Received: 10 October 2022 | Accepted: 9 January 2023

DOI: 10.1002/ajb2.16158

SPECIAL ISSUE ARTICLE

American Journal of Botany

Conflicting constraints on male mating success shape reward size in pollen-rewarding plants

Jacob M. Heiling[1,2] | **Rebecca E. Irwin**[1] | **William F. Morris**[3]

[1]Department of Applied Ecology, North Carolina State University, Raleigh, NC, USA

[2]Department of Biological Sciences, Clemson University, 132 Long Hall, Clemson, SC, USA

[3]Department of Biology, Duke University, Durham, NC, USA

Correspondence
Jacob M. Heiling, Department of Biological Sciences, Clemson University, 132 Long Hall, Clemson, SC 29634, USA.
Email: jheilin@clemson.edu and jacob.michael.heiling@gmail.com

This article is part of joint special issues of the *American Journal of Botany* and *Applications in Plant Sciences*: “Pollen as the Link Between Phenotype and Fitness.”

Abstract

Premise: Pollen-rewarding plants face two conflicting constraints: They must prevent consumptive emasculation while remaining attractive to pollen-collecting visitors. Small pollen packages (the quantity of pollen available in a single visit) may discourage visitors from grooming (reducing consumptive loss) but may also decrease a plant's attractiveness to pollen-collecting visitors. What package size best balances these two constraints?

Methods: We modeled the joint effects of pollinators' grooming behaviors and package size preferences on the optimal package size (i.e., the size that maximizes pollen donation). We then used this model to examine Darwin's conjecture that selection should favor increased pollen production in pollen-rewarding plants.

Results: When package size preferences are weak, minimizing package size reduces grooming losses and should be favored (as in previous theoretical studies). Stronger preferences select for larger packages despite the associated increase to grooming loss because loss associated with nonremoval of smaller packages is even greater. Total pollen donation increases with production (as Darwin suggested). However, if floral visitation declines or packages size preference increases with overall pollen availability, the fraction of pollen donated may decline as per-plant pollen production increases. Hence, increasing production may result in diminishing returns.

Conclusions: Pollen-rewarding plants can balance conflicting constraints on pollen donation by producing intermediate-sized pollen packages. Strictly pollen-rewarding plants may have responded to past selection to produce more pollen in total, but diminishing returns may limit the strength of that selection.

KEYWORDS

floral reward, foraging preferences, male mating success, mathematical model, pollen donation, pollen packaging, pollen presentation theory, pollinator grooming, pollinator reward preferences

Angiosperms present different types of “rewards” (nectar, pollen, oils, resins, and even ovules/seeds; e.g., Ramírez et al., 2023 in this special issue) to entice animals to visit their flowers and, in so doing, provide the plant with reproductive services (delivery of pollen to a flower's stigmas, and delivery of the flower's pollen to stigmas). Among these rewards, pollen perhaps most commonly serves two functions: It is a reward, but it also carries gametes (the same is true of ovules in pollinating seed parasitic mutualisms, but they are relatively rare). While plants often use alternative rewards such as nectar to entice floral visitors and may safeguard pollen via morphological (Thorp, 2000) or chemical (Rivest and Forrest, 2020) means, nearly 20,000 species of insect-pollinated angiosperms (representing ~7% of all angiosperm species) use pollen as their sole floral reward (Willmer, 2011). In this situation, plants may be faced with a dilemma: They must present enough pollen to entice (pollen-collecting) animals to visit their flowers but prevent at least some of their pollen from being consumed so that it can transport male gametes.

One well-known mechanism that can shelter at least some of the pollen that visitors remove from flowers from being consumed or lost is the presentation of pollen in relatively small packages (Harder and Thomson, 1989). The reason packaging can prevent excessive pollen loss is that pollinators are more likely to groom after receiving a large amount of pollen during a flower visit, either to simply clean their bodies (likely true even of nectar-collecting visitors) or, for pollen-collecting visitors, to immediately consume the pollen or pack it into structures (e.g., bees' corbiculae) for transport and later consumption (Boggs and Gilbert, 1979; Thomson, 1986; Inouye et al., 1994). Either way, the removed pollen does not transport gametes. For pollen-collecting visitors, it may not be efficient to groom after receiving only a small pollen reward, even though pollen is the reward of interest. As Harder and Thompson (1989; also see Klinkhamer and de Jong, 1993) showed, when the probability of grooming increases with the amount of pollen that visitors can remove from a flower during a visit, the total amount of pollen delivered to stigmas will be increased by a plant presenting as little pollen as possible at one time in each flower (i.e., by making pollen package size as small as possible) and distributing its total pollen production into many small packages.

However, if the size of pollen packages becomes too small, a plant's flowers may become unattractive to pollen-collecting visitors, who should prefer to get a relatively large reward for the time invested in visiting each flower. Thus, pollen-rewarding plants must negotiate two conflicting constraints: Making large packages will likely increase pollen loss to grooming, while making small packages will likely result in low visitation and many unremoved packages that therefore will not function to transport gametes. While Harder and Thomson (1989) presented theory to examine the advantages of packaging to minimize grooming losses, we are not aware of any theoretical investigation of how pollen-rewarding plants should best negotiate the twin constraints of pollen grooming and attractiveness to pollinators. Hence, here we construct a simple model to assess optimal package size when both constraints operate.

In *The Origin of Species*, Darwin (1859, p. 90) argued that when floral visitors view pollen as a reward, "[plant] individuals which produced more and more pollen, and had larger anthers, would be selected", even when most of the pollen is consumed by the visitors. But is it inevitably true that pollen-rewarding plants that produce more pollen will have greater male fitness? Darwin drew an analogy between nectar and pollen as rewards, suggesting that greater production of either would increase a plant's attractiveness to visitors seeking that reward, and thus increase male success. As pollen is the only reward presented by strictly pollen-rewarding species, Darwin's conjecture might suggest that strictly pollen-rewarding plants should produce more pollen than their relatives that produce both nectar and pollen. There is some empirical evidence that this is indeed the case (Simpson and Neff, 1983; Golubov et al., 1999; Etcheverry et al., 2012). However, greater production of pollen per plant will also alter the pollen standing crop in the plant population. Greater pollen availability could potentially alter pollinator visitation rates and the preferences of pollen-collecting floral visitors, which in turn may influence whether increasing pollen production actually does increase male fitness. To examine this possibility, we modify our simple model to explore possible scenarios of increasing pollen production and whether it enhances pollen donation (one component of male fitness).

In this paper, we use simple mathematical models to address the following questions: (1) How do grooming and reward size preference interact to affect optimum pollen package size in pollen-rewarding plants? (2) Does optimum package size depend on additional factors such as total pollen production by a plant and the amount of passive pollen loss (i.e., pollen that simply falls out of flowers during a pollinator visit)? (3) Does making more pollen increase the amount of pollen a plant donates, and does the answer to this question depend on other changes that accompany increased pollen production, such as changes in floral visitation rate and pollinators' reward size preferences?

OPTIMAL PACKAGE SIZE WITH GROOMING AND REWARD PREFERENCES

Pollen donation with passive and active pollen loss

Many animal-pollinated plants have mechanisms to control the release of pollen over a period of time (Lloyd and Yates, 1982; Thomson et al., 2000). A large array of architectural and phenological mechanisms can control pollen release within individual flowers and across the entire floral display (Lloyd and Yates, 1982; Harder and Thomson, 1989). We use "pollen package" to refer to the amount of pollen available in a flower to a visitor during a single visit. Our focus is on how a plant's package size affects the absolute number and fraction of its pollen grains that are deposited on stigmas, whether in flowers on other plants, in other flowers on the same plant, or in the same flower. Mechanisms to reduce autogamy and geitonogamy are described elsewhere in the pollen presentation literature (e.g., Harder and Thomson, 1989; Harder and Wilson, 1994; Castellanos et al., 2005; Thomson, 2006; Leme da Cunha and Aizen, 2023 in this special issue).

We adopted an equation from Harder and Thomson (1989) (Eq. 1) to represent the number of grains donated to stigmas, D, from a package containing R pollen grains, conditional on its removal by a visitor and accounting for passive loss and grooming, which are governed by the parameters a and g, respectively (see Table 1 for definitions of all model parameters):

$$D = aR^g \tag{1}$$

with $0 \le a \le 1$ and $0 < g \le 1$. "Passive loss" refers to pollen that cannot transport gametes due to processes other than

TABLE 1 Parameter meanings, ranges, and values used.

Parameter	Meaning	Range or values
A	Total pollen grains produced per flower	10,000; 50,000; and 100,000
R	Pollen package size, number of grains released/flower/visit	100 up to A
a	Attenuation coefficient for passive loss	0–1 constant at $a = 0.9$
g	Attenuation coefficient for grooming/consumptive loss	0–1
y	Reward size preference	0–1
H	Half-saturation constant for removal probability	$A/2$

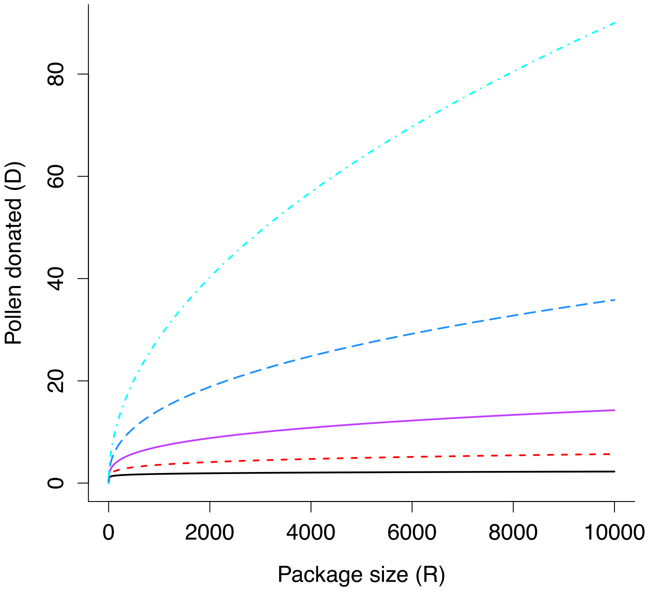

FIGURE 1 Effect of grooming on pollen donation as described by Eq. 1, taken from Harder and Thomson (1989). From top to bottom, lines show values of grooming parameter g of 0.5, 0.4, 0.3, 0.2, and 0.1. In all cases, the passive loss parameter $a = 0.9$.

grooming and consumption by pollinators, including pollen that falls from the flower during a visit or from the pollinator's body in fight (Thomson, 1986; Inouye et al., 1994). The passive loss parameter a is the amount of removed pollen that is *not* passively lost; thus $a = 0$ represents passive loss of all pollen removed during a visit and passive loss declines to zero as a approaches 1. The grooming parameter g governs active loss of pollen that is not lost passively and is inversely related to grooming intensity such that if $g = 1$, the fraction donated is independent of the amount removed, but if $g < 1$, the fraction deposited declines with the amount removed, as would be expected if the visitor is more likely to groom or to groom more thoroughly after picking up a larger amount of pollen (Harder, 1990a; Castellanos et al., 2005; Weinman et al., 2023 in this special issue). If $g < 1$, D is an increasing but decelerating function of R (Figure 1), and therefore the proportion of grains donated per package, D/R, declines as R increases. Therefore, the smallest possible packages will lead to more donation, and all else being equal, a plant dividing its total pollen production into many packages, each as small as possible, will be favored.

Harder and Thomson (1989) found that a mean of 14% of the pollen available in nectar-rewarding *Erythronium americanum* flowers was lost passively during manipulation of flowers by nectar foraging *Bombus* (*B. ternarius* and *B. terricola*) queens and *Apis mellifera* workers, while Rademaker et al. (1997) found that approximately 50% of the pollen removed during single visits to nectar-rewarding *Echium vulgare* flowers failed to adhere to nectar foraging *B. terrestris* workers. These values translate to passive loss parameter values of $a = 0.86$ and 0.5, respectively. Because pollen-rewarding plants often exhibit some degree of specialized pollen placement on the floral visitor (Dunn, 1956; Harder, 1990b; Vallejo-Marín et al., 2009), which should reduce passive loss, we set the passive loss parameter at $a = 0.9$ throughout. Actual passive loss values may be considerably lower (i.e., $a > 0.9$) in plants that exhibit very specialized placement or produce adhesive pollenkitt (e.g., *Lupinus* spp.), or higher in those with large open and unspecialized corollas (e.g., *Papaver* spp.).

Incorporating pollen reward size preference

However, for a pollen package to contribute to a plant's male success, it must first be removed by a floral visitor. Pollinators are known to discriminate among flowers based on pollen reward size (e.g., Cresswell and Robertson, 1994; Rasheed and Harder, 1997a, b). To account for the effect of pollinator reward size preferences on pollen removal, we used a modified Michaelis–Menten equation to represent the probability p that a package of size R is removed from the flower:

$$p = \frac{R^y}{H^y + R^y}. \tag{2}$$

The preference parameter y governs pollinators' preferences for larger rather than smaller packages. The case $y = 0$ represents visitors that are indifferent with respect to the size of pollen rewards, and preference for larger packages increases with y (Figure 2A). For simplicity, we have assumed that if $y > 0$, the probably of removal approaches 1 as package size approaches infinity, but one could easily

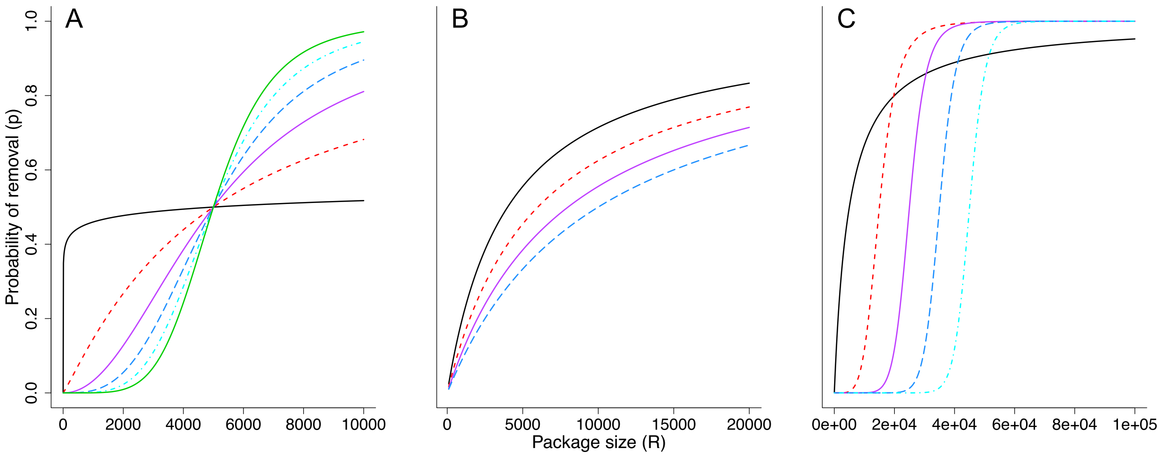

FIGURE 2 Effect of pollinator preferences on the probability that a pollen package of size R is removed from a flower by a visitor, according to Eq. 2. Panel A shows the effect of changing the preference parameter y from 0.1 (solid black) to 5.1 (solid green); here the half-saturation constant $H = 5000$. Panel B shows the effect of increasing the half-saturation constant H from 4000 to 10,000 pollen grains in increments of 2000 grains; here $y = 1$. Panel C shows the effect of simultaneously changing y and H from $(y, H) = (1, 5000)$ (solid black) to $(y, H) = (17, 45000)$ (dashed cyan) in equal increments.

introduce another parameter to the numerator on the right-hand side of (2) to represent the asymptotic probability of removal. As y approaches infinity, the probability of removal approaches a step function, with no removal below a threshold package size and complete removal above. The parameter H is similar to the Michaelis–Menten half-saturation constant; when visitors show preferences ($y > 0$), H is the package size at which the probability of removal equals 0.5. Increasing H decreases the probability of removal at all package sizes (Figure 2B). Thus, the effects of package size on removal are determined by both y and H (Figure 2C).

Total pollen donation and optimum package size

The product of (1) and (2) gives f, the total pollen donation expected per pollen package:

$$f = pD. \tag{3}$$

If a plant makes a total of A pollen grains and divides them into packages of size R, then the number of packages n is

$$n = \frac{A}{R}. \tag{4}$$

Thus, the total expected pollen donation per plant F is the product of the number of packages (n) and the total pollen donation expected per pollen package (f)

$$F = nf = \frac{pDA}{R}. \tag{5}$$

The optimal package size $\bar{R}$ is the one that maximizes F. In Appendix S1, we show that the optimum package size predicted by (5) is

$$\bar{R} = \left(\frac{y}{1-g} - 1\right)^{1/y} H. \tag{6}$$

Three conclusions are immediately apparent from Eq. 6. First, if y, g, and H are stand-alone parameters (i.e., not functions of other parameters in the model), then because passive pollen loss (governed by the parameter a) and total pollen production (A) do not appear in Eq. 6, they do not influence the optimal package size (but below, we will relax the assumption that y and H are stand-alone parameters). Second, it is easy to see that if $y \leq 1 - g$, then $\bar{R} \leq 0$ (see Appendix S2). Of course, zero or negative package sizes are impossible, but what this condition says is that if pollinator preference is weak (i.e., y is closer to zero) relative to the intensity of grooming (i.e., $1 - g$ is closer to 1), then the optimum is for the plant to make packages as small as possible. However, if $y > 1 - g$, then plants should make packages larger than the minimum size, *even though* a greater proportion of pollen will be lost to grooming, simply because too many smaller packages would never be removed. Third, we see from Eq. 6 that $\bar{R}$ increases linearly with H, the half-saturation constant of the pollinator preference function. Because the probability of removal declines for all package sizes as H increases (Figure 2B), higher H means that plants must make larger packages to ensure a reasonable probability of removal.

The relationship between optimal package size and parameter y is nonlinear (Figure 3A). As noted above, $\bar{R}$ is effectively a single pollen grain when y is small. As y increases, initially increases to a maximum value and then declines. As y increases to very large values, the exponent

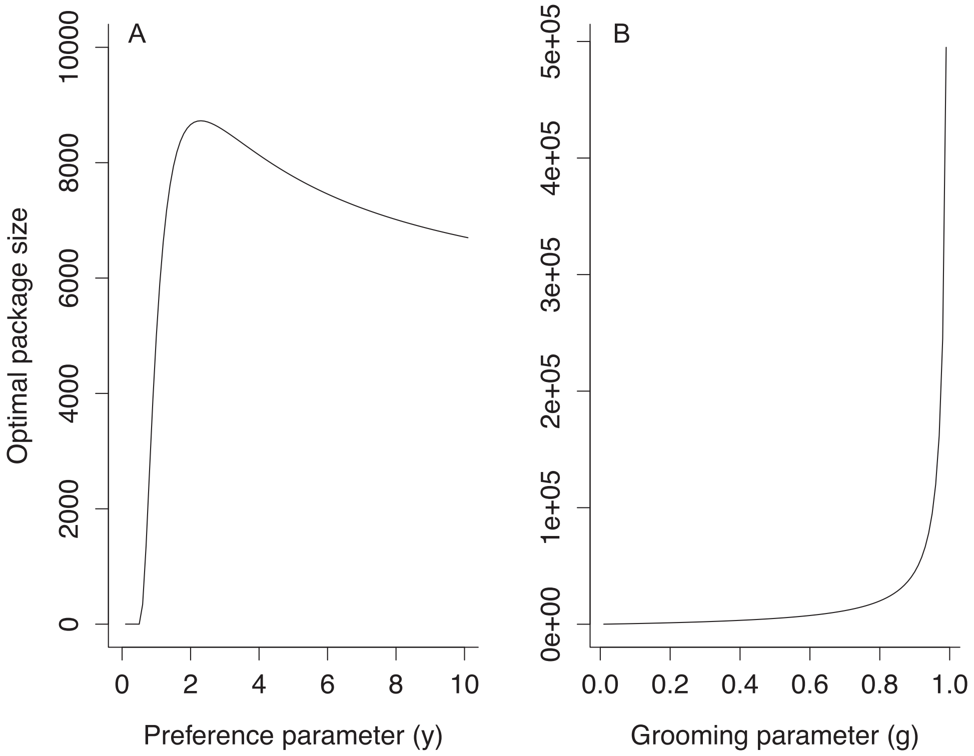

FIGURE 3 Optimal package size $\overline{R}$ given by Eq. 6. Panel A shows $\overline{R}$ for different values of the preference parameter y with $g = 0.5$. Panel B shows $\overline{R}$ for different values of the grooming parameter g with $y = 1$. In both panels, $H = 5000$.

$1/y$ in the first term on the right-hand side of Eq. 6 approaches zero, so the first term goes to 1, and therefore, the asymptotic optimal package size as y goes to infinity is H. The reason that $\overline{R}$ initially increases with y is straightforward; as pollinators discriminate more against small packages in favor of larger ones (Figure 2A), plants must make larger packages to ensure pollen removal. However, as y becomes very large, the probability of removal begins to plateau for package sizes above H (Figure 2A), and therefore there is little advantage in producing very large packages that are only slightly more likely to be removed but face high losses to grooming, causing $\overline{R}$ to decline. As the probability of removal approaches a step function as y approaches infinity, all packages above H in size have removal probability 1 (and all packages below H are not removed); hence, the best package size is H, which ensures removal but minimizes grooming losses. For a given value of the preference parameter y, optimal package size increases as grooming intensity decreases (i.e., as g approaches 1; Figure 3B). In other words, once the grooming constraint is relaxed, larger packages are favored to increase removal.

Does increased pollen production increase pollen donation in pollen-rewarding plants?

Was Darwin correct that plants can increase pollen donation by producing more pollen? The simplest possibility is that pollinators' package size preferences and grooming behaviors remain fixed as pollen production increases. If Eqs. 1 and 2 are independent of pollen production A, then Eq. 5 predicts that total pollen donation will increase linearly with pollen production, or equivalently, that the fraction of pollen that is delivered to stigmas, $F/A = pD/R$, will be constant as pollen production increases. Under this scenario, greater pollen production does increase total pollen donation despite pollen consumption, as Darwin predicted, and the value of the additional pollen produced does not decline as more and more pollen is produced.

However, there are good reasons to expect that pollen removal may not always be independent of total pollen production. At least two possibilities come to mind, both related to the fact that if all plants in a population make more pollen, the pollen standing crop should increase. First, if pollen availability increases across the plant population, but if pollinator abundance is limited by other factors such as nest site availability, predation, or disease or by availability of resources (e.g., nectar or pollen) in other plant species at critical times in the year, then the ratio of pollinators to available pollen might decrease as per-capita pollen production increases. Thus, greater pollen production might lead to a decrease in the probability that a package will be removed at all package sizes. The second possibility is that as pollen becomes more available population-wide, pollen-collecting pollinators might come to prefer larger packages even more. Looked at another way, when pollen is scarce, pollinators may be forced to take some smaller packages to meet their pollen needs, but as pollen availability increases, it may be more efficient for pollinators to learn which plants are presenting larger packages and concentrate their foraging only on those plants. In the following sections, we explore how these two possibilities influence whether greater pollen production increases pollen donation.

Scenario I: Consequences of feedbacks between pollen abundance and pollen removal

The simplest way to introduce a reduction in pollen removal as pollen production increases is to make the half-saturation constant H in our simple model an increasing function of A. Because increasing H decreases the probability of removal for packages of all sizes (Figure 2B), making H a simple linear function of A (i.e., $H = A/2$) achieves the desired reduction in removal probability as A increases. To isolate the effect of increasing A, we assess donation for plants making the optimal package size at each level of A (the optimal size is given by Eq. 6 with $H = A/2$). In this and the subsequent scenarios, we vary pollen production from 10,000 to 100,000 pollen grains, which spans the range of per-flower pollen production in three strictly pollen rewarding plant species, *Lupinus sericeus* (Harder, 1990b), *Desmodium uncinatum* (Etcheverry et al., 2012), and *Solanum chimborazense* (Mione and Anderson, 1992), but the results we present hold for larger amounts of pollen produced per plant.

Not surprisingly, when removal declines with pollen abundance, plants need to make larger packages to have them removed (Figure 4A; note that for the parameter values used in Figure 4A, the optimal package size equals A, so the best option is to produce a single large package). Also unsurprisingly, when plants must make larger and larger packages to achieve removal, grooming losses increase, total pollen donation increases but less steeply than does pollen production (compare x- and y-axis scales in Figure 4B), and the fraction of all pollen that is donated declines with A (Figure 4C). Thus, reduced removal as pollen production increases impedes plants' ability to increase donation by increasing production, and plants face diminishing returns as they produce more and more pollen.

Scenario II: Simple adaptive pollinator preferences

To mimic pollinators that adapt their package size preferences to the level of pollen availability in the plant population, the simplest modification to the model is to make the parameter y a linearly increasing function of per-capita pollen production A (again treating H as a constant as in our original model, and again tracking donation for plants making the optimal package size at each level of A). With this change, pollinators' preferences for larger packages, and discrimination against smaller packages, increases as the pollen standing crop increases (see Figure 2A). Because the optimal package size is a nonlinear function of y (Figure 3A), optimal package size can increase, decrease, or remain constant with increasing A (and thus y) over different ranges of A. In the scenario illustrated in Figure 4B, E, and H, optimal package size equals A when A is small (<20,000), i.e., the largest possible packages are favored (Figure 4B), and as package size increases, grooming losses increase and the fraction of pollen donated declines (Figure 4H), as in Scenario I. However, once y becomes sufficiently large that optimal package size begins to decrease (Figure 4B; compare to Figure 3A) as packages larger than H are converging in attractiveness, grooming losses decrease, and fractional pollen donation now increases (Figure 4H). Eventually, as A continues to increase, fractional donation will asymptote as the optimal package size converges on H (see Figure 3A). Thus, in this model, increasing pollen production can decrease, increase, or have no effect on pollen donation, depending on the range of pollen production being considered, a more complex situation than Darwin envisioned.

Scenario III: Pollinators prefer increasingly larger packages as pollen production increases

One perhaps unrealistic consequence of the assumption that only the preference parameter y increases as pollen production A increases is that pollinators increasingly act as though they care only about whether a package is above a threshold size (H), refusing all smaller packages and making no distinctions on the basis of size for packages above the threshold. Thus, to mimic increasingly picky pollinators, in Scenario III we make *both* the preference parameter y and the half-saturation constant H linearly increasing functions of pollen production A (compare to Figure 2C). The result is that pollinators increasingly favor larger and larger packages as pollen production increases (Figure 4C). Plants can no longer avoid high grooming losses if they are to have their pollen removed by pollinators, total pollen delivery increases less steeply than pollen production (Figure 4F), and the fraction of pollen donated declines as A increases (Figure 4I). Thus, as in Scenario I, under Scenario III plants again face diminishing returns as they increase pollen production, not because packages of all sizes suffer reduced removal but because increasingly pollinators are interested only in the largest packages. However, depending on the parameter values in the two scenarios, the diminishing returns in Scenario III may be less steep than in Scenario I (compare Figure 4F and H).

DISCUSSION

The fundamental message that emerges from our simple model and the scenarios we explored here is that multiple constraints on male success must be considered when we try to understand the reward sizes presented by

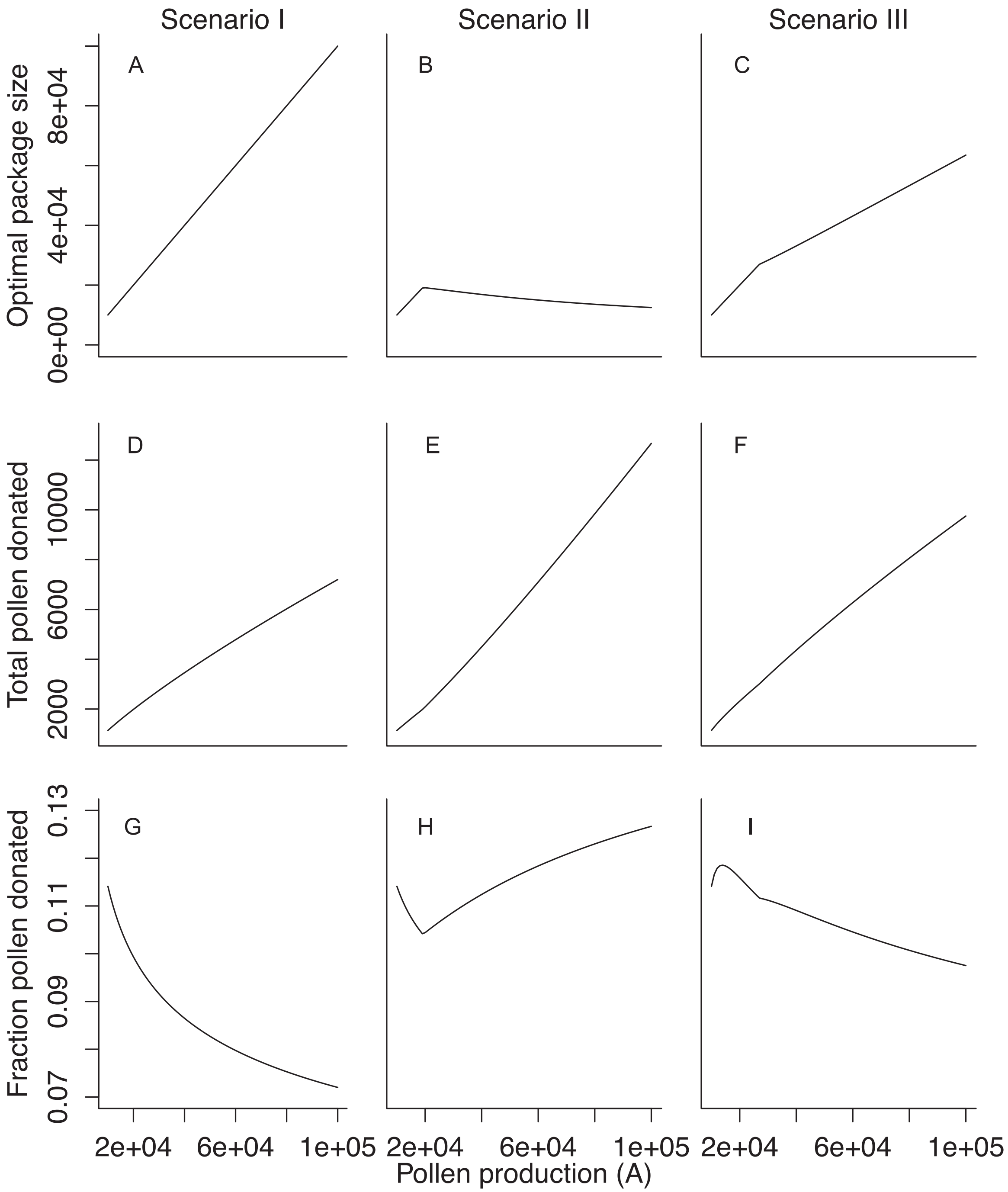

FIGURE 4 Effects of increasing total pollen production by a plant (A) on the optimal package size $\overline{R}$ (panels A–C), total pollen donation (panels D–F), and the fraction of pollen that is donated to stigmas (panels G–I), according to three scenarios (described in the text) for how floral visitation and pollinator preferences change in response to increasing pollen availability. Pollen donation is shown for the optimal pollen package size at each level of total pollen production A. The left column of panels corresponds to Scenario I in which the pollen preference parameter y in Eq. 2 increases linearly with pollen production A (according to the function $y = 1 + 0.0002 \times (A - 10000)$); see Figure 2A; here $H = 5000$). The middle column of panels corresponds to Scenario II in which the half-saturation constant H increases linearly with pollen production A (according to the function $H = A/2$; see Figure 2B; here $y = 1$). The right column of panels corresponds to Scenario III in which both the preference parameter y and the half-saturation constant H increase linearly with pollen production A (following the linear equations just given; see Figure 2C). A baseline of $y = 1$, $H = 5000$ at pollen production $A = 10000$ applies to all panels, to make the scenarios comparable. In all scenarios, pollen packages were not allowed to be larger than a plant's total pollen production. Other parameter values: $a = 0.9$, $g = 0.8$.

pollen-rewarding plants. Specifically, when only grooming losses are considered, presenting the smallest possible packages will yield the highest pollen donation, but when pollinator preferences are also considered, plants may need to make packages that are larger to ensure removal and maximize donation even though doing so increases grooming losses, simply because a different loss (pollen that is never removed) is even more severe for smaller packages.

Our simple model and its modifications also shed light on Darwin's conjecture that pollen-rewarding plants should be selected to increase pollen production despite consumption of pollen by visitors, a problem that is particularly acute for strictly pollen-rewarding plants. The answer to the question of whether Darwin was correct seems to be: It depends. In particular, whether the *fraction* of pollen that is donated to stigmas should remain constant or increase as pollen production increases depends on the details of whether and how floral visitation rate (and thus overall probability of pollen removal) and pollinator preferences (and thus differential removal of packages of different sizes) change as pollen production increases (see Figure 4). Note that in all three scenarios in Figure 4, total pollen donation does increase as pollen production per plant increases (see Figure 4D–F). Thus, if Darwin intended to say that greater pollen production would increase total donation, then he appears to have been generally correct. However, we have focused here on the fraction of pollen donated, which we believe better indicates the marginal value to a plant of producing additional pollen. In two of our three scenarios (I and III), the marginal value declines as production increases (because of declining removal overall in Scenario I and ever-increasing preferences for larger and larger packages in Scenario III). Furthermore, one could argue that Scenarios I and III are perhaps more realistic than Scenario II, which assumes pollinators' choices become binary (i.e., accepting any package above a threshold size) at high pollen production levels. When the fraction of pollen donated declines with increasing production, one must ask: Rather than producing more pollen at diminishing returns, would the plant be better off investing those resources in other fitness components, such as female success in hermaphroditic plants (i.e., producing more ovules, or increasing the seed to ovule ratio) or survival and growth in perennial plants? Perhaps those strictly pollen-rewarding plants that produce more pollen than their nectar- and pollen-rewarding relatives (Simpson and Neff, 1983; Golubov et al., 1999; Etcheverry et al., 2012) have reached the point where any additional increase in pollen production would come at too great a cost in terms of other fitness components. This speculation cannot be answered without knowing the relative costs of pollen and other fitness components, as well as how pollinator visitation rate and reward size preferences respond to increasing pollen availability. One step in this direction would be a multi-family comparative analysis of pollen production, package size, and reward strategy which would facilitate hypothesis testing regarding the evolution of the pollen reward strategy. We are not aware that such an analysis has been performed.

Indeed, our model also highlights how much remains to be understood about how visitors respond to variation in pollen rewards. The preference function we have used (Figure 2) could in principle be fitted to data on floral visitation and package removal rates measured in field arrays of plants from genotypes that vary in package size. Ideally, such an experiment should also vary total pollen availability, e.g., by increasing the number of flowers or the density of plants in the array. While such an experiment would face logistical challenges, it is tractable, but we are not aware that such an experiment has been performed.

While our model considers the conflicting constraints of pollen grooming and pollinator preferences, it neglects at least two other constraints that could shape optimal package size and that could form the basis for future extensions of the model. First, we assumed there is no limit to the size of a package pollinators can remove (cf. Figure 4A, C). In practice, pollinator body mass or the size of the regions on pollinators' bodies where they carry pollen may limit the size of the package they can carry. If so, pollinators might discriminate not only against packages that are too small but also those that are too large, or only partially remove packages above a given size. In this case, a unimodal preference function might be more appropriate than Eq. 2. All else being equal, a unimodal preference function should favor packages that are smaller, but perhaps not as small as possible. Second, we ignore how constraints on pollen package size in pollen-rewarding species might be influenced by other species in the community that present other rewards. For example, Tong et al. (2018) have argued that differentiation between nectar- and pollen-rewarding strategies in pairs of co-occurring *Pedicularis* species may facilitate their co-existence. If the presence of heterospecifics presenting rich nectar rewards causes pollinators to depend more on pollen-rewarding species for their pollen needs, pollinators might be willing to accept smaller packages, as long as they are larger than the packages presented by their nectar rewarding neighbors, and of comparable nutritional quality. Indeed, pollen quality (e.g., protein–lipid–starch ratio) represents another axis (besides package size) that could influence the preferences of pollen-collecting visitors, and that could be incorporated into next-generation models.

While we have presented our model as representing a pollen-rewarding plant, our results also apply to plants that present both pollen and nectar, so long as the pollen is viewed as a reward by at least some visitors (whose grooming behaviors and pollen preferences then become relevant). We expect that the main differences between these two reward strategies are not qualitative but rather quantitative differences in visitors' grooming intensity and strength of pollen preferences. Bees constitute perhaps the most important pollen-foraging pollinators in most terrestrial plant communities (Michener, 2000; Thorp, 2000; Heinrich, 2004; Willmer, 2011) due to their dependence on pollen as a protein and lipid source (Simpson and Neff, 1983) coupled with their abundance, wide occurrence, morphological and behavioral characteristics, and high foraging efficiency. Bees are known to discriminate on the basis of both reward size and quality when pollen-foraging (Buchmann and Cane, 1989; Harder, 1990a; Muth et al., 2016; Rasheed and Harder, 1997a; Ruedenauer et al., 2015), and the economics of pollen foraging with respect to reward assessment may mirror that of nectar foragers (Rasheed and Harder, 1997a, 1997b). Even when foraging for nectar, bees efficiently remove pollen from their bodies (Thomson and Plowright, 1980; Thomson, 1986; Harder and Thomson, 1989). Grooming efficiency should be at least as high when bees are pollen-foraging. Indeed, there is empirical evidence to suggest that grooming rates are particularly high during pollen foraging (Buchmann and Cane, 1989) and increase with pollen reward size (Harder, 1990a). Thus, when comparing pollen-rewarding to pollen- and nectar-rewarding plants, we expect the former will face both more intense grooming and stronger pollen preferences. But these differences are easily incorporated in our model simply by changing the values of the parameters g and y (or both y and H), respectively.

Many plant species have long maintained or secondarily derived a strictly pollen-rewarding strategy, with strictly pollen-rewarding genera, subgenera, and species scattered throughout lineages containing many nectar-rewarding taxa (e.g., many Fabaceae, Etcheverry et al., 2012; *Papaver* spp., Simpson and Neff, 1983; some *Pedicularis* spp., Macior, 1970; *Solanum* spp., Kessler and Halitschke, 2009). Thus, many plants have been able to successfully navigate over evolutionary time the conflicting constraints on pollen rewards that we have highlighted here.

AUTHOR CONTRIBUTIONS

J.H. conceived the study and wrote the original draft with input and resources provided by R.I.; W.M. and J.H. developed the model; R.I. and W.M. provided revisions.

ACKNOWLEDGMENTS

The authors thank G. Calabrese and I. Hennes for programming advice and J. Bronstein, J. Thomson, and two anonymous reviewers for insightful comments on the manuscript. Research was supported by NSF grants DEB-1354061/1641243 to R.E.I. and by NSF grant DEB-1753980 to W.F.M.

DATA AVAILABILITY STATEMENT

R scripts (R Core Team, 2018) are available through Open Science Framework at: https://doi.org/10.17605/OSF.IO/QVCFY.

ORCID

Jacob M. Heiling http://orcid.org/0000-0002-3654-1701
Rebecca E. Irwin http://orcid.org/0000-0002-1394-4946
William F. Morris http://orcid.org/0000-0001-5914-5974

REFERENCES

Boggs, C. L., and L. E. Gilbert. 1979. Male contribution to egg production in butterflies: evidence for transfer of nutrients at mating. *Science* 206: 83–84.

Buchmann, S. L., and J. H. Cane. 1989. Bees assess pollen returns while sonicating *Solanum* flowers. *Oecologia* 81: 289–294.

Castellanos, M. C., P. Wilson, S. J. Keller, A. D. Wolfe, and J. D. Thomson. 2005. Anther evolution: pollen presentation strategies when pollinators differ. *American Naturalist* 167: 288–296.

Cresswell, J. E., and A. W. Robertson. 1994. Discrimination by pollen-collecting bumblebees among differentially rewarding flowers of an alpine wildflower, Campanula rotundifolia (Campanulaceae). *Oikos* 69: 304–308.

Darwin, C. 1859. On the origin of species by means of natural selection. Murray, London, UK.

Dunn, D. B. 1956. The breeding systems of *Lupinus*, group *Micranthi*. *American Midland Naturalist* 55: 443–472.

Etcheverry, A. V., M. M. Alemán, T. Figueroa-Fleming, D. López-Spahr, C. Anselmo Gómez, C. Yáñez, D. M. Figueroa-Castro, and P. Ortega-Baes. 2012. Pollen:ovule ratio and its relationship with other floral traits in Papilionoideae (Leguminosae): an evaluation with Argentine species. *Plant Biology* 14: 171–178.

Golubov, J., L. E. Eguiarte, M. C. Mandujano, J. López-Portillo, and C. Montaña. 1999. Why be a honeyless honey mesquite? Reproduction and mating system of nectarful and nectarless individuals. *American Journal of Botany* 86: 955–963.

Harder, L. D. 1990a. Behavioral responses by bumble bees to variation in pollen availability. *Oecologia* 85: 41–47.

Harder, L. D. 1990b. Pollen removal by bumble bees and its implications for pollen dispersal. *Ecology* 71: 1110–1125.

Harder, L. D. 1998. Pollen-size comparisons among animal-pollinated angiosperms with different pollination characteristics. *Biological Journal of the Linnean Society* 64: 513–525.

Harder, L. D., and J. D. Thomson. 1989. Evolutionary options for maximizing pollen dispersal of animal-pollinated plants. *American Naturalist* 133: 323–344.

Harder, L. D., and W. G. Wilson. 1994. Floral evolution and male reproductive success: optimal dispensing schedules for pollen dispersal by animal-pollinated plants. *Evolutionary Ecology* 8: 542–559.

Heinrich, B. 2004. Bumblebee economics. Harvard University Press, Cambridge, MA, USA.

Inouye, D. W., D. E. Gill, M. R. Dudash, and C. B. Fenster. 1994. A model and lexicon for pollen fate. *American Journal of Botany* 81: 1517–1530.

Kessler, A., and R. Halitschke. 2009. Testing the potential for conflicting selection on floral chemical traits by pollinators and herbivores: predictions and case study. *Functional Ecology* 23: 901–912.

Klinkhamer, P. G., and T. J. de Jong. 1993. Attractiveness to pollinators: a plant's dilemma. *Oikos* 66: 180–184.

Leme da Cunha N., and M. A. Aizen. 2023. Pollen production per flower increases with floral display size across animal-pollinated flowering plants. *American Journal of Botany* 110 (in press).

Lloyd, D. G., and J. M. A. Yates. 1982. Intrasexual selection and the segregation of pollen and stigmas in hermaphrodite plants, exemplified by *Wahlenbergia albomarginata* (Campanulaceae). *Evolution* 36: 903–913.

Macior, L. W. 1970. The pollination ecology of *Pedicularis* in Colorado. *American Journal of Botany* 57: 716–728.

Macior, L. W., T. Ya, and J. Zhang. 2001. Reproductive biology of *Pedicularis* (Scrophulariaceae) in the Sichuan Himalaya. *Plant Species Biology* 16: 83–89.

Michener, C. D. 2000. The bees of the world, 1. Johns Hopkins University Press, Baltimore, MD, USA.

Mione, T., and G. J. Anderson. 1992. Pollen–ovule ratios and breeding system evolution in *Solanum* section *Basarthrum* (Solanaceae). *American Journal of Botany* 79: 279–287.

Muth, F., J. S. Francis, and A. S. Leonard. 2016. Bees use the taste of pollen to determine which flowers to visit. *Biology Letters* 12: 20160356.

Rademaker, M. C. J., T. J. De Jong, and P. G. L. Klinkhamer. 1997. Pollen dynamics of bumble-bee visitation on *Echium vulgare*. *Functional Ecology* 11: 554–563.

Rasheed, S. A., and L. D. Harder. 1997a. Economic motivation for plant species preferences of pollen-collecting bumble bees. *Ecological Entomology* 22: 209–219.

Ramírez, M. J., C. Escanilla-Jaramillo, and M. M. Murúa. 2023. Phenotype restrictions to self-pollination in the specialized oil-rewarding genus *Calceolaria*. *American Journal of Botany* 110 (in press).

Rasheed, S. A., and L. D. Harder. 1997b. Foraging currencies for non-energetic resources: pollen collection by bumblebees. *Animal Behaviour* 54: 911–926.

Rivest, S., and J. R. K. Forrest. 2020. Defence compounds in pollen: Why do they occur and how do they affect the ecology and evolution of bees? *New Phytologist* 225: 1053–64.

Ruedenauer, F. A., J. Spaethe, and S. D. Leonhardt. 2015. How to know which food is good for you: Bumblebees use taste to discriminate between different concentrations of food differing in nutrient content. *Journal of Experimental Biology* 218: 2233–2240.

Simpson, B. B., and J. L. Neff. 1983. Evolution and diversity of floral rewards. *In* C. E. Jones and R. J. Little [eds.], Handbook of experimental pollination biology, 142–159. Van Nostrand Reinhold, NY, NY, USA.

Thomson, J. D. 1986. Pollen transport and deposition by bumble bees in erythronium: influences of floral nectar and bee grooming. *Journal of Ecology* 74: 329–341.

Thomson, J. D. 2006. Tactics for male reproductive success in plants: contrasting insights of sex allocation theory and pollen presentation theory. *Integrative and Comparative Biology* 46: 390–397.

Thomson, J. D., and R. C. Plowright. 1980. Pollen carryover, nectar rewards, and pollinator behavior with special reference to *Diervilla lonicera*. *Oecologia* 46: 68–74.

Thomson, J. D., P. Wilson, M. Valenzuela, and M. Malzone. 2000. Pollen presentation and pollination syndromes, with special reference to *Penstemon*. *Plant Species Biology* 15: 11–29.

Thorp, R. W. 2000. The collection of pollen by bees. *In* A. Dafni, M. Hesse, and E. Pacini [eds.], Pollen and pollination, 211–223. Springer Science and Business Media, Vienna, Austria.

Tong, Z. Y., X. P. Wang, L. Y. Wu, and S. Q. Huang. 2018. Nectar supplementation changes pollinator behaviour and pollination mode in *Pedicularis dichotoma*: implications for evolutionary transitions. *Annals of Botany* 123: 373–380.

Vallejo-Marín, M., J. S. Manson, J. D. Thomson, and S. C. H. Barrett. 2009. Division of labour within flowers: heteranthery, a floral strategy to reconcile contrasting pollen fates. *Journal of Evolutionary Biology* 22: 828–839.

Weinman, L. R., T. Ress, and R. Winfree. 2023. Individual bees, but not all bee species, transport proportionally less pollen for the plants from which they collect the most pollen. *American Journal of Botany* 110 (in press).

Willmer, P. 2011. Pollination and floral ecology. Princeton University Press, Princeton, NJ, USA.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Derivation of an expression for the optimal package size using the simple grooming/preference model in the main text.

Appendix S2. Regions of the parameter space defined by the grooming and preference parameters in which the optimal package size $\overline{R}$ is as small as possible ($\overline{R} \leq 0$) or larger than the smallest possible size ($\overline{R} > 0$). Note that low values of the grooming parameter correspond to high levels of grooming.

How to cite this article: Heiling, J. M., R. E. Irwin, and W. F. Morris. 2023. Conflicting constraints on male mating success shape reward size in pollen-rewarding plants. *American Journal of Botany* e16158. https://doi.org/10.1002/ajb2.16158