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# Systematic increase in pollen carryover and its consequences for geitonogamy in plant populations

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The fraction of pollen that is carried over from one flower to the next as a pollinator visits a sequence of flowers has a strong effect on patterns of mating in plant populations. Although most studies have used simple exponential or geometric functions to represent carryover, pollen deposition patterns often show longer-than-geometric tails, suggesting a systematic increase in the carryover fraction. We introduce a changing carryover model that allows the carryover fraction to increase or decrease during a sequence of visits. Maximum Likelihood methods were used to fit constant and changing carryover models to twelve previously published data sets. A model with an increasing carryover fraction provided a better fit than a constant carryover model in 75% of the cases examined. We found only partial evidence for one proposed cause of increasing carryover, the burial of donor pollen beneath pollen collected from recipient flowers. Finally, we use the results for *Ipomopsis aggregata*, a hummingbird-pollinated plant that presents many flowers simultaneously, to show that the changing carryover model predicts less pollen will be transferred among flowers on the same plant (geitonogamy) than does a constant carryover model fit to the same experimental data.

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Carryover of pollen as pollinators move from flower to flower has long been recognized as a factor that affects the extent of gene flow in plant populations (Levin and Berube 1972, Levin and Kerster 1974, Schaal 1980). As a result, the extent of pollen carryover has now been quantified for several plant-pollinator systems (Thomson and Plowright 1980, Price and Waser 1982, Waser and Price 1982, Campbell 1985, Galen and Plowright 1985, Geber 1985, Svensson 1985, Thomson 1986, Thomson et al. 1986, Waser 1988, Thomson and Thomson 1989, Robertson 1992, Morris et al. 1995). The picture that emerges from these studies is that, although the amount of donor pollen deposited does decline after the first flower visit, some pollen continues to be deposited even after many visits. Faced with ubiquitous pollen carryover, pollination biologists have now realized that a range of carryover patterns are likely, and that different patterns may have different consequences for reproduction and gene flow.

In previous studies, the most commonly used description of carryover has been either an exponential function (Lertzman and Gass 1983, Geber 1985, Svensson 1985) or its discrete analog, a geometric function (Bateman 1947, Primack and Silander 1975, Plowright and Hartling 1981, Crawford 1984, Campbell 1985, Galen and Rotenberry 1988, Robertson 1992, de Jong et al. 1992a, b, 1993). Such curves would be expected if the fraction of donor pollen remaining on the pollinator that is carried over to the next flower (hereafter denoted the "pollen carryover fraction") remains constant throughout a visitation sequence. However, several authors have noted de-

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Table 1. Pollen carryover data sets analyzed.

| Data set | Plant species | Pollinator species | Special treatments | No. of runs | Total no. of visits | Reference |
|---|---|---|---|---|---|---|
| Pollen carryover | | | | | | |
| 1 | *Ipomopsis aggregata* | Hummingbirds* | Recipients emasculated | 11 | 250 | Waser and Price 1982 |
| 2 | *Delphinium nelsonii* | *Bombus flavifrons* | Recipients emasculated | 7 | 85 | Waser 1988 |
| 3 | *Delphinium nelsonii* | *Bombus appositus* | Recipients emasculated | 6 | 133 | Waser 1988 |
| 4 | *Delphinium nelsonii* | *Selasphorus platycercus* | Recipients emasculated | 6 | 203 | Waser 1988 |
| 5 | *Linaria vulgaris* | *Bombus fervidus* | Recipients emasculated | 9 | 86 | Thomson 1986 |
| 6 | *Erythronium americanum* | *Bombus ternarius* | None | 24 | 303 | Thomson 1986 |
| 7A | *Erythronium grandiflorum* | *Bombus occidentalis* | None | 10 | 385 | Thomson et al. 1986 |
| 7B | *Erythronium grandiflorum* | *Bombus occidentalis* | Anthers of recipients brushed | 6 | 212 | Thomson et al. 1986 |
| 8 | *Erythronium grandiflorum* | *Bombus occidentalis* | None | 23 | 822 | Thomson and Thomson 1989 |
| Dye carryover | | | | | | |
| 9A | *Ipomopsis aggregata* | Hummingbirds* | None | 11 | 148 | Price and Waser 1982 |
| 9B | *Ipomopsis aggregata* | Hummingbirds* | Recipients emasculated | 6 | 247 | Price and Waser 1982 |
| 9C | *Ipomopsis aggregata* | Hummingbirds* | Anthers of recipients brushed | 6 | 144 | Price and Waser 1982 |

* *Selasphorous rufus* and *S. platycercus*.

viations from a simple exponential pattern; typically, the observed amount of pollen deposited late in the visitation sequence is greater than predicted by the best-fit exponential model (e.g. see Fig. 1 in Thomson et al. 1986). Such longer-than-exponential tails suggest that the carryover fraction may increase systematically during a flower visitation sequence. Morris et al. (1995) presented a suite of mechanistic models that predict deposition patterns with longer-than-exponential tails, and found that the long-tailed models fit experimental data for *Brassica campestris* better than a simple exponential model. Because long-tailed deposition has significant ecological and evolutionary implications, pollination biologists need to determine how often an exponential (or geometric) model fails to adequately describe pollen carryover.

Here, we evaluate the evidence for increasing pollen carryover (and the long-tailed deposition patterns it generates) in previously published studies. We first propose a discrete model that allows pollen carryover to vary systematically during the course of a visitation sequence. Specifically, the model can portray either increasing or decreasing carryover; the geometric model represents the special case of constant carryover. We then use Maximum Likelihood methods both to estimate the carryover fraction and to determine whether a constant or changing carryover model provides a better fit to 12 previously published data sets. Finally, we discuss the potential consequences of changing carryover for mating patterns in plant populations.

# Methods

## Sources of data

The twelve data sets used in the analysis are summarized in Table 1. The data represent all the carryover studies the authors have published in which the sample size was sufficient to characterize the carryover pattern. Details of the experimental methods are provided in the original papers. In a typical pollen deposition experiment, pollinators were allowed to collect pollen from one or more donor flowers, and then to pay single visits to a sequence of recipient flowers whose stigmas were censused for donor pollen grains. The studies in Table 1 used two techniques to avoid confusing donor and non-donor pollen grains on recipient stigmas. Thomson and colleagues took advantage of a pollen color polymorphism in *Erythronium* spp. to differentiate donor and recipient pollen (Table 1, data sets 6, 7A, 7B and 8). The other studies used emasculated recipient flowers to assure that any pollen grains deposited were produced by the donor flower(s) (see also Thomson and Plowright 1980, Campbell 1985, Galen and Plowright 1985, Geber 1985, Thomson 1986, Waser 1988, Robertson 1992). One concern regarding the emasculated recipient method is that it may preclude the normal layering of pollen on the pollinator's body, a process that might retard the deposition of donor pollen due to its temporary burial beneath non-donor pollen acquired at later visits (Price and Waser 1982,

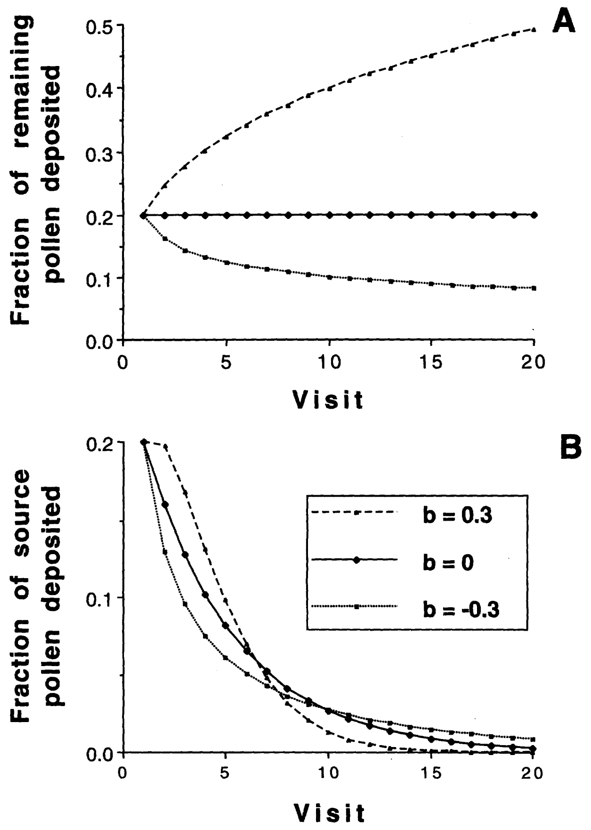

Fig. 1. The effect of the parameter b in eq. 2 on A) the fraction of pollen deposited (or one minus the pollen carryover fraction) and B) deposition pattern of donor pollen.

Lertzman and Gass 1983, Thomson et al. 1986, Robertson 1992, Morris et al. 1995). Re-emergence of buried pollen could produce a long tail to the carryover curve, which might not be seen with emasculated recipients. A second concern is that the absence of anthers may change a pollinator's stance, thus influencing the degree of stigmatic contact. To examine the effect of recipient pollen on the deposition pattern of donor pollen, we included in our analysis data from two studies that explicitly manipulated recipient pollen. First, Thomson et al. (1986) compared deposition of pollen from the red pollen morph of *Erythronium grandiflorum* on yellow-pollen recipient flowers that were either unmanipulated (Table 1, data set 7A) or whose anthers were brushed to remove pollen, leaving the empty anther sacs in place to encourage a normal stance (data set 7B). Second, Price and Waser (1982) compared the deposition patterns of fluorescent dye on recipient flowers of *Ipomopsis aggregata* whose anthers were either unmanipulated (data set 9A), brushed (data set 9B) or removed (data set 9C). We caution that these last 3 data sets quantified deposition of dye and not actual pollen grains. Carryover of dye may not be exactly comparable to pollen carryover (Waser and Price 1982, Thomson et al. 1986, Waser 1988), but the processes are certainly analogous; we included these data sets in order to address the potential importance of pollen layering.

## Models of pollen deposition

We fit two models to each data set to determine whether pollen carryover was constant. The constant carryover or geometric model has the general form (cf. Bateman 1947, Primack and Silander 1975, Plowright and Hartling 1981, Crawford 1984, Campbell 1985, Robertson 1992):

$$P_n = \alpha\ (1-\beta)^{n-1};\ n>0,\ 0<\beta<1 \qquad (1)$$

where $P_n$ is the number of donor pollen grains deposited on the $n^{th}$ visit and $\alpha$ and $\beta$ are constants that can be interpreted as follows. The parameter $\beta$ represents the fraction of donor pollen removed from the pollinator at each visit. Pollen may be removed by deposition onto stigmas or other flower parts, by grooming activities of the pollinator, or by simply falling off. The total number of donor pollen grains deposited on stigmas after a large number of recipient flowers has been visited equals $\alpha/\beta$ (see Appendix). If we assume that removal occurs only through deposition onto stigmas, then eq. 1 becomes:

$$P_n = \lambda\ P_o\ (1-\lambda)^{n-1} \qquad (2)$$

where $\lambda$ is the fraction of donor pollen remaining on the pollinator that is deposited per visit (hence $1-\lambda$ is the carryover fraction, and $(1-\lambda)^{n-1}$ is the fraction of the donor pollen remaining on the pollinator after n-1 visits) and $P_o$ represents the total number of pollen grains delivered to recipient stigmas (since $\alpha/\beta = \lambda\ P_o/\lambda$). In this case, $P_o$ is also the number of pollen grains collected from the donor flower.

If there are multiple avenues by which pollen may leave the pool on a pollinator's body, then we require additional information to estimate the deposition fraction $\lambda$ (see Appendix). For some of the data sets listed in Table 1, we do not know if processes other than deposition are responsible for pollen removal (exceptions are the *Erythronium* spp. (Harder and Thomson 1989) and *Ipomopsis aggregata* (de Jong et al. 1993), in which substantial amounts of non-depositional pollen loss have been observed or estimated). Thus, although we used eq. 2 to represent constant carryover, we make the following caveat (see Appendix). When non-depositional pollen losses are important, then 1) the estimated $\lambda$ represents the total fraction of pollen removed per visit, not just the fraction deposited onto the recipient stigma; and 2) the estimate of $P_o$ represents the total pollen delivery to recipients, which will be less than the amount of pollen removed from the donor.

We compared eq. 2 to a changing carryover model:

$$P_n = P_o\ \lambda n^b \prod_{k=1}^{n-1} (1-\lambda k^b) \qquad (3)$$

Table 2. Maximum likelihood parameter estimates and BIC values for the constant (eq. 2) and changing (eq. 3) pollen carryover models. Best-fit models are indicated by asterisks. †: simplex algorithm did not converge; no parameter estimates were obtained.

| Data set | Model | Parameter values $P_o$ | $\lambda$ | b | Max. log likelihood | BIC |
|---|---|---|---|---|---|---|
| 1 | Constant | 444 | 0.0486 | na | 5126 | 5121 |
| | Changing | 618 | 0.0442 | −0.201 | 5142 | 5134* |
| 2 | Constant | 767 | 0.132 | na | 13175 | 13171 |
| | Changing | 1012 | 0.120 | −0.289 | 13208 | 13201* |
| 3 | Constant | 1091 | 0.0725 | na | 15404 | 15399 |
| | Changing | 1048 | 0.0695 | 0.0699 | 15408 | 15401 |
| 4 | Constant | 462 | 0.0146 | na | 870 | |
| | Changing | † | † | † | † | † |
| 5 | Constant | 2682 | 0.202 | na | 99661 | 99656 |
| | Changing | 3555 | 0.179 | −0.368 | 99844 | 99837* |
| 6 | Constant | 59.0 | 0.303 | na | 1582 | 1576 |
| | Changing | 64.3 | 0.372 | −0.487 | 1676 | 1667* |
| 7A | Constant | 185 | 0.181 | na | 2978 | 2972 |
| | Changing | 186 | 0.251 | −0.265 | 3043 | 3034* |
| 7B | Constant | 293 | 0.208 | na | 3912 | 3906 |
| | Changing | 298 | 0.335 | −0.461 | 4073 | 4065* |
| 8 | Constant | 279 | 0.176 | na | 12781 | 12774 |
| | Changing | 281 | 0.241 | −0.260 | 12985 | 12974* |
| 9A | Constant | 244 | 0.0931 | na | 1563 | 1558 |
| | Changing | 301 | 0.116 | −0.369 | 1595 | 1587* |
| 9B | Constant | 867 | 0.0247 | na | 7115 | 7111 |
| | Changing | $4.25\times10^5$ | $7.4\times10^{-5}$ | −0.304 | 7187 | 7178* |
| 9C | Constant | 1122 | 0.0392 | na | 9666 | 9661 |
| | Changing | 1348 | 0.0361 | −0.0895 | 9669 | 9662 |

in which the fraction of remaining pollen deposited on the $n^{th}$ visit is $\lambda n^b$ (thus $\lambda$ in the changing carryover model represents the fraction of the initial pollen load that is deposited on the first visit). A negative value of the parameter b corresponds to a deposition fraction that declines with visit number (Fig. 1A); hence the carryover fraction increases. An increasing carryover fraction results in a pattern of pollen deposition with longer-than-geometric tails (Fig. 1B). Conversely, positive b values indicate increasing deposition (or declining carryover), which produces sigmoidal deposition patterns with shorter-than-geometric tails. When $b=0$, the changing carryover model reduces to the constant carryover model.

We used Maximum Likelihood techniques to estimate the best-fit parameter values for the two models. We first assumed that the number of pollen grains (or dye particles) deposited on the stigma of recipient n represents a Poisson random variable with expectation $P_n$, as given by eq. (2) or (3). The likelihood of an experimental data set given a particular model is:

$$L = \prod_{j=1}^{N} (P_{n_j})^{v_j} \exp\{-P_{n_j}\} / v_j!$$

where N is the total number of recipient flowers in a data set (Table 1), $v_j$ is the observed number of pollen grains deposited on flower j, and $n_j$ is the position of flower j in a visitation sequence (note that we have calculated the likelihood by combining the data from all runs in a data set). Taking logarithms and subtracting a constant term yields the log likelihood function:

$$\hat{L} = \prod_{j=1}^{N} v_j \ln P_{n_j} - P_{n_j}.$$

For all combinations of models and data sets, we used the simplex algorithm (Press et al. 1986: 326–330) to identify the parameter values that maximized $\hat{L}$ (Pascal program available upon request from W. F. Morris).

To determine which model provided a better fit to a particular data set, we computed the Bayesian Information Criterion (BIC) for each model:

$$\text{BIC} = \hat{L}_{\max} - \frac{1}{2} p \ln N$$

where p is the number of parameters in the model (Schwarz 1978). If one model produces a BIC value that exceeds the corresponding value for the competing model by 1 or more, the model with the greater BIC value is judged to provide a superior fit to the data (Sakamoto et al. 1986). Since increasing the number of parameters in a model tends to decrease the BIC value, this criterion discriminates against overly parameterized models. For $N \geq 3$, the BIC is more conservative than the more familiar Akaike Information Criterion (Akaike 1973) in that it is

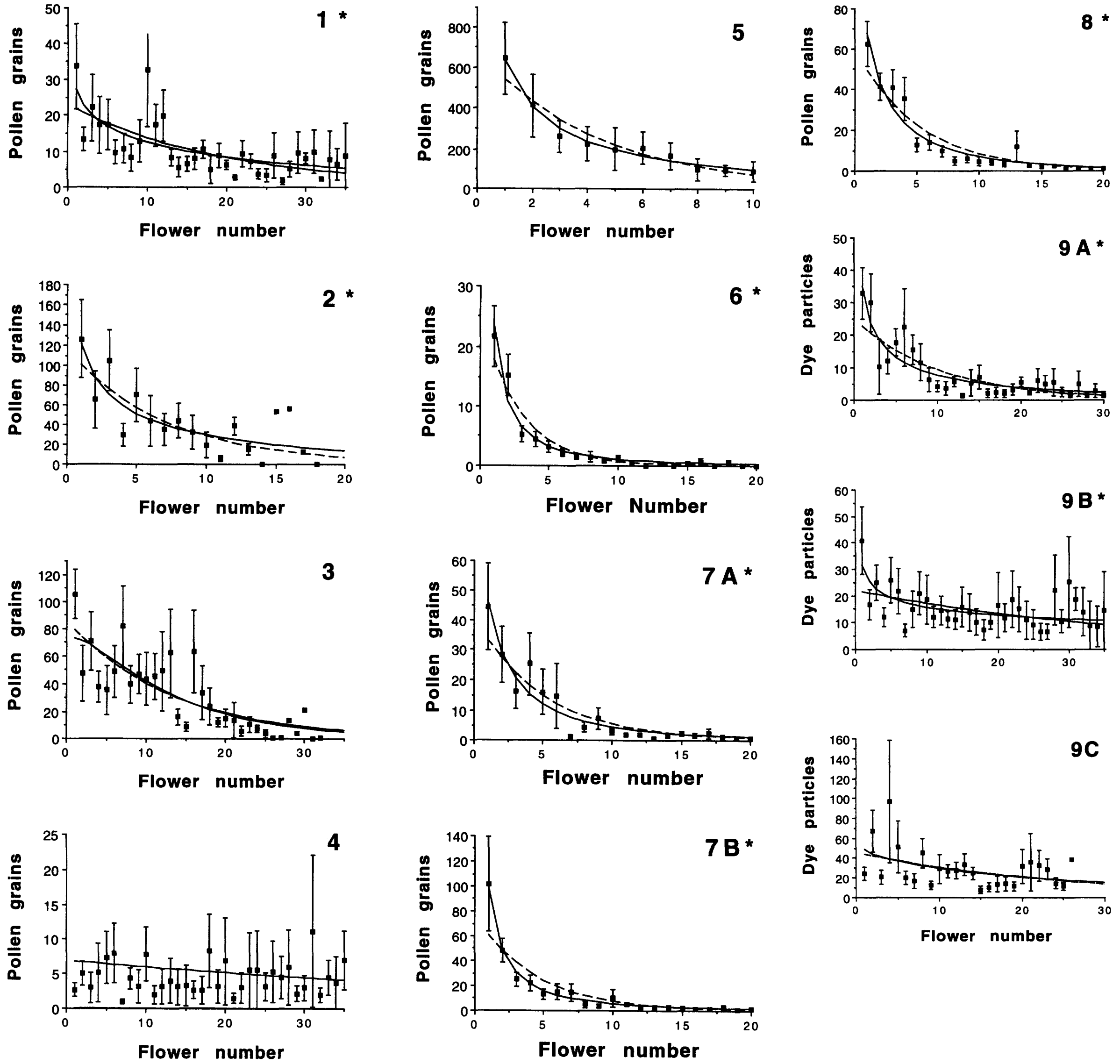

Fig. 2. The observed number of donor pollen grains or dye particles (means ± 1 s.e.) compared to the predictions of the best-fit constant (dashed lines) and changing (solid lines) carryover models. Numbers in the upper right corner of each graph correspond to the data sets listed in Table 2, and asterisks indicate that the changing carryover model provides a better fit than the constant carryover model (see Table 2).

more likely to reject the model with more parameters in favor of the simpler model.

# Results

## Constant vs changing carryover fraction

The Maximum Likelihood parameter estimates and BIC values for both carryover models are given in Table 2. For 9 of the 12 data sets we examined, the changing carryover model fit the experimental data better than the constant model. (For data set 4, in which carryover was especially erratic (see Fig. 2), the search algorithm failed to converge upon reasonable parameter estimates for the changing carryover model; hence the constant model is superior by default). Furthermore, in all 9 of these data sets, the best estimate of the parameter b was negative, indicating that the pollen carryover fraction increased with increasing visit number. The observed deposition patterns are compared to the predictions of the two deposition models in Fig. 2. For all data sets in which the changing carryover model was judged to provide a better fit, the predicted pattern of rapid initial deposition followed by a longer-than-geometric tail accords better with the experimental data.

## The effect of recipient pollen on carryover of donor pollen

For both *Erythronium grandiflorum* and *Ipomopsis aggregata*, pollen carryover increased with visit number when recipient anthers were unmanipulated (data sets 7A and 9A, Table 2). Increasing carryover was still observed when the anthers of *E. grandiflorum* recipients were brushed (data set 7B, Table 2), while the difference in BIC values between the two models was too small to be conclusive for brushed-anther recipients of *I. aggregata* (data set 9C, Table 2). Finally, emasculated recipients of *I. aggregata* also exhibited an increasing carryover fraction (data set 9B, Table 2).

# Discussion

The most striking result of our analysis is that, in 75% of the data sets examined, the pollen carryover fraction appears to increase over the course of a pollination sequence. Furthermore, we detected increasing carryover at least once for each of the six plant species represented in the data, and for both bumblebee and hummingbird pollinators, suggesting that systematic variation in carryover may be a widespread feature of plant-pollinator systems (see also Morris et al. 1995). If so, the earlier view that the interaction between a plant and a pollinator can be characterized by a single pollen carryover fraction is probably too simplistic. Our intent in presenting alternative models and Maximum Likelihood methods for estimating parameters is to encourage future studies to test for changes in carryover.

The changing carryover model (eq. 3) is phenomenological in that it does not explicitly include the mechanism generating the change. Several authors have discussed possible mechanisms that would cause carryover to deviate from a geometric pattern. Pollen grains could differ in how well they are attached to the pollinator, so that weakly adhering grains are deposited rapidly, resulting in increasing carryover of the more firmly attached pollen grains (Thomson et al. 1986). The rapid deposition of weakly adhering pollen may be hastened by the grooming activities of the pollinator (Thomson 1983, 1986). A carryover fraction that has a constant mean but varies stochastically from visit to visit will also generate a long-tailed pattern of pollen deposition that mimics an increasing carryover fraction (Morris et al. 1995). A third mechanism that would increase carryover is the layering of pollen acquired from recipient flowers on top of donor pollen (Price and Waser 1982, Lertzman and Gass 1983, Thomson 1983, Morris et al. 1995). Our analysis of studies that explicitly manipulated recipient pollen (data sets 7A,B and 9A,B,C) yielded only partial evidence for pollen layering. If the increase in carryover in later visits were due entirely to burial of donor pollen beneath recipient pollen, we would expect a geometric deposition pattern when recipient pollen is eliminated, but a long-tailed pattern for intact recipients. Yet we observed a long-tailed pattern of carryover for brushed-anther recipients of *Erythronium* visited by bumble bees (data set 7B, Table 2), suggesting that mechanisms other than layering are primarily responsible for the change in carryover fraction. One possible mechanism is a decline in pollinator grooming over the visitation sequence. Harder (1990a) has shown that bumble bees are more likely to groom after visiting rewarding flowers. Since bumble bees did not acquire pollen from brushed-anther recipients, their propensity to groom may have been highest immediately after they left the donor flower, resulting in lower initial carryover. This hypothesis would also explain why the carryover pattern actually had longer tails when recipient anthers were brushed to remove pollen ($b=-0.461$) than when intact recipients were used ($b=-0.265$), since bumble bees would be expected to continue active grooming while visiting pollen-rich recipients. For *Ipomopsis aggregata* visited by hummingbirds, carryover did shift from a long-tailed pattern for intact recipients (data set 9A, Table 2, $b=-0.369$) to a geometric pattern when recipient anthers were brushed (data set 9C, Table 2), which is consistent with pollen layering. However, factors other than pollen layering must also be operating in this system, since removal of recipient pollen by emasculation rather than by brushing anthers yielded long-tailed carryover (data set 9B, Table 2, $b=-0.304$). One possibility is that mechanical disturbance by anthers homogenizes the donor pollen on a hummingbird's bill by loosening the subset of pollen grains that would otherwise adhere tightly. Emasculation would then lead to long-tailed carryover as weakly adhering pollen is deposited quicker than more "sticky" pollen. For this hypothesis to be true, the effect of mechanical disturbance by anthers must be masked by pollen layering in order to be consistent with long-tailed carryover in intact recipients. These results point to the need for experiments that explicitly manipulate pollen layering and other aspects of pollen transfer mechanics in order to resolve this issue definitively. Nevertheless, our analysis does demonstrate that layering is not required to generate non-geometric deposition patterns, since such patterns were observed in the absence of recipient pollen.

Regardless of the causal mechanism, long-tailed patterns of carryover have important implications for plant reproduction. Morris (1993) and Morris et al. (1995) have discussed the impact of long-tailed carryover on pollen dispersal distance. Pollen carryover also determines in part the relative rates of selfing vs outcrossing in plant populations. Several authors have argued that a high pollen carryover fraction will reduce the amount of geitonogamous transfer of self pollen among flowers on a plant (Crawford 1984, Geber 1985, Richards 1986, de Jong et al. 1992a, b, 1993, Robertson 1992). By analogy, we expect that by increasing the relative amount of pollen that is not deposited until late in a visitation sequence (Fig. 1B), a systematically increasing carryover fraction will reduce geitonogamous pollen transfer in plants with multiple open flowers, and thereby increase pollen export.

To examine the quantitative effect of changing carryover for geitonogamy, we used the results for hummingbirds visiting *Ipomopsis aggregata* (data set 1, Tables 1 and 2) to compare the levels of geitonogamy predicted by the best-fit constant and changing carryover models. *I. aggregata* individuals present as many as 50 flowers simultaneously at peak flowering (de Jong et al. 1992b), and hummingbird visits to multiple flowers on the same plant are common. In addition, the application of self pollen to stigmas of *I. aggregata* strongly reduces seed set (Waser and Price 1991), suggesting a strong advantage to factors that reduce geitonogamy. We computed two measures suggested by de Jong et al. (1993) to summarize the consequences of within-plant pollen transfer. The "fraction geitonogamy", G, is the average over all flowers visited of the fraction of the pollen deposited on a stigma that originates from other flowers on the same plant. The fraction geitonogamy provides an index of the potential impact of interfloral pollen transfer on female fitness in plants such as *I. aggregata* in which self pollen is lower in quality than outcross pollen. The "fraction pollen export" F is the fraction of all pollen collected from a plant that is exported to other plants; by reducing F, geitonogamy may reduce the male fitness of a plant through pollen discounting.

We assume that a hummingbird forages on a long series of donor flowers, and that $\varrho$ pollen grains are transferred to the bird's bill at each visit. We also assume that during a visit, a bird first deposits pollen on the stigma and then acquires pollen from the anthers. That is, we neglect autodeposition of self pollen within a flower (including autodeposition does not alter the consequences of changing carryover rates for geitonogamy). We then calculate G and F for an increasing number of visits to flowers on a recipient plant.

In calculating G, we compute the amount of self and outcross pollen deposited on each flower of a recipient plant in the course of a hummingbird visit. To do so, we first recognize that a changing carryover fraction imparts an age structure to the pollen load attached to a hummingbird's bill, because a greater fraction of recently collected pollen is deposited per visit than older pollen. Hence if $\lambda_i = \lambda i^b$ represents the fractional deposition of pollen that has resided on the pollinator for i visits, the first flower on the recipient plant will receive $\lambda_1\varrho$ outcross pollen grains from the last donor flower visited, $\lambda_2(1-\lambda_1)\varrho$ grains from the penultimate donor flower, and in general

$$\varrho\lambda_i \prod_{j=1}^{i-1} (1-\lambda_j)$$

grains from the donor flower that contributed to the pollen load i visits previously. The total outcross pollen deposited on the first recipient flower $O_1$ is the sum over all age classes of donor pollen on the bird:

$$O_1 = \varrho\left[\lambda_1 + \sum_{i=2}^{\infty}\left(\lambda_i \prod_{j=1}^{i-1}(1-\lambda_j)\right)\right].$$

The term inside the square brackets is the probability that a pollen grain will eventually be deposited after an infinite number of visits, which must equal 1; hence $O_1 = \varrho$. The second and subsequent flowers visited on the recipient plant will receive fewer than $\varrho$ outcross pollen grains, because some of the pollen on the bird will now be self pollen from earlier recipient flowers. In general, the amount of outcross pollen deposited on the nth recipient flower is:

$$O_n = \begin{cases} \varrho & \text{if } n=1; \\ \varrho\left[\sum_{i=n}^{\infty}\left(\lambda_i \prod_{j=1}^{i-1}(1-\lambda_j)\right)\right] & \text{if } n>1. \end{cases}$$

By our assumption that birds first deposit pollen on the stigma and then pick up pollen from the anthers, the first recipient flower receives no self pollen, the second receives $\lambda_1\varrho$ self pollen grains from the first recipient flower, and in general, the number of self pollen grains deposited on the nth recipient flower is:

$$S_n = \begin{cases} 0 & \text{if } n=1; \\ \lambda_1\varrho & \text{if } n=2; \\ \varrho\left[\lambda_1 + \sum_{i=2}^{n-1}\left(\lambda_i \prod_{j=1}^{i-1}(1-\lambda_j)\right)\right] & \text{if } n>2. \end{cases}$$

The fraction geitonogamous pollen deposited on recipient flower n is $g_n = S_n/(S_n + O_n)$. Because $S_1 = 0$, the fraction geitonogamy for the first recipient flower, $g_1$, is zero. Next we observe that

$$\begin{aligned} S_n + O_n &= \varrho\left[\lambda_1 + \sum_{i=2}^{n-1}\left(\lambda_i \prod_{j=1}^{i-1}(1-\lambda_j)\right)\right] \\ &\quad + \varrho\left[\sum_{i=n}^{\infty}\left(\lambda_i \prod_{j=1}^{i-1}(1-\lambda_j)\right)\right] \\ &= \varrho\left[\lambda_1 + \sum_{i=2}^{\infty}\left(\lambda_i \prod_{j=1}^{i-1}(1-\lambda_j)\right)\right] = \varrho. \end{aligned}$$

That is, the total amount of pollen deposited equals the amount of pollen acquired by the hummingbird, as expected when the pollen load on the bird has reached equilibrium. Consequently,

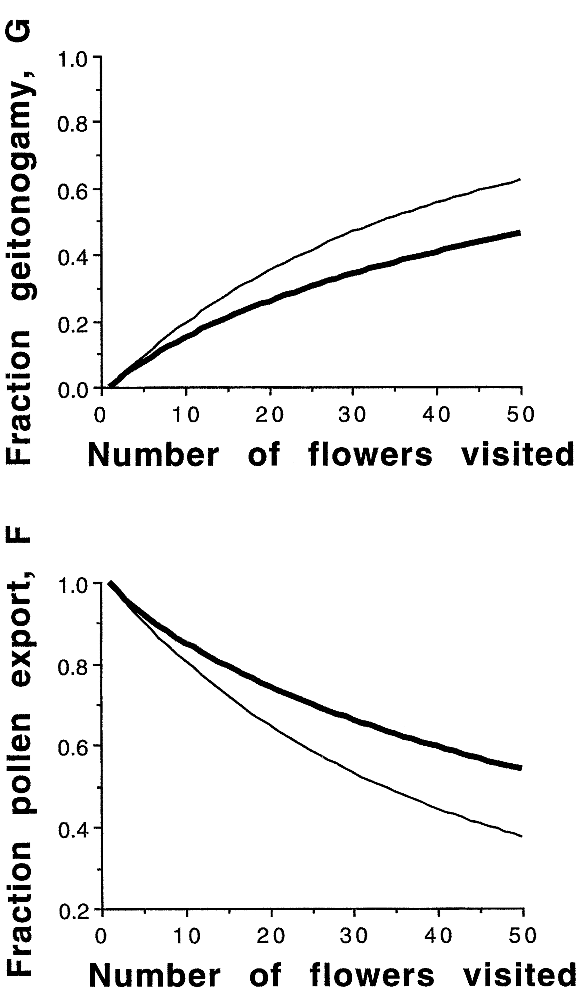

Fig. 3. The predicted fraction geitonogamy and fraction pollen export (see text, eqs 4 and 5) for the best-fit constant (thin lines) and changing (heavy lines) carryover models for hummingbirds visiting *Ipomopsis aggregata.*

$$g_n = \frac{S_n}{\varrho} = \begin{cases} 0 & \text{if } n=1 \\ \lambda_1 & \text{if } n=2 \\ \lambda_1 + \sum\limits_{i=2}^{n-1} \left( \lambda_i \prod\limits_{j=1}^{i-1} (1-\lambda_j) \right) & \text{if } n>2 \end{cases}$$

Note that the fraction geitonogamy does not depend on the amount of pollen that adheres to the bill per visit. The average fraction geitonogamy when N recipient flowers are visited is:

$$G = \frac{1}{N} \sum_{n=1}^{N} g_n. \tag{4}$$

The fraction pollen export F is simpler to calculate. If a hummingbird visits only a single recipient flower, it will carry off $\varrho$ recipient pollen grains, and F will equal 1. If $N > 1$ recipient flowers are visited, the bird will carry off $\varrho$ grains from the last recipient flower, $(1-\lambda_1)\varrho$ grains from the penultimate flower, etc. In general,

$$E_N = \varrho \left[ 1 + \sum_{i=1}^{N-1} \left( \prod_{j=1}^{i} (1-\lambda_j) \right) \right]$$

pollen grains will be exported. The total amount of recipient pollen collected is $N\varrho$; hence the fraction pollen export is:

$$F = \frac{E_N}{N\varrho} = \frac{1}{N} \left[ 1 + \sum_{i=1}^{N-1} \left( \prod_{j=1}^{i} (1-\lambda_j) \right) \right]. \tag{5}$$

As is true for G, F is independent of the amount of pollen acquired per visit.

We substituted the parameter estimates $\lambda = 0.0442$ and $b = -0.201$ for the changing carryover model (data set 1, Table 2) into eqs 4 and 5 to calculate G and F. To calculate the expected levels of geitonogamy for the constant carryover model, we set $\lambda_i$ for all pollen age classes equal to the best-fit estimate of the constant deposition fraction (i.e. we set $\lambda = 0.0486$ and $b = 0$ in eqs 4 and 5; for equivalent expressions for G and F when carryover is constant, see de Jong et al. 1992a, 1993). The two carryover models make strikingly different predictions about geitonogamy, despite the fact that the parameters for the 2 models were estimated from the same data set (Fig. 3). For example, if a hummingbird visits 12 flowers per plant (which equals the mean number of open flowers per plant at the Rocky Mountain Biological Laboratory (de Jong et al. 1992b)), G is 24.6% lower (0.172 vs 0.228) and F is 7.2% higher (0.828 vs 0.772) for the changing carryover model than for the constant model. For any number of flowers visited, the changing carryover model predicts a lower fraction geitonogamy and a higher fraction pollen export than the constant carryover model. This example illustrates that accurate descriptions of pollen carryover patterns are needed to correctly predict patterns of mating in plant populations. It also supports the view that a systematic increase in the pollen carryover fraction will reduce the effects of geitonogamy on both male and female fitness in mass-blooming plants such as *I. aggregata.*

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## Appendix

### *Estimating multiple routes of pollen removal from pollinators*

If the donor pollen collected by a pollinator can have multiple fates, the appropriate model for constant pollen carryover is more complex than eq. 2. For example, let us assume that a constant fraction λ of the remaining donor pollen is deposited on each flower visited, but that an additional fraction *d* is dropped or groomed from the pollinator's body, and hence is never deposited onto recipient stigmas (see de Jong et al. 1993 for a slightly different measure of pollen loss). This scenario is portrayed by the model:

$$P_n = \lambda\ P_o\ [1-(\lambda + d)]^{n-1}. \qquad (A1)$$

Like eq. 2, eq. A1 predicts a geometric decrease in the number of pollen grains deposited in the course of a visitation sequence. However, we cannot estimate all three parameters λ, *d*, and $P_o$ if we know only the number of pollen grains deposited on recipient stigmas. The reason is that there are only two free parameters in eq. A1, since the model can be rewritten in the form of eq. 1 by setting $\alpha = \lambda\ P_o$ and $\beta = \lambda + d$. Maximization procedures (such as the simplex algorithm that we used to fit carryover models to deposition data) will invariably set $d = 0$, inflate the estimate of λ, and deflate the estimate of $P_o$. However, if an independent estimate of the amount of donor pollen collected by the pollinator (i.e. $P_o$) is available, then values for both λ and *d* can be determined from deposition data. (For methods of estimating $P_o$, see Harder and Thomson 1989 and Harder 1990b). One would simply fit eq. 1 to the data to obtain estimates of $\alpha$ and $\beta$, set $\lambda = \alpha/P_o$, and set $d = \beta - \lambda$.

*Total pollen delivery*

The total number of donor pollen grains that arrive on recipient stigmas (S) can be calculated by summing eq. 1 over all recipients:

$$S = \sum_{n=1}^{\infty} \alpha\ (1\text{-}\beta)^{n-1} = \alpha + \alpha\ (1\text{-}\beta) + \alpha\ (1\text{-}\beta)^2 + \ldots \quad \text{(A2)}$$

Because $\beta < 1$, the infinite geometric series A2 converges to $\alpha/\beta$. Note that this result is valid regardless of whether pollen removal occurs via deposition only ($\beta = \lambda$ as in eq. 1) or via deposition combined with other losses ($\beta = \lambda + d$ as in eq. A1). Hence the total pollen delivery when non-depositional pollen removal occurs is $\lambda P_o/(\lambda + d)$.

*Caveat for using eq. 2 when non-depositional pollen removal occurs*

If one were to use eq. 2 when significant non-depositional pollen removal occurs, then the parameter estimates $\hat{\lambda}$, and $\hat{P}_o$ no longer represent the true values of the deposition fraction and the amount of donor pollen collected, respectively. Comparison of eqs (2) and (A1) shows that $\hat{\lambda}$ is an estimate of $\lambda + d$, the total fraction of donor pollen removed per visit, and $\hat{P}_o$ is an estimate of $\lambda P_o/(\lambda + d)$ (which is the total pollen delivery with non-depositional pollen removal; see above).