 396–405. (doi:10.1046/j.1365-2435.2001.00536.x.)

Ishii, H. S. & Sakai, S. 2001*b* Implications of geitonogamous pollination for floral longevity in *Iris gracilipes*. *Funct. Ecol.* **15**, 633–641. (doi:10.1046/j.0269-8463.2001.00560.x.)

Iwasa, Y., de Jong, T. J. & Klinkhamer, P. G. L. 1995 Why pollinators visit only a fraction of the open flowers on a plant: the plant's point of view. *J. Evol. Biol.* **8**, 439–453. (doi:10.1046/j.1420-9101.1995.8040439.x.)

Johnson, S. D. 1997 Insect pollination and floral mechanisms in South African species of *Satyrium* (Orchidaceae). *Plant Syst. Evol.* **204**, 195–206. (doi:10.1007/BF00989205.)

Johnson, S. D., Neal, P. R. & Harder, L. D. In press. Pollen fates and the limits on male reproductive success in an orchid population. *Biol. J. Linn. Soc.*

Karrenberg, S. & Jensen, K. 2000 Effects of pollination and pollen source on the seed set of *Pedicularis palustris*. *Folia Geobot.* **35**, 191–202.

Kirk, R. E. 1995 *Experimental design: procedures for the behavioural sciences*, 3rd edn. Pacific Grove, CA: Brooks/Cole.

Lloyd, D. G. 1992 Self- and cross-fertilization in plants. II. The selection of self-fertilization. *Int. J. Plant Sci.* **153**, 370–380. (doi:10.1086/297041.)

MacDonald, S. E., Chinnappa, C. C. & Reid, D. M. 1988 Evolution of phenotypic plasticity in the *Stellaria longipes*: complex comparisons among cytotypes and habitats. *Evolution* **42**, 1036–1046.

McCullagh, P. & Nelder, J. A. 1989 *Generalized linear models* 2nd edn. London: Chapman & Hall.

Meagher, T. R. & Delph, L. F. 2001 Individual flower demography, floral phenology and floral display size in *Silene latifolia*. *Evol. Ecol. Res.* **3**, 845–860.

Neter, J., Kutner, M. H., Nachtsheim, C. J. & Wasserman, W. 1996 *Applied linear statistical models* 4th edn. Chicago: Irwin.

Ohashi, K. & Yahara, T. 2001 Behavioural responses of pollinators to variation in floral display size and their influences on the evolution of floral traits. In *Cognitive ecology of pollination* (ed. L. Chittka & J. D. Thomson), pp. 274–296. Cambridge: Cambridge University Press.

Peakall, R. 1989 A new technique for monitoring pollen flow in orchids. *Oecologia* **79**, 361–365. (doi:10.1007/BF00384315.)

Primack, R. B. 1985 Longevity of individual flowers. *Annu. Rev. Ecol. Syst.* **16**, 15–37. (doi:10.1146/annurev.es.16.110185.000311.)

Relyea, R. A. 2002 Costs of phenotypic plasticity. *Am. Nat.* **159**, 272–282. (doi:10.1086/338540.)

SAS Institute Inc. 2001 SAS OnlineDoc, Version 8.2. Cary, North Carolina: SAS Institute Inc.

Schemske, D. W. & Horvitz, C. C. 1984 Variation among floral visitors in pollination ability: a precondition for mutualism specialization. *Science* **225**, 519–521.

Schemske, D. W. & Horvitz, C. C. 1989 Temporal variation in selection on a floral character. *Evolution* **43**, 461–464.

Schoen, D. J. & Ashman, T.-L. 1995 The evolution of floral longevity: resource allocation to maintenance versus construction of repeated parts in modular organisms. *Evolution* **49**, 131–139.

Snow, A. A., Spira, T. P., Simpson, R. & Klips, R. A. 1996 The ecology of geitonogamous pollination. In *Floral biology: studies on floral evolution in animal-pollinated plants* (ed. D. G. Lloyd & S. C. H. Barrett), pp. 191–216. New York: Chapman & Hall.

van Doorn, W. G. 1997 Effects of pollination on floral attraction and longevity. *J. Exp. Bot.* **48**, 1615–1622. (doi:10.1093/jexbot/48.314.1615.)

van Doorn, W. G. 2001 Categories of petal senescence and abscission: a re-evaluation. *Ann. Bot.* **87**, 447–456. (doi:10.1006/anbo.2000.1357.)

Worley, A. C. & Barrett, S. C. H. 2000 Evolution of floral display in *Eichhornia paniculata* (Pontederiaceae): direct and correlated responses to selection on flower size and number. *Evolution* **54**, 1533–1545.

Young, H. J. 1986 Beetle pollination of *Dieffenbachia longispatha* (Araceae). *Am. J. Bot.* **73**, 931–944.

Young, H. J. & Gravitz, L. 2002 The effects of stigma age on receptivity in *Silene alba* (Caryophyllaceae). *Am. J. Bot.* **89**, 1237–1241.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.