Why pollinators visit only a fraction of the open flowers on a plant: The plant’s point of view

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Abstract

We analyze the so-called 'exponential decay' model of pollen transfer for the case in which pollinators visit a fraction of the open flowers on a plant. The analysis is limited to the simplest case of a self-incompatible species, in which self pollen does not interfere with seed set. Plants can manipulate the number of flowers visited per pollinator approach by adjusting attractiveness of flowers so as to maximize pollen export (male fitness). In the model the length of the visitation sequence that is optimal for the plant always decreases with pollen deposition rate $k_1$, pollen uptake rate $k_2$, and the number of pollinator approaches to the plant $X$, but increases with the total number of flowers $F$. We assume that the average number of pollinator approaches $X$ increases with the total number of flowers $F$, but slower than proportionality. It then follows that the optimal fraction of flowers a pollinator visits after arriving on the plant ($f/F$) decreases with the total number of flowers $F$. Furthermore, the male fitness gain per flower generally decreases with number of flowers, except for the condition of 'inefficient' pollen transfer with very small values of $k_1$, $k_2$, and $X$, or when the plant has only a few flowers. The latter conditions should favour high nectar production and mass blooming. The known range of parameters suggests that male fitness increases with the total number of flowers slower than proportionality.

Introduction

The so-called 'exponential decay' model of pollen transfer (Lertzman and Gass, 1983) is now frequently used to calculate fitness consequences of different pheno-
types of plants (Crawford, 1984; Galen and Rotenberry, 1988; Robertson, 1992; de Jong et al., 1992). The model traces the amount of pollen deposition and pollen transfer in each flower, and gives an estimate of the number of pollen grains exported to other plants, which is the male fitness component of the plant. In two previous papers (de Jong et al., 1992; Klinkhamer et al., 1993) we examined the question how male plant fitness increases with number of open flowers on the plant. This shape of the fitness curve is relevant for sex-allocation theory (Charnov, 1982) and life-history theory (Iwasa and Cohen, 1989; Pugliese, 1988; Stearns, 1992).

The drawback of de Jong et al. (1992) is that pollinators were assumed to visit all flowers, whereas in nature they clearly visit only a fraction of the available flowers (see references in discussion). Klinkhamer et al. (1993) did allow pollinators to visit a fraction of the flowers, but at the expense of relying heavily upon simulation results.

The foraging behavior of pollinators has been studied extensively (e.g. Best and Biezczudek, 1982; Hodges and Miller, 1981; Levin and Kerster, 1973; Pyke, 1981; reviewed by Waddington, 1983). In these models, however, plants are regarded as patches supplying food for the foragers, and are often treated as passive entities. Alternatively one can study the plant’s adaptation to influence pollinator behavior (Waser, 1983). We here examine what would happen if the plant can somehow manipulate the number of flowers visited per approach. This manipulation can be possible by modifying the reward, such as nectar supply. For simplicity, we mainly analyze the case in which the cost of increasing the reward is small, but later we will discuss how the solution would be modified if the cost is important.

There are two goals of the theoretical work in the present paper: It is known that only a fraction of flowers are visited by pollinators, and that the number of flowers visited increases with the total number of flowers but at a rate slower than proportionality (e.g. Klinkhamer and de Jong, 1990; Klinkhamer et al., 1989; Robertson, 1992; Andersson, 1988; Thomson, 1988; Schmid-Hempel and Speiser, 1988; Pleasants and Zimmerman, 1990; Geber, 1985; Schmitt, 1983). We try to explain this observation as a result of plant’s strategy to manipulate the number of flowers visited in a single pollinator visit.

The second goal of the present paper is to examine the shape of the male reproductive success curve as a function of the number of flowers. According to dynamic resource allocation theory for life-history strategies (Iwasa and Cohen, 1988; Pugliese, 1988), the curvature of reproductive success as a function of reproductive investment is important: the optimal strategy is polycarpy (repeated reproduction) if reproductive success increases with the investment at a decreasing rate, while it is monocarpy (“big bang” reproduction) or intermittent reproduction if the reproductive success increases at an increasing rate. Attracting pollinators at an accelerating rate of increase was proposed to explain monocarpy of Agaves and Yuccas by Schaffer and Schaffer (1977), although later studies (Aker, 1982) did not confirm this. Here we restrict ourselves to a limited case that can be analyzed mathematically. We analyze the exponential decay model mathematically in more detail, especially concerning how the optimal fraction of flowers visited during each approach depends on various parameters, such as pollen deposition rate, pollen
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removal rate, the number of flowers per plant, the number of pollinator approaches per plant, and the number of flower visits per approach. For each given number of open flowers on the plant we calculate the optimal length of the visitation sequence and then describe the relationship between male fitness and the total number of open flowers on the plant. These fitness curves are discussed in relation to the evolution of monocarp.

**The model**

Here we explain briefly the pollination model, first presented in Klinkhamer et al. (1993). We denote the number of flowers visited per pollinator after its arrival (the length of the visitation sequence) by $f$. The plant may affect this number by varying nectar production rates of flowers. $f$ may also depend on other factors, such as the total number of flowers on the plant $F$. For plants with a given number of flowers, $f$ will be closely related to the plant's attractiveness to pollinators. We assume that the plant is self-incompatible and self-pollen does not interfere with seed set.

First, we note that the pollen export per flower ($E$) is the product of two factors: (1) the number of pollen grains removed from the anthers ($R$) and (2) the average fraction of these removed pollen to be exported to other plants instead of being deposited to other flowers of the same plant ($1 - D$). If pollinators visit a single flower per approach, all the pollen grains removed from the flower will be exported ($1 - D = 1$, i.e. $D = 0$). However, in general, pollinators tend to visit several flowers of the same plants in a sequence before leaving the plant. Then, some fraction of pollen ($D$) is lost through pollen deposition from one flower on other flowers of the same plant (geitonogamy) and will not contribute to pollen export to other plants. Holsinger (1993) referred to $D$ as the discounting factor. The fraction changes with the location of the flower in the sequence, but we can simply calculate the average under the assumption that pollinators visit flowers in random order, with the restriction that no flower is visited more than once during a single pollinator approach. Hence the number of flowers visited per approach ($f$) should not exceed the total number of flowers on the plant $F$. The effects of multiple visits to the same flower in a single visitation sequence will be discussed later.

When a pollinator visits a flower, it deposits a fraction $k_1$ of the pollen on its body on the flower. Although we expect most pollen to be deposited on the stigma, it does not matter for the outcome of the model if some deposition is on other parts of the flower. Also, the pollinator removes a fraction $k_2$ of the pollen from the anthers of the flower, of which a fraction $k_3$ adheres to the pollinator's body. We call $k_1$ pollen deposition rate and $k_2$ pollen removal rate. For simplicity, we set $k_3 = 1$ and we ignore $k_3$ in what follows. This does not affect our conclusions, because the argument remains the same if a constant fraction of the pollen that is removed from the flower is picked up by the pollinator, so that the rest is wasted. Let $B$ be the amount of pollen produced by each flower. The amount of pollen removed from a flower visited by $n$ pollinators is $B(1 - (1 - k_2)^n)$. It is unlikely that all the flowers on the plant receive exactly the same number of visits. In addition the
number of pollinator approaches has variance among plants of the same number of flowers. We take the average of this pollen removal by assuming that the number of visits \( n \) follows a Poisson distribution. The mean of this distribution is the average number of pollinator visits per flower, which is the product of the average number of approaches of pollinators \( X \) and the number of flowers visited per approach \( f \), divided by the total number of flowers \( F \). The result is:

\[
R = \left( \frac{\text{pollen grains removed from a flower}}{} \right) = B \left( 1 - e^{-k_2 \frac{Xf}{F}} \right).
\]

To compute the average fraction of the pollen grains removed to be exported to the other plants, consider a pollinator that approaches a plant and visits \( f \) flowers before leaving the plant. The fraction of pollen removed from a single flower and still remaining on the body of the pollinator when it leaves the plant after visiting \( j \) other flowers of the same plant is \( (1 - k_1)^j \), and if averaged over \( j \) from 1 to \( f \) with the equal probability \( 1/f \), it becomes:

\[
1 - D = \left( \frac{\text{fraction of pollen grains transported}}{} \right) = \frac{(1 - (1 - k_1)^f)}{f k_1}.
\]

The amount (per flower) of pollen that is exported to the other plants \( (E) \) is the product of \( R \) and \( (1 - D) \):

\[
E = \frac{B(1 - (1 - k_1)^f)}{f k_1} \left( 1 - e^{-k_2 \frac{Xf}{F}} \right).
\]

which is rewritten as

\[
E(f, F) = c \left( 1 - e^{-\beta f} \right) \left( 1 - e^{-\gamma f} \right)
\]

where \( \alpha = -\log (1 - k_1) \), \( \beta = k_2 X/F \) and \( c = B/k_1 \).

We can see that the parameters \( k_2, X \) and \( F \) affect the fitness only through a combined parameter \( \beta = k_2 X/F \). Hence the effect of doubled \( k_2 \) on fitness, with all the other parameters kept constant, is the same as twice as many pollinator approaches \( X \), or half the number of flowers \( F \). Note also that \( E \) (and the whole analysis that follows) does not depend on the pollen load of the pollinator when it arrives at the plant.

However, all parameters are not independent. Plants with many flowers will attract more pollinators. We assume that the average number of pollinator visits to a plant, denoted by \( X(F) \) or \( X \), increases with the number of flowers \( F \), but the rate of increase becomes slower for large \( F \). Realized number of pollinator visits experienced by a plant with \( F \) flowers may have a large variance around \( X(F) \). Specifically, we assume that \( X(F) \) increases with \( F \) but slower than linearly, so that

\[
X(F) = x_0 F^\gamma, \quad 0 < \gamma < 1,
\]

where power \( \gamma \) is a positive constant less than 1. This assumption is supported by the field data (Thomson, 1988; Andersson, 1988, Pleasants and Zimmerman, 1990;
Klinkhamer et al., 1989; Klinkhamer and de Jong, 1990), which we will discuss in more detail later. As can be seen from Eq. (2), we assume in contrast with Klinkhamer et al. (1993) that \( X \) and \( f' \) vary independently.

Eq. (1) is the fitness through male function, or pollen export. Because we consider self-incompatible species in which self pollen does not interfere with seed set, female function (seed production, etc.) is not affected by the pollination processes that are considered here (e.g. Burd, 1994). If we further assume that the cost of construction and maintenance of flowers is constant per flower (i.e. it is proportional to the total number of flowers \( F \)), the pollen export, Eq. (1), is the currency that measures plant fitness.

**How does the optimal number of flowers visited \( (f) \) depend on the total number of flowers \( (F) \)?**

By the optimal number of flowers visited \( f \), we mean the optimal value for the plant, i.e. the value at which maximum pollen export is attained, Eq. (1). If the cost of increasing \( f \) by increasing reward (nectar supply) is small, and with total number of flowers fixed, \( f \) corresponds to optimal nectar reward. \( f \) is optimized for a given number of flowers \( F \) so that the male fitness \( E(f, F) \) is maximized under the constraint

\[
0 \leq f \leq F. \tag{3}
\]

Later we discuss the case in which to increase \( f \) is costly. For the moment we assume that the \( f \) value computed below satisfies \( f < F \) and we can neglect the upper bound of Eq. (3). Later we discuss the situation in which pollinators visit all flowers \( (f = F) \).

To obtain the optimal \( f(F) \), we calculate the partial derivative of the male fitness per flower \( E(f, F) \) with respect to \( f \) and set this equal to zero:

\[
\frac{\partial}{\partial f} \log E = \frac{1}{f} + \frac{\alpha e^{-\alpha f}}{1 - e^{-\alpha f}} + \frac{\beta e^{-\beta f}}{1 - e^{-\beta f}} = 0, \tag{4}
\]

which can be rearranged as

\[
1 = \frac{\alpha f}{e^{\alpha f} - 1} + \frac{\beta f}{e^{\beta f} - 1}. \tag{5}
\]

Note that \( f \) is a function of \( F \), because \( \beta \) decreases with \( F \).

Now we examine the dependency of \( f \), computed by Eq. (5), on the model parameters. The solution of \( f \) as a root of Eq. (5) may be written as \( f(\alpha, \beta) \). Let

\[
V(\alpha f) = \frac{\alpha f}{e^{\alpha f} - 1} \text{ and } V(\beta f) = \frac{\beta f}{e^{\beta f} - 1},
\]

which satisfies \( V(0) = 1, V' < 0, V'' > 0 \). Then after taking the partial derivative of Eq. (5) with respect to \( \alpha \), we have

\[
0 = V'(\alpha f)\left( \alpha \frac{\partial f}{\partial \alpha} + f \right) + V'(\beta f) \beta \frac{\partial f}{\partial \beta},
\]
Fig. 1. $\hat{j}$ as the solution of Eq. (5). This is the optimal number of flowers visited per pollinator approach, which attains the maximum pollen export per plant, provided that it is less than the total number of flowers $F$. One horizontal axis is for pollen deposition rate $k_1$, and the other for the product of pollen removal rate $k_2$ and average number of pollinator approaches per plant $x$, divided by the total number of flowers $F$.

hence

$$
\frac{\partial f}{\partial x} = \frac{V'(af)f}{-V'(af)x - V'(bf)\beta} < 0.
$$

Similarly, we obtain

$$
\frac{\partial f}{\partial \beta} < 0.
$$

This means that $\hat{j}$ decreases with $k_1$, $k_2$, and $X$ and increases with $F$ (Fig. 1). Since the average number of pollinator visits $X$ increases with $F$ slower than linearly, as indicated by Eq. (2), $\hat{j}$ increases with the number of flowers $F$. Hence we expect that pollinators should visit more flowers per approach for plants with more flowers. Note that this is not necessarily mean that large plants should produce more nectar per flower.

How does the optimal fraction of flowers visited ($\hat{j}/F$) depend on total number of flowers ($F$)?

Since $\hat{j}$ depends on $F$ only through $\beta$, we have

$$
\frac{d}{dF} \ln \left( \frac{\hat{j}(F)}{F} \right) = \frac{d\hat{j}/dF}{\hat{j}} = \frac{1}{F} \frac{\partial \hat{j}}{\partial \beta} \frac{\partial \beta}{\partial F} \frac{1}{F} = \left( \frac{\beta}{\hat{j}} \frac{\partial \hat{j}}{\partial \beta} \left( \frac{F \partial \beta}{\beta \partial F} \right) - 1 \right) \frac{1}{F}.
$$

(7)
First we note that, from Eq. (2), $\beta$ is proportional to $F^{-2}$, which decreases with $F$. Then $\frac{\partial f}{\partial F} = -(1 - \gamma)$ is between $-1$ and $0$. Second, from a computation similar to Eq (6a), we have

$$\frac{\beta \partial f}{\partial \beta} = \frac{V'(ff)\beta}{V'(xf)x} = \frac{V'(ff)\beta}{V'(\beta f)\beta}.$$ 

Noting that $V'(x) < 0$ in general we have

$$-1 < \frac{\beta \partial f}{\partial \beta} < 0.$$ 

From these two relationships, Eq. (7) becomes

$$\frac{d}{dF} \ln \left( \frac{f(F)}{F} \right) = 0.$$ 

Eq. (7) tells us that the fraction of flowers that a pollinator visits $\frac{f(F)}{F}$ should decrease with $F$, although $f$ increases with $F$. In other words, if plants can adjust their attractiveness and affect pollinator behaviour, it is expected that pollinators visit a smaller fraction of the flowers on plants with many flowers.

Under what conditions should all flowers be visited ($\hat{f} = F$)?

In all the analyses above, we neglected the constraint of Eq. (3). This is because the $f$ computed by Eq. (5) is normally smaller than $F$ and then the solution $f$ given by (5) is the optimal value $f$. However, we can prove that $\hat{f}$ may reach the total number of flowers $F$ when either $k_1$, $k_2$, or $X$ are very small. This can be shown by simply noting that Eq. (5) includes $\alpha f$ and $\beta f$, and hence if both $x$ and $\beta$ are multiplied by a small factor $\varepsilon$, then the value of $\hat{f}$ satisfying (5) (that makes the partial derivative of $E$ equal zero for given $F$) is simply multiplied by $1/\varepsilon$, which is a large factor. Hence the solution $f$ of Eq. (5) can be larger than any upper bound, and then the optimal $f$ is equal to the total number of flowers $F$.

The solution $f$ of Eq. (5) also can be very large if one of $\alpha$ and $\beta$ is very small but the other is not. This can be derived by noting that Eq. (5) becomes

$$1 = 1 - \frac{\alpha f}{2} + \beta f e^{-\beta f}$$

when say $\alpha f$ is much smaller than $\beta f$. We have

$$\hat{f} = \frac{1}{\beta} \ln \frac{2\beta}{\alpha},$$

which can be as large as possible if $\alpha f$ is very small. This implies that the value of $f$ given by Eq. (5) should be very large if either the efficiency of pollen deposition, pollen removal, or the pollinator availability is small. Then we expect that pollinators visit all the flowers in each approach ($\hat{f} = F$).
Now we consider the case in which $F$ increases and $X$ also increases following Eq. (2), but all the other parameters are fixed. Since $\beta$ decreases with the total number of flowers $F$, there exists a critical value $F_*$ such that the value of $f$ given by Eq. (5) is larger than $F$ if $F > F_*$, but smaller than $F$ if $F < F_*$. In such a situation, optimal length of visitation sequence is $\hat{f} < F$ and $\partial E/\partial f < 0$ holds for $F > F_*$, but $\hat{f} = F$ and $\partial E/\partial f > 0$ for $F < F_*$. 

How does male fitness $E$ depend on total number of flowers $F$?

A) Length of visitation sequence fixed: We examine whether the male fitness per flower (or pollen export to other plants per flower) decreases with the number of flowers. The male fitness per flower depends both on length of the visitation sequence $f$ and on the number of flowers $F$, as indicated by $E(f, F)$. From Eq. (2), $\beta$ is proportional to $F^{-(1-\gamma)}$, which decreases with $F$. Therefore, when $f$ is fixed, the male fitness per flower decreases with the number of flowers $F$:

$$\frac{\partial E(f, F)}{\partial F} < 0.$$ 

This implies that the pollen export per flower is smaller on plants with many open flowers, even though plants with many flowers attract more pollinators.

B) Length of visitation sequence can be adjusted: The plant may adjust nectar production to make $f$ equal to $\hat{f}$, corresponding to the total number of flowers $F$ as discussed in the last section. We denote this by $\hat{E}(\hat{f}, F)$, which satisfies:

$$\frac{\partial E(\hat{f}, F)}{\partial \hat{f}} = 0.$$ 

Now the male fitness, at $\hat{f}$ and at a given $F$, is $\hat{E}(\hat{f}, F)$. The derivative of this function is:

$$\frac{d}{dF}E(\hat{f}, F) = \frac{\partial \hat{E}(\hat{f}, F)}{\partial \hat{f}} \frac{d\hat{f}}{dF} + \frac{\partial \hat{E}(\hat{f}, F)}{\partial F},$$

where the first term is zero, because of Eq. (11), and the second term is negative because of Eq. (10). Hence we conclude that in this case the male fitness per flower also decreases with the number of flowers $F$; at least if $k_1$, $k_2$, and $X$ are not too small.

As discussed before, if $k_1$, $k_2$, and $X$ are small, $f$ computed by Eq. (5) becomes larger than $F$. Under the constraint $f \leq F$, the fitness is

$$E(F, F) = \frac{c}{F}(1 - e^{-x})(1 - \exp \left[ -k_2X(F) \right])$$

$$= \frac{c}{F}(1 - e^{-x})(1 - \exp \left[ -k_2X(F) \right]).$$

(13)
Fig. 2. (A) \( \bar{f} \), the optimal number of flowers visited per pollinator approach; (B) pollen export per flower \( E(f, F) \) when pollinators visit the optimal number of flowers, and (C) pollen export per plant \( F \bar{E}(f, F) \). Horizontal axis is \( F \), the total number of flowers of a plant. For \( F \) larger than a critical value \( F > F_c \), \( \bar{f} \) is less than \( F \) and is given by a solution of Eq. (5). For \( F > F_c \), \( \bar{f} \) is equal to the total number of flowers, \( F \). The pollen export per flower increases with \( F \) for small \( F \), attains the maximum at \( F = F^* \) (0 < \( F^* < F_c \)) and then decreases afterwards (\( F > F^* \)). Here the number of pollinator approaches are assumed to increase with the total number of flowers \( F \), following Eq. (2). Parameters are: \( k_1 = 0.1, k_2 = 0.1, x_0 = 2, \gamma = 0.5, B = 100,000 \).

(D), (E), and (F) correspond to (A), (B), and (C), respectively, but for the case with a much smaller efficiency of pollen deposition \( k_1 = 0.005 \) (Other parameters are the same).

Note that \( \bar{E}(F, F) \) becomes zero as \( F \) converges to zero, implying that pollen export per flower \( \bar{E}(F, F) \) increases with \( F \) for very small \( F \). On the other hand, it decreases with \( F \) near \( F = F_c \), which can be shown by examining Eq. (12) together with Eq. (10) and \( \frac{\partial \bar{E}}{\partial f} = 0 \) at \( F = F_c \). For \( F \) smaller than \( F_c \), pollen export per flower \( \bar{E}(F, F) \) is maximum at an intermediate value \( F^* \), s.t. 0 < \( F^* < F_c \).
Fig. 2A illustrates the optimal length of visitation sequence \( \hat{f} \) that achieves the maximum pollen export per flower \( E \) for different number of flowers per plant \( F \). \( \hat{f} \) increases with \( F \) for \( F \) less than a critical level \( F_c \), in which case \( \hat{f} = F \) holds. In contrast, for \( F \) larger than this critical level, \( \hat{f} < F \) holds. In such a region, \( \hat{f} \sim F \) holds. Fig. 2B illustrates the pollen export per flower, \( E \). It increases with \( F \) for small \( F \), but has a peak at \( F = F^* \), and then decreases with \( F \) for larger \( F \). \( F^* \) is smaller than the critical value \( F_c \). Fig. 2C illustrates how the total pollen export of the plants (male fitness) increases with the total number of flowers \( F \). Note that for \( \hat{f} < F \) the pollen export increases more slowly than proportionally with \( F \). In this particular case, the range of \( F \) smaller than \( F_c \) is very small.

Figs. 2D, 2E and 2F illustrate a case with a very low rate of pollen deposition (small \( k_1 \)) and consequently less geitonogamy. \( F^* \) is larger, and the region in which the pollen export per flower increases with \( F \) becomes more important. In this region, male fitness (or pollen export) would be an accelerating function of the number of flowers (Fig. 2F). Note however that the pollen deposition rate used to generate this example is outside the observed parameter range in Appendix 3 of de Jong et al. (1992).

In summary, only when pollination is 'inefficient' (\( k_1 \) and \( k_2 \) low) and pollinators are sparse (\( X \) low) would we expect selection for increased nectar reward luring the pollinators into visiting all flowers. Sparse pollination may be the result if plants are unattractive with few open flowers. Only in that case will fitness gained per flower be higher for plants with many flowers (Fig. 2E).

Discussion

Conclusion

The main predictions of the analysis in this paper are that, if plants can adjust nectar reward to affect visitation sequences by pollinators, then the following hold:

- In a large part of the parameter space, the pollinators should visit (from the plants point's of view) only a small fraction of the open flowers on the plant during each approach.
- The length of the optimal visitation sequence increases with total number of open flowers but less than proportionally. The same conclusion was also reached by Klinkhamer et al. (1993) for a fixed number of pollinator approaches. In this paper we have shown that this conclusion also holds if the number of approaches increases with flower number.
- Male fitness is generally a saturating function of number of open flowers, except when pollination is inefficient (\( k_1 \) and \( k_2 \) low) and pollinators are scarce (\( X \) low).
- Under the latter conditions plants should provide high nectar rewards, inducing pollinators to visit all flowers and resulting in an accelerating fitness curve at low flower numbers.
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Plant size, number of approaches and flower visits

The main assumption of the paper is that plants with many flowers attract more pollinators, but less than proportionally. The exponent \( \gamma \) in Eq. (2) has been found to be between 0.18 and 0.52 for bumblebees on *Echium vulgare* (Klinkhamer and de Jong, 1990) and between 0.62 and 0.84 for bumblebees on *Cynoglossum officinale* (Klinkhamer et al., 1989). Thomson (1988) experimented with *Aralia hispida* plants with 1 and 3 umbels which were visited by bumblebees. His results show that approaches increase 2.1–2.5 fold (\( \gamma = 0.69–0.81 \)). Schmid-Hempel and Speiser (1988) compared arrival of bumblebees at small (8 flowers) and large (16 flowers) inflorescences of *Epilobium angustifolium*. The small inflorescences received 59 and the large ones 88 approaches per hour (\( \gamma = 0.57 \)). Further reports of a saturating relationship between number of flowers and number of pollinator approaches come from Geber (1985), Andersson (1988) and Pleasants and Zimmerman (1990). Thus there seems to be unanimous support for the assumption that plants with many flowers attract more pollinators, but proportionally less per flower.

We predicted that the fraction of flowers visited is smaller on large plants. The proportionality constant (the slope on the log-log plot) for number of flowers visited vs. total number of flowers ranged between 0.31 and 0.60 for *Echium vulgare* (Klinkhamer and de Jong, 1990) and between 0.49 and 0.82 for *Cynoglossum officinale* (Klinkhamer et al., 1989). A value of 0.54 was obtained by Robertson (1992) who studied foraging of tachinid flies on *Myosotis colensoi*. Andersson (1988) estimated the proportionality constant to be 0.69 for bumblebees on *Anchusa officinalis*. Thomson (1988) found that 1.5–2.2 times more flowers were visited on plants with 3 umbels, as compared to plants with a single umbel (proportionality constant 0.41–0.73). Schmid-Hempel and Speiser (1988) noticed that bumblebees visited on average 3.2 flowers on small inflorescences (8 flowers) and 4.3 flowers on large inflorescences (16 flowers) (proportionality constant 0.42). Pleasants and Zimmerman's (1990) data on *Delphinium nelsonii* and *Aconitum columbianum* showed that flowers visited increased less than proportionally with total number of flowers. Geber (1985) reached the same conclusion for bumblebees on *Mertensia ciliata*. Schmitt (1983) reported that the proportion of open flowers visited on *Senecio* plants was negatively correlated with the number of open flowerheads per plant for both bumblebees and butterflies.

Revisitation

For simplicity, we explained the model as if each pollinator visits *f* flowers in each visitation sequence. Instead of a fixed number of flowers visited per approach, we may consider a distribution of the number of flowers visited per sequence. Also, the same flower can be revisited within a single approach. In fact all the analyses still hold in such situations. What is needed is the assumption that the total number of pollinator visits per flower follows a Poisson distribution. There are two sources for the variance of the number of pollinator approaches experienced by each flower: (1)
the variance of the number of approaches to an individual plant and (2) the variance of the number of visits to an individual flower during a single pollinator visit. The latter variance would become zero if $f = F$, but the former variance would remain to generate the variance in the number of pollinator visits to an individual flower, thus making a Poisson distribution feasible.

Multiple visits to the same flower during a single visitation sequence of an individual pollinator tend to increase the variance of the number of pollinator visits per flower. This can be demonstrated by a specific example, in which the number of pollinator visits to an individual plant follows a Poisson distribution with mean $X(F)$. If the pollinator visits $f$ different flowers chosen among $F$ flowers of the individual, the number of pollinator visits experienced by an individual flower follows a Poisson distribution with mean $X(F)f/F$. By contrast, if the pollinator may visit the same flower more than once during a single approach to a plant, the total number of pollinator visits per flower has a variance larger than the one given by a Poisson distribution (but with the same mean).

Revisitation of the same pollinator to the plant may require the modification of the model if a considerable fraction of pollen grains collected from a plant can come back to the same plant by revisitation, and if pollinators tend to revisit the flower where they enjoyed a higher foraging success before. These aspects of pollinator behavior could be an important theme for future theoretical study, but is beyond the scope of the present paper.

**Effects of costs of nectar and more approaches**

Our analysis in this paper is based on the simplifying assumption that the increase or decrease of $f$, the number of flowers visited in a single pollinator approach to a plant, is costless. Giving a higher or a lower reward to a pollinator is one way for the plant to manipulate $f$. If the reward is costly, as shown by Pyke (1991), the plant should set a value of $f$ which is smaller than the value that maximizes the fitness, as calculated in the present paper. We then have an even stronger argument to explain why pollinators visit only a fraction of the open flowers on a plant.

However, to optimize $f$ when nectar is costly may not be as simple as it looks, because next to production costs, the investment to pollinator attraction may modify both number of approaches by pollinators $X$ and the length of visitation sequence per visit $f$ (the "dilemma"; Klinkhamer and de Jong, 1993). In such a case the optimal $f$ would be a compromise between cost of nectar, effect of nectar, effect of nectar on $X$, and effect on $f$. If the main problem of the plant is to attract pollinators, then the value of $f$ can be set to a level higher than the optimal value calculated in the present model without such interaction.

It is always beneficial for the plant to increase the total number of pollinator approaches $X$, but it is not always profitable to increase the length of the visitation sequence $f$. Hence plants may give a high reward to increase $X$ but may try to decrease $f$. By which strategies (e.g. variable nectar reward) the plant can partly
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resolve this dilemma is an interesting question in its own (Robertson, 1992), which falls beyond the scope of this paper.

Monocarpy and the shape of the fitness curve

According to life history theory, the shape of the fitness curve as a function of reproductive investment has a profound effect. If the reproductive success increases either linearly or slower than linearly with the reproductive investment, the life history pattern that optimizes the lifetime reproductive success is polycarpy, i.e. the plant should continue to reproduce over many years (Iwasa and Cohen, 1989). By contrast, if the reproductive success increases faster than linearly, then the optimal reproductive schedule can be monocarpy, or mass blooming (Pugiese, 1988). The present paper suggests that the condition favoring monocarpy is difficult to meet because male fitness tends to increase with the number of flowers, and thus with the investment slower than linearly.

The experimental estimates of parameters included in the model were listed in a table in Appendix 3 of de Jong et al. (1992); from this, pollen deposition rate is $0.02 < k_1 < 0.47$ and pollen removal rate is $0.07 < k_2 < 0.65$, and the parameters used to draw Fig. 2A–C are realistic. In order to generate an example in which the male fitness (pollen export) per plant increases faster than linearly, as illustrated in Fig. 2D–F, we need to use extremely small rates of pollen deposition rate or pollen uptake. Based on known parameter ranges, we tentatively conclude that male fitness tends to increase slower than linearly for the observed range of parameters. However, these basic parameters of the pollination processes were studied for only few plants. Mass blooming species may typically have low values of pollen deposition efficiency and it would be interesting if more data on transfer of pollen were available for this group of species.

The benefit of large flowering plants through attracting more pollinators is one of the explanations for the evolution of monocarpy (references in Young, 1990). We showed that this explanation is unlikely, at least for frequently visited plants with efficient pollination. Of interest is Schemske’s (1980) report on the orchid Brassavola nodosa that produces between one and five flowers. Removal of pollinia increased more than proportionally with flower number. If $k_1$ is low, this may potentially lead to accelerating fitness with flower number. Although no pollinator observations were reported this might correspond to our case where pollinators visit all flowers, so that plants that produce flowers in synchrony may be most fit, i.e. export more pollen per flower.

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