

Rates of pollen deposition and removal in *Myosotis colensoi*

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Summary

1. The flowers of *Myosotis colensoi* are protogynous. The stigma is accessible for pollination for several hours before pollen is presented. One or two days after a flower opens, scales at the mouth of the corolla tube change colour, signalling the start of a protracted post-pollination phase. Flowers in this phase present neither pollen nor receptive stigmas and they are avoided by the principal visitor — a tachinid fly.

2. Hand pollination of protected stigmas shows that they remain receptive throughout the life of the flower. During favourable weather, however, pollen is deposited on most stigmas before the anthers dehisce. The effective female phase is thus shorter than the nominal period based on either the period of stigma receptivity or the end of the period before pollen presentation. The effective male phase is much longer, requiring as many as 12–14 separate visits to complete.

3. Pollen presentation is staggered because the five anthers dehisce sequentially over several hours. This process extends the period over which pollen is removed.

4. Periods of poor weather alter the presentation schedule and pollen removal and deposition rates, lengthen the effective phase durations and cause a partial temporal overlap in sexual functions. These results are discussed with reference to theories of sexual selection.

Key-words: Dichogamy, effect of climate, phenology, pollen presentation, sexual selection

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Introduction

Bateman (1948) observed that, for oogamous plants and animals, the maternal expenditure on an offspring is usually much higher than the paternal expenditure. He postulated that, as a consequence, maternal fitness is more often limited by the resources available for reproduction, while paternal success is more limited by the number of offspring able to be sired. He argued that this leads to competition between males and that there is sexual selection for traits that confer an advantage in maximizing the number of offspring sired. This concept has come to be known as 'Bateman's Principle' and has been recognized as an important component of the reproductive strategies of animals and, more recently, plants (Charnov 1979; Willson 1979; Lloyd & Yates 1982; Queller 1983). Charnov (1979) argued that where the conditions of Bateman's Principle hold, most gains in fitness from

expenditure on attraction structures occur through the male function. Hence selection in hermaphrodites should principally favour traits that improve the successful export of pollen to compatible stigmas. Sexual selection has been invoked to explain the apparent over-production of hermaphrodite flowers that do not set seed (Willson & Rathcke 1974; Willson & Price 1977; Queller 1983; Couvet, Henry & Gouyon 1984; Sutherland & Delph 1984; Spalik 1991). Some empirical data have been collected that indicate that the female function becomes saturated with relatively little expenditure on attraction structures, and that most fitness gains from increasing the structures are made on the paternal side (Bell 1985; Stanton, Snow & Handel 1986). Willson (1979) suggested that sexual selection may be important in explaining the evolution of other traits including sex expression, resource allocations, pollinator mechanisms and the relative duration of staminate and pistillate phases.

Unfortunately, the relative duration of male and female phases has often been measured in ways that give ambiguous or misleading results. Phase dur-

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ations are usually assessed by the physical appearance of anthers and stigmas (e.g. Schoen 1977; Schemske 1978; Willson & Schemske 1980; Bertin 1982; Lloyd & Yates 1982; Devlin & Stephenson 1984, 1985) or by the duration of stigma receptivity and pollen viability (Schoen 1977; Palmer, Travis & Antonovics 1989). However, as Lloyd & Webb (1986) point out, 'what matters in nature is the time when pollen is available to be transferred from a blossom compared with the time when stigmas are capable of receiving pollen that has a prospect of fertilising ovules.' Information on the period of effective presentation of pollen and stigmas is what is needed. These types of data are almost completely lacking in the literature (but see Wells & Lloyd 1991).

Several workers have described mechanisms that prolong the presentation and pickup of pollen by pollinators (Lloyd & Yates 1982; Devlin & Stephenson 1984; Haynes & Mesler 1984; Lloyd 1984; Harder *et al.* 1985; Harder & Thomson 1989). Lloyd & Yates (1982) argued that selection will favour prolonged duration of the staminate phase and staggered presentation of pollen. Flowers that are able to lengthen the time over which their pollen is removed are likely to export pollen to more receptive stigmas because more pollinators will be involved in transport. Sib competition among pollen grains from the same parent on one pistil is thereby reduced and the risk of failure is also diminished. Moreover, Harder & Thomson (1989) show that in *Erythronium* pollen deposition efficiency is greatest when only a small amount of pollen is initially picked up, as this results in less wastage of pollen. Two strategies for prolonging pollen presentation may be distinguished (Harder & Thomson 1989). *Pollen dispensing strategies* involve mechanisms that allow only a portion of the pollen of a flower to be made available at one time. A variety of mechanisms that do this has been noted (Lloyd & Yates 1982; Brantjes 1983; Haynes & Mesler 1984; Devlin & Stephenson 1985). *Pollen packaging strategies* stagger the presentation of pollen by packaging it into small bundles (anthers, flowers, inflorescences) which present their pollen sequentially (Percival 1955; Harder *et al.* 1985). Either or both mechanisms are particularly likely to be selected whenever the conditions assumed under Bateman's Principle occur, i.e. adequate pollination for 100% fertilization and more than one visit per flower during pollen presentation (Lloyd & Yates 1982; Harder & Thomson 1989).

There has been very little study of the proximate factors that influence flower longevity and dichogamy (Primack 1985). Frequently an incidental or anecdotal reference to the influence of weather is made (e.g. Percival 1950) but only rarely has an attempt been made to substantiate this (Wells & Lloyd 1991). This paper attempts to (1) describe visitation patterns to flowers of different phases; (2) determine the timing

of pollen removal and receipt; (3) contrast these effective durations for presentation of pollen and stigmas with the nominal durations; (4) examine pollen packaging strategies; and (5) determine the effect of weather on phenology in *Myosotis colensoi*.

Materials and methods

THE PLANT

Myosotis colensoi (Kirk) Macbride is a herbaceous, prostrate perennial forming patches up to 0.4 m across. Flowers are produced in November and December in New Zealand and are white, hermaphrodite and tubular. They are c. 12 mm wide with a corolla tube of c. 7 mm. Nectar is produced at the base of the corolla tube. The flowers are protogynous with a short exclusively female phase of on average one to two hours, followed by a longer male phase after the anthers dehisce. The five anthers dehisce sequentially over several hours. After approximately one day, the flowers enter an equally long phase during which neither pollen nor stigmas are presented but the corolla is still conspicuous (Robertson 1989; Robertson & Lloyd 1991). The change from the period when pollen is received or donated (pollination phase) to the post-pollination phase is signalled by a change of colour of a set of scales that form a ring at the mouth of the corolla tube. During the female and male phases these scales are bright yellow but they fade to white over a relatively short period after the functional pollination period has passed.

The most important floral visitor is a tachinid fly, *Protohystricia huttoni* (Malloch). These relatively large flies visit *M. colensoi* to collect nectar from the floral tubes.

PHASE PREFERENCES OF POLLINATORS

To assess the preference pollinators may have for flowers either in the pollination phase (yellow corolla scales with stigma and/or pollen presented) or post-pollination phase (scales fading or faded, anthers usually brown), individuals of the tachinid fly *Protohystricia huttoni* were observed foraging on *M. colensoi*. It was not possible to distinguish whether the flowers visited were in the male or female phase, as this would have required closer scrutiny of the flowers than could be managed without disturbing the fly. Flies were observed as they moved over a plant, and the number of pollination phase and post-pollination phase flowers that were visited were counted. The total numbers of flowers in each phase were also counted. The observations were made during peak flowering on 14 November 1987 and again on the 18 November 1987. An analysis of variance (not shown) revealed no difference between

days, so the data for the two days were pooled for subsequent analyses.

A paired *t*-test was performed on the difference between the proportions of visits to the two phases and the proportions of the two phases available on a plant. The null hypothesis tested was that the flies were utilizing each of the flower types in proportion to their abundance, i.e. that they were not preferentially selecting one or other type.

It was not possible to measure the minute amounts of nectar in the flowers because the quantities of nectar were too small. Hence it was not possible to determine whether post-pollination flowers produce nectar.

PERIOD OF STIGMA RECEPTIVITY

To investigate the period of stigma receptivity, previously covered flowers of varying age were hand-pollinated in the field, and the seed set was subsequently measured. Flowers from four plants were assigned to four sexual stages:

1. Female — flowers open but anthers yet to dehisce.
2. Male — anthers dehiscent or dehisced and scales still bright yellow.
3. Fading — flowers just entering the post-pollination phase, with scales beginning to fade.
4. Faded — scales fully faded.

Pollen from a flower of another plant was brushed onto each recipient stigma, and the stigma was examined with a 20× hand-lens to ensure that it had ample pollen. The calyx was marked with a small spot of enamel model-maker's paint, the ages of flowers being indicated with different coloured paints. After approximately four weeks the nutlets had reached maturity and the number of nutlets per calyx was recorded. An analysis of variance was performed on the mean number of seeds per flower for each plant using the statistical package MINITAB.

EFFECTIVE PHASE DURATION — FEMALE FUNCTION

On 12 November 1987, 50 flowers that were just beginning to open in the morning were marked with toothpicks. Each hour subsequently the stigmas were examined with a 20× hand-lens to check if the flower had opened and if so, whether pollen had been deposited on the stigma. At the same time the sexual phase of the flower was also recorded, including the number of dehiscent anthers, if any. It was not possible to count the number of pollen grains on the stigmas, but it was noted whether some pollen had been deposited or not. Since there are four ovules per flower, only a small amount of pollen is required to set full seed.

POLLINATOR ACTIVITY INDEX

Each hour, the number of individuals of *P. huttoni* entering a semicircular plot of c. 8m radius over a period of 15 minutes was recorded as an index of pollinator activity. This plot was adjacent to the area containing the plants with marked flowers.

EFFECTIVE PHASE DURATION — POLLEN REMOVAL

The rate of pollen removal was measured, beginning on 22 November 1988, by counting the pollen remaining after known periods of time. This was compared with the amount of pollen found in flowers with intact anthers (Robertson & Lloyd 1991). Flowers were chosen at random at 09.00h just as they were opening and were marked with toothpicks. In total 80 flowers were marked and approximately 10 of these were removed at each of the following times: 1.5, 2, 4, 7 hours after opening; at 10.00h and 14.00h the next day; and finally at 10.00h and 14.00h on the third day. Because pollinator activity occurs only between approximately 09.00h and 18.00h, the times of sampling were equivalent to the following periods of pollinator activity: 1.5, 2, 4, 7, 10, 14, 19 and 23 hours after flower opening. As each flower was removed its sexual stage, including the number of anthers dehiscent and the condition of the scales, was recorded. Each flower was placed in a small glass vial containing formaldehyde, acetic acid and ethanol (1:3:9). In the laboratory the amount of pollen remaining was determined. The entire contents of the vial were squashed and rinsed through a sieve with distilled water. The wash was centrifuged at 3000rpm for 5 minutes and decanted. The pollen pellet was re-suspended in 0.1 ml of a mixture of 3:1 lactic acid and glycerol (Lloyd 1965) and a sub-sample counted on a haemocytometer slide.

The relative amount of pollen remaining was expressed as a proportion of the amount contained in flowers with intact anthers. The pollen remaining declined exponentially. The exponential decline was fitted by taking the natural logarithm of the means at each time and fitting a line of best fit to these means. It was necessary first to subtract a residual amount of pollen — 7500 grains, the number that was left as a seemingly unremovable fraction (see Fig. 3). The line was forced through 1.0 — the point which corresponds to all pollen remaining at time 0.

THE EFFECT OF CLIMATIC CONDITIONS ON PHENOLOGY

The measurements of pollen presentation and deposition and pollinator activity were repeated on two further days, 18 November 1987 and 21 November 1987. The three days were dissimilar in climatic conditions. On 12 November the weather was fine

Table 1. The frequency of visits to receptive and non-receptive flowers

	Proportion of visits	Proportion of available flowers
Receptive flowers	0.844	0.543
Non-receptive flowers	0.156	0.457
Standard error ($n = 24$)	0.039	0.039

Receptive flowers have bright yellow corolla scales, non-receptive flowers have fading or faded scales.

and warm and pollinators were abundant. On 18 November it was cold and windy but with periods of bright sun. Finally 21 November was overcast and cool. On the second and third days pollinators were relatively scarce.

On 13 November 1987 and on the morning of 14 November 1987 steady rain fell. In the late morning of the second day the rain stopped and the sun came out. To determine the effect of rain on the flower phases, the proportion of flowers in each of the various stages was estimated after the rain had stopped. As the flowers on a plant open any time at a uniform rate (Robertson 1989), these proportions should correspond with the relative durations of the phases. One sample was taken shortly after the rain had stopped, and the other was taken three hours later in the afternoon. An additional class of flower was recognized on this day. These flowers had bright yellow scales but brown anthers that bore no pollen. It was apparent that these flowers had opened and begun dehiscing their pollen before the rain and subsequently the pollen had been damaged or washed away. Though they were presenting no pollen, their scales had not faded, so they had not entered the post-pollination phase.

Results

PHASE PREFERENCES OF POLLINATORS

Individuals of the tachinid fly *Protophystricia huttoni* clearly prefer to visit flowers that are in the male or

female phase rather than those flowers that have entered the post-pollination phase (Table 1). Post-pollination flowers represent almost 50% of the flowers available, yet only 16% of the visits are to these flowers ($t = 6.95$, $P < 0.0001$). The preference may be expressed as the following preference ratio,

$$\frac{\text{visits to receptive flowers}}{\text{visits to non-receptive flowers}} \bigg/ \frac{\text{no. of receptive flowers}}{\text{no. of non-receptive flowers}}$$

In this case,

$$\frac{0.844}{0.156} \bigg/ \frac{0.543}{0.457} = 4.55 \quad \text{eqn 1}$$

Individual flies, therefore, display almost a five-fold preference for flowers in the pollination phases. Moreover, it was noticeable that the post-pollination flowers that were visited were generally those with scales that were just starting to fade and so represent the youngest of the post-pollination flowers.

PERIOD OF STIGMA RECEPTIVITY

Results of hand-pollination of stigmas from flowers of different ages show that the stigma remains receptive throughout the life of the flower (Table 2). An analysis of variance reveals that there are no significant differences in stigma receptivity throughout the flower lifetime, although different plants have different overall mean seed sets. Thus the duration of nominal female function in a flower encompasses the entire period when the corolla is fresh and conspicuous.

EFFECTIVE PHASE DURATION — FEMALE FUNCTION

Figure 1 presents the results of the time taken for stigmas to receive their first pollen for flowers marked on 12 November. It is clear that pollination

Table 2. The effect of the plant and the age class of the pollen-receiving flower on the success of hand pollinations

Plant	Mean seed set \pm SE (n)			
	Female	Male	Fading	Post-pollination
12	1.5 \pm 1.50 (2)	4.0 (1)	2.2 \pm 0.75 (6)	3.5 \pm 0.40 (10)
117	4.0 (1)	3.0 \pm 1.00 (2)	2.6 \pm 0.75 (5)	2.6 \pm 0.60 (8)
110	4.0 \pm 0.00 (2)	2.7 \pm 0.74 (7)	3.7 \pm 0.33 (6)	2.8 \pm 0.49 (8)
119	0.0 (1)	1.5 \pm 1.50 (2)	0.0 \pm 0.00 (3)	0.0 \pm 0.00 (5)
Average	2.5 \pm 0.81 (6)	2.7 \pm 0.50 (12)	2.4 \pm 0.39 (20)	2.5 \pm 0.31 (31)
ANOVA				
Source of variation	df	M.S.	F	P
Plant	3	6.043	7.45	<0.01
Age class	3	0.312	0.38	<0.8
Error	9	0.811		

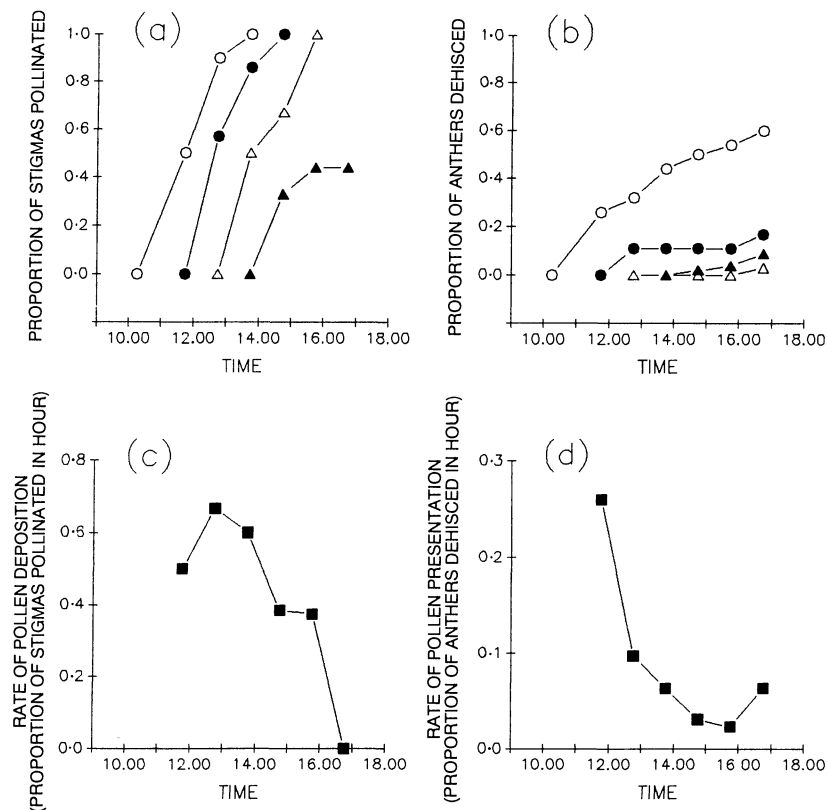


Fig. 1. The fate of flowers from their opening on a fine and warm day (12 November 1987). The different samples represent the different opening times of the flowers. (a) The proportion of flowers with pollen on their stigmas. (b) The proportion of anthers dehiscing. (c) The hourly rates of pollen deposition. (d) The hourly rate of anther dehiscence.

occurred quickly, within a few hours (Fig. 1a) in all flowers. With the exception of the flowers that opened after 13.00h, all stigmas had received pollen by the end of the afternoon. Moreover, the rate of pollen deposition on previously unpollinated stigmas remained high throughout the day until about 17.00h (Fig. 1c). This relatively high rate of deposition coincided with high rates of pollinator activity (Fig. 2a).

The onset of anther dehiscence was variable but generally had only just started or had yet to begin by the time pollination had occurred (Fig. 1b). For only a small fraction of flowers were any anthers dehiscing before the stigmas were pollinated. This result was particularly evident during the afternoon, when anther dehiscence was slow (Fig. 1d). Table 3 presents a comparison between nominal and effective phase duration. The 'half-life' of the female

Table 3. The half-life of nominal and effective phases (hours). 1. The time taken for half the flowers to dehiscence the first anther (nominal stigma presentation). 2. The time taken for the stigmas on half of the flowers to be pollinated (effective stigma presentation). 3. The time taken for half the flowers to begin to have faded scales (nominal pollen presentation). 4. The time taken for half the pollen to be removed (effective pollen presentation)

Date	Stigma presentation		Pollen presentation	
	1. Nominal	2. Effective	3. Nominal	4. Effective
12.11.87 Fine and warm	2.0	0.9	—	—
18.11.87 Fine but cold	1.3	5.3	—	—
21.11.87 Overcast	1.5	4.0	—	—
22.11.88 Fine and warm	—	—	11.5	4.0

Only flowers that opened before 14.00h were used above.

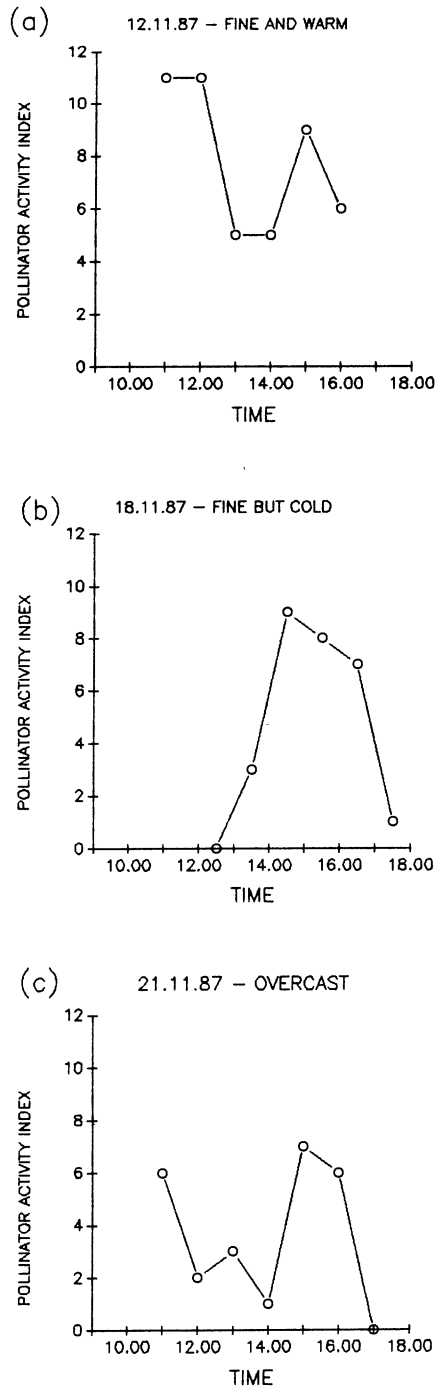


Fig. 2. The rates of pollinator activity on the 3 days that the female function was surveyed. The index of pollinator activity is the number of individuals of *Protohystricia* observed foraging in a semi-circular plot over a 15-min period.

phase is given by interpolation of the curves in Fig. 2. The period over which 50% of the flowers had had pollen deposited was estimated for each run of flowers and averaged. Additionally, the time taken for half the flowers to dehisce one anther was also estimated from Fig. 1. Thus it is possible to compare directly the accuracy of an estimate of the length of the female phase made from the timing of pollen

release with the estimate of the period of effective stigma presentation derived from observations of pollen deposition. Considering for the moment only the fine and warm day (12 November 1987), the rate of pollen deposition exceeds the rate of initial anther dehiscence. On average, half the flowers are estimated to have been pollinated in just under one hour (Table 3). In comparison it takes approximately two hours before the first anther is dehisced. In this case, the effective period of stigma presentation is shorter than the nominal female phase duration assessed by the rate of anther dehiscence. The data for the two later dates will be considered below.

EFFECTIVE DURATION OF POLLEN REMOVAL

Figure 3(a) presents the results of the observations on the removal of pollen from a set of marked flowers on a series of fine days. The results show a gradual removal of pollen down to a residual level. This residue is apparently not able to be removed, either because it has been dislodged to inaccessible regions of the flower or remains stuck in the anther sacs. The results reveal that pollen removal is a slow process and takes approximately 12–14 hours of pollinator activity to reach the basal level. Using a rate of visitation of one visit per flower per hour — the average rate reported in another study of the same population (Robertson 1989) — it is estimated that 12–14 visits are required to complete the male function. A model of exponential decline was fitted to the data. The line of best fit was back-transformed and plotted on Fig. 3(a). This line corresponds to a removal rate of 14.3% of the removable pollen per hour, which corresponds roughly to each visit (Table 4).

Figure 3(b) shows the rate of anther dehiscence and the rate of onset of the fading of corolla scales. It can be seen that the period of active pollen removal slightly exceeds the period over which anthers are dehisced. In fact, by similarly fitting a curve of exponential decline of undehisced anthers, it can be shown that 25% of previously undehisced anthers dehisced each hour (Table 4). Throughout the first eight hours of pollen removal, anthers are being dehisced and presenting new pollen to be removed. There is a short period of time in which no new anthers are dehisced, but pollen removal continues.

A comparison between nominal and effective phases can also be made for the male function. In this case the time taken for half the pollen to be removed is compared to the time taken for half the flowers to enter the post-pollination phase. The point at which 50% of the flowers have reached either the post-pollination phase or had half their pollen removed is interpolated from Fig. 3 as before. The results (Table 3) reveal that the average flower has half of its pollen removed after approximately four hours. It takes almost twice as long again for half the flowers to enter

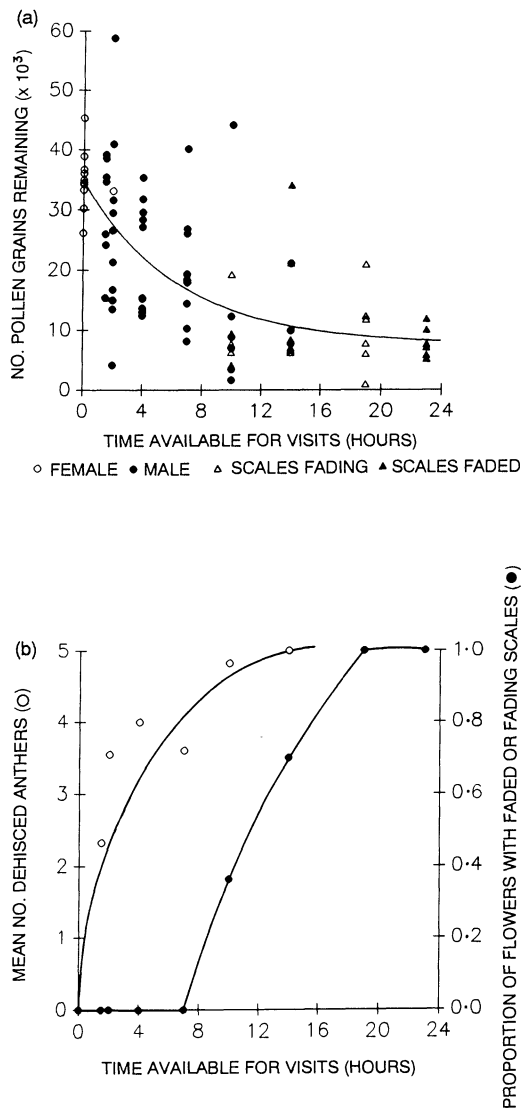


Fig. 3. Pollen removal and phase development. (a) Removal of pollen from marked flowers over time. The symbols represent the phase the flowers were in at the time of sampling. (b) The mean number of anthers dehiscent and the proportion of flowers that have reached the post-pollination phase against time.

the post-pollination phase. However, because of the exponentially declining rate of pollen removal, a considerable amount of additional time is required to remove the remaining fraction of pollen that is eventually removed. As a result, pollen removal continues for as long as 16 hours after flower opening. In this sense there is good correspondence between when pollen ceases being removed and the onset of the post-pollination phase.

THE EFFECT OF CLIMATIC CONDITIONS ON PHENOLOGY

The rate at which pollen is deposited varies from day to day and presumably depends on the rate of pollinator activity. Pollinator activity in turn seems to be related to weather conditions. However, the rate of pollen presentation is also affected by weather, setting up a complex interaction between these factors. On the two cooler days, a much longer time is required for half the flowers to have pollen deposited. This corresponds with less pollinator activity as estimated by the pollinator activity index (Fig. 2). However, the rate of new pollen presentation remains similar to the rates on the fine and warm days (Table 4). On 18 November 1987 approximately five hours had elapsed before 50% of stigmas had received pollen. However, anther dehiscence was occurring at a similar rate as on the previous fine day. The rates of deposition on 21 November 1987 were slightly higher while pollen presentation was slower. However, anther dehiscence was much faster on another fine day (22 November 1988, Table 4). The timing of dehiscence seems to be complex; it may involve an interaction between temperature, light and the time of day. In general, where conditions lead to slow rates of pollination, there may be considerable overlap between male and female functions. This will presumably lead to an increase in the level of self-pollination.

Table 4. Rates of pollen deposition, presentation and removal per hour

Date	Average proportion stigmas pollinated	Average rate of anther dehiscence	Average rate of pollen removal
12.11.87 Fine and warm	0.51	0.09	—
18.11.87 Fine but cold	0.10	0.10	—
21.11.87 Overcast	0.25	0.07	—
22.11.88 Fine and warm	—	0.25	0.14

Only flowers that opened before 14.00h were used above.

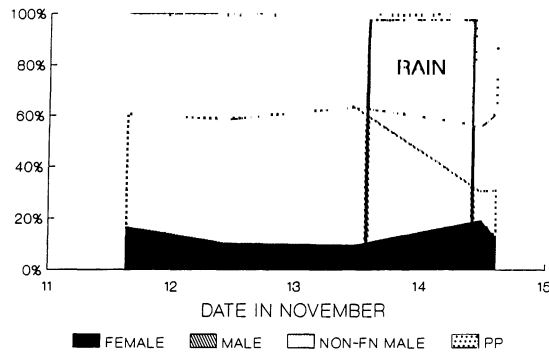


Fig. 4. The effect of overnight rain on the proportion of flowers in four recognized age classes. (Non-fn male, flowers that have damaged anthers but yellow scales; PP, post-pollination phase flowers).

The importance of weather in the phenology of flowers is confirmed by the effect of overnight rain on 13 November 1987 on the proportion of flowers in the various age classes (Fig. 4). Prior to the rain there was the usual balance of flower classes, with a small number of female-phase flowers and approximately equal numbers of male- and post-pollination-phase flowers. After the rain, however, there was an increase in the number of female-phase flowers, presumably because the onset of anther dehiscence was delayed. In addition, a number of flowers that were presenting pollen the previous day were rendered non-functional by the rain. The pollen had been lost from these flowers despite their having bright corolla scales. The net effect of these changes was a swing in the balance of phases towards an increase of the female stage flowers and a loss of pollen-presenting flowers. Thus, the female function of flowers that were opening or opened during this time was maintained, while the male function suffered from the unavoidable loss of pollen and opportunities for visitation. Once the period of bad weather was over, the flowers whose dehiscence was delayed, quickly presented their pollen and the balance of phases was swiftly restored.

Discussion

Applying the concept of sexual selection to plants has led to the suggestion that many of the adaptations of hermaphrodite flowers are concerned more with the dispersal of pollen than with its receipt (Willson 1979; Bell 1985). It is expected that in addition to allocating more resources to the male function at anthesis, there will be selection for the presentation of pollen over a long period, thereby increasing the number of visitors that can remove pollen from a flower (Lloyd & Yates 1982; Queller 1983; Harder & Thomson 1989). There are two principal advantages in having pollen removed from a flower in smaller packages during a greater number of visits. First, smaller

quantities of pollen are likely to be more efficiently picked up and subsequently redeposited on stigmas, reducing wastage (Harder & Thomson 1989). Second, pollen that is transferred in more numerous but smaller packages is carried to more stigmas. Hence it competes less with other pollen from the same male parent and more with pollen with other plants. Both the enhanced efficiency and the reduced sib competition associated with more pollen-removing visits increase the opportunities for pollen in intrasexual selection. An increase in the duration of the pollen phase of a flower is likely to be cheaper than increasing the number of flowers, which requires expenditure on additional corollas, pedicels, etc. On the other hand, the strategy of dispensing pollen in smaller quantities over a longer period is eventually limited by the numbers of pollinators that are available to remove pollen before it deteriorates or is spoiled by the weather, or by exhaustion of a nectar reward. Moreover, many species must present a considerable amount of pollen at one time as an adequate reward for pollen-seeking pollinators.

Although the relative duration of pistillate and staminate phases has often been given in studies of the reproductive biology of species, generally these results are in terms of the physical appearance of anthers and stigmas; alternatively the period of stigma receptivity has been measured (Devlin & Stephenson 1985; Palmer, Travis & Antonovics 1989; Richardson & Stephenson 1989). However, the effective time over which pollen is actually available for removal to other flowers or is able to be deposited on stigmas with a chance of successful fertilization is likely to be shorter than the nominal phases indicated by the physical conditions (Lloyd & Webb 1986). Unfortunately, there are very few studies that measure both pollen availability and time of pollen receipt. Webb & Bawa (1983) working with *Malvaviscus arboreus* found that both functions are satisfied early in these one-day flowers. Wolfe & Barrett (1989) found that flowers of the tristylous *Pontederia cordata* are visited between 10 and 20 times per day, and pollen is able to be removed throughout the day. In contrast, a single visit deposits, on average, 14–53 compatible grains on a stigma. There is only one ovule in this species, so a single visit is easily able to satisfy the female function.

Data collected here for *Myosotis colensoi* show that nominally stigmas may be pollinated successfully throughout the life of a flower. Similarly, results (unpublished) show that pollen from the very oldest flowers is still able to father seeds successfully. It might appear, therefore, that the female-phase duration exceeds the duration of the male function. However, stigmas usually have pollen deposited within two hours of opening on fine days. It is likely that these first grains will successfully fertilize the four available ovules. A comparison of the effective stigma presentation (the period when pollination is

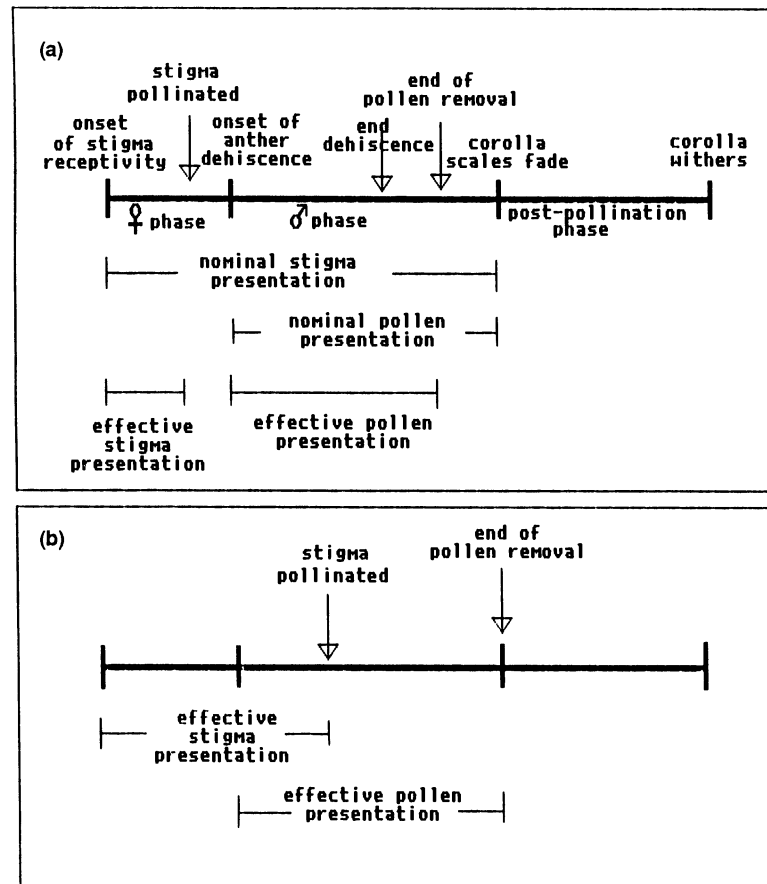


Fig. 5. Schematic representation of average durations of floral events under differing weather conditions. (a) Good weather — no overlap of effective male and female function. (b) Poor weather — extensive overlap of functions and an increased chance of autogamy.

possible) with the time taken for anthers to dehisce, reveals that the effective female time is approximately half the nominal female time (as measured by the onset of the male phase). The total period of stigma receptivity is therefore a very poor measure of the effective female phase; the nominal phase length based on the start of pollen presentation is also approximate.

The male function takes much longer to satisfy. The results indicate that as many as 12–14 visits may be received before all pollen which can be removed is removed. This period on average is slightly shorter than a visual assessment of the male phase (Fig. 5a). New pollen is presented over much of this period. The five anthers do not dehisce their pollen simultaneously but do so over most of the period of pollen presentation. Such packaging is likely to extend the number of visits that are able effectively to disperse pollen. Previous studies have shown that some flower visitors remove most of the pollen accessible in just one visit (Strickler 1979; Harder *et al.* 1985; Harder & Thomson 1989; Wolfe & Barrett 1989). Hence a flower that presents all of its pollen at once is likely to have its pollen transported by fewer pollinators, and thus to fewer potential mates, than one that staggers

its release. The gradual release of pollen will confer advantage on the male function as long as visits are relatively common and certain (Lloyd & Yates 1982; Wells 1988; Harder & Thomson 1989). Pollinators are reluctant to visit flowers that have fading or faded scales. This result is confirmed by the completion of pollen removal by the time of the phase change. Clearly, therefore, these flowers spend a long time in a phase in which they make no direct contribution to pollen donation or receipt. The adaptive significance of maintaining such non-productive flowers is considered elsewhere (Robertson 1989). For the purposes of this paper it is necessary to note only that the period of post-pollination cannot be assigned directly to either male or female functions; the function of these post-pollination flowers, if any, must be accessory to pollen transfer.

Until now we have considered pollen deposition and removal in periods of optimal weather. However, it seems likely that on days on which pollinator activity is restricted, the flowers that open will in general face a very different fate from those that open under better circumstances. Despite its potential importance, few studies have addressed this aspect directly. Wells & Lloyd (1991) found signifi-

cant correlations between the time taken for anthers to dehisce in *Pseudowintera colorata* and ambient temperature, and that the weather pattern imparted a loose synchrony of plants within a population. Similar temporal synchrony has been found in *Aralia* (Thomson & Barrett 1981) and *Lobelia* (Devlin & Stephenson 1987) but neither of the latter studies related the differences observed to the weather. Such fluctuations in gender are likely to have important influences on the success of plants as male or female parents. In particular, male–male competition will be less intense when phenotypic gender swings towards a female emphasis (usually in periods of and immediately following bad weather). In addition, male fitness of a flower will be increased if its pollen can be protected or conserved in periods of bad weather (Percival 1955) and yet made available as soon as conditions allow transport to receptive stigmas (for an early expression of this argument see Kerner 1902).

In *M. colensoi* periods of rain delay the dehiscence of anthers. This protects flowers from losing pollen but also causes a change in the proportions of male and female flowers. During rain flowers continue to open but do not dehisce their anthers. Once rain stops, therefore, there is an over-representation of female flowers and a flower that enters the male phase will experience a period of relatively lax competition for stigmas. There may be selection for rapid presentation of the pollen as soon as conditions become favourable. This may explain why flowers continue to open during rain.

While there is a strong effect of rain on flower development, the relationship between weather conditions, pollinator activity and pollen presentation on days without rain is less clear. It appears that the rate of pollen deposition is slower on cooler or cloudy days and that this rate depends on pollinator activity. Many stigmas have not been pollinated before the anthers begin to dehisce on a flower. Consequently, there may be an extensive overlap between the male and female functions on cooler days (Fig. 5b). Pollinator-mediated selfing is therefore more likely when an insect visits the flower. In situations where bad weather limits female success through pollinator limitation, the maintenance of stigma receptivity may allow a more assured reproductive success. This argument is parallel to that for delayed selfing which follows opportunities for outcrossing (Becerra & Lloyd 1992).

The results presented here show that periods of male and female activities cannot be determined accurately by merely observing when stigmas become receptive and anthers dehisce. The time when pollen receipt and donation start and finish is what is important and for this species shows that on fine days the male function takes much longer to satisfy than the female function and usually begins after the female phase is concluded. However, circumstances

vary for particular flowers and depend on the weather conditions immediately before and during anthesis.

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