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LINKING POLLINATOR VISITATION RATE AND POLLEN RECEIPT[1]

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The majority of flowering plants require animals for pollination, a critical ecosystem service in natural and agricultural systems. However, quantifying useful estimates of pollinator visitation rates can be nearly impossible when pollinator visitation is infrequent. We examined the utility of an indirect measure of pollinator visitation, namely pollen receipt by flowers, using the hummingbird-pollinated plant, *Ipomopsis aggregata* (Polemoniaceae). Our a priori hypothesis was that increased pollinator visitation should result in increased pollen receipt by stigmas. However, the relationship between pollinator visitation rate and pollen receipt may be misleading if pollen receipt is a function of both the number of pollinator visits and variation in pollinator efficiency at depositing pollen, especially in the context of variable floral morphology. Therefore, we measured floral and plant characters known to be important to pollinator visitation and/or pollen receipt in *I. aggregata* (corolla length and width and plant height) and used path analysis to dissect and compare the effect of pollinator visitation rate vs. pollinator efficiency on pollen receipt. Of the characters we measured, pollinator visitation rate (number of times plants were visited multiplied by the mean percentage of flowers probed per visit) had the strongest direct positive effect on pollen receipt, explaining 36% of the variation in pollen receipt. Plant height had a direct positive effect on pollinator visitation rate and an indirect positive effect on pollen receipt. Despite the supposition that floral characters would directly affect pollen receipt as a result of changes in pollinator efficiency, corolla length and width only weakly affected pollen receipt. These results suggest a direct positive link between pollinator visitation rate and pollen receipt across naturally varying floral morphology in *I. aggregata*. Understanding the relationship between pollinator visitation rate and pollen receipt may be of critical importance in systems where pollinator visitation is difficult to quantify.

Key words: floral morphology; hummingbird pollination; *Ipomopsis aggregata*; path analysis; Polemoniaceae; pollen receipt; pollinator efficiency; pollinator visitation.

Estimates of pollinator visitation are critically important to address a variety of ecological questions, including the impact of pollinators on selection on floral traits and the role of interspecific plant competition on pollinator visitation and pollination success. Moreover, because approximately 90% of flowering angiosperms rely on insects or other animals for pollination (Tepedino, 1979; Buchman and Nabhan, 1996), animal pollination represents an important ecosystem service (Costanza et al., 1997). Estimating pollinator visitation (i.e., number of visits, percentage of flowers probed per visit), however, to link pollinator visitation to plant reproduction is often time-consuming and challenging (Kearns and Inouye, 1993). For example, when pollinator visitation is infrequent (Campbell et al., 1991; Mitchell, 1992; Ackerman et al., 1997; Parker, 1997), a researcher may observe only a handful of pollinator visits during hundreds of observation hours. Moreover, external factors, such as the presence of the researcher, may influence the behavior of floral visitors (akin to the ''herbivory uncertainty principle''; Cahill et al., 2001, 2002). Unfortunately, we know relatively little about the reliability of indirect estimates of pollinator visitation rates, such as counting mechanically tripped flowers or recording pollination-mediated floral color changes (reviewed in Kearns and Inouye, 1993).

Here we examine the utility of one indirect measure of pollinator visitation, namely pollen receipt by flowers. We are assuming that any pollen that was deposited on the stigma must have been put there by a pollinator, and increased pollinator visitation should result in increased pollen receipt by stigmas. Although a positive association between pollinator visitation and pollen receipt may hold in some natural systems (e.g., Galen and Stanton, 1989; Young and Stanton, 1990; Jones and Reithel, 2001) or under controlled conditions (Mitchell and Waser, 1992), pollen receipt as an estimate of pollinator visitation may be misleading if, among other factors, (1) dehiscing anthers directly contact the stigma (reviewed in Barrett, 2002), (2) stigmas close after pollinator visitation (Fetscher and Kohn, 1999), (3) pollen receipt is a function of both the number of times flowers are visited by pollinators and pollinator effectiveness at picking up pollen from anthers and depositing pollen on stigmas (Murcia, 1990; Campbell et al., 1994; Conner et al., 1995), (4) pollinators groom pollen from their bodies in successive floral visits (Conner et al., 1995), (5) pollinators dislodge pollen from the stigma surface (Gori, 1983; Young, 1988), or (6) pollen receipt follows a saturating curve because the stigmatic surface area is limited (Galen and Stanton, 1989). Moreover, if hermaphroditic flowers vary in the proportion of time they spend in the pistillate vs. staminate

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phase (Campbell, 1989a; Campbell et al., 1994), variation in the duration of stigma receptivity may further disrupt the relationship between pollinator visitation and pollen receipt. These factors are not mutually exclusive.

To reduce the probability that pollen receipt is a function of stigma-anther contact or other forms of autogamous pollen transfer, pollinator visitation can be estimated using emasculated flowers. Emasculating flowers eliminates self-pollen deposition. However, functional anthers are necessary for the growth and development of many flowers (Greyson and Tepfer, 1967), and anther removal may sever hormonal relationships among floral organs and cause developmental abnormalities in flowers (Kiss and Konig, 1990). Not only does emasculation change floral morphology and development, but it may affect pollinator activity. For example, Rademaker et al. (1997) found that bumble bees approached emasculated flowers but, compared to unemasculated flowers, landed on the corollas in a ''clumsy'' manner and usually did not come in contact with the stigma. And when pollen serves as the reward for floral visitors, pollinators may avoid emasculated flowers. In addition, emasculation may reduce levels of geitonogamy (within-plant pollen movement), affecting subsequent plant fitness (e.g., de Jong et al., 1992).

If there is temporal separation between the maturation of anthers and stigma receptivity (dichogamy) or spatial separation (herkogamy), pollen receipt may provide a reliable estimate of pollinator visitation without emasculation. However, the temporal separation between anther and stigma maturation is often incomplete. Any overlap in reproductive structures could lead to autodeposition of pollen on receptive stigmas (Waser and Price, 1991), resulting in misleading estimates of pollinator visitation.

Moreover, pollen receipt may not only be a function of the number of times pollinators visit flowers but also a function of pollinator efficiency. We are defining pollinator efficiency as the stigma pollen load deposited per pollinator visit (Inouye et al., 1994). In this definition, we are ignoring the male component of pollinator efficiency, removing pollen from anthers (Inouye et al., 1994). Different species of floral visitors often vary in their pollinator efficiency at flowers of the same plant species. For example, Arnold (1982) found that bumble bees (*Bombus* spp.) transferred over two times more pollen per visit to flowers of *Linaria vulgaris* Miller (Scrophulariaceae) than halictid bees (*Halictus* and *Dialictus* spp.). In addition, natural phenotypic variation in floral morphology may affect the efficiency of the same pollinator species. For example, Campbell et al. (1994) found that natural variation in floral morphology (stigma exsertion) influenced hummingbird efficiency at depositing pollen on the stigmas of flowers of *Ipomopsis aggregata* (Pursh) V. Grant (Polemoniaceae). Given these scenarios, variation in pollinator efficiency because of a diversity of pollinators or because of variation in floral morphology may further affect the relationship between pollinator visitation rate and pollen receipt.

Here we examine the link between pollinator visitation rate and pollen receipt by unemasculated flowers in a naturally growing population of the hummingbird-pollinated *Ipomopsis aggregata*. *Ipomopsis aggregata* provides an ideal model plant with which to address the links between pollinator visitation and pollen receipt because *I. aggregata* is pollinated by a relatively simple pollinator assemblage (primarily two species of hummingbirds). Therefore, variation in pollinator assemblage likely will not impact the relationship between visitation rate and pollen receipt. Quantifying useful estimates of hummingbird pollinator visitation rates to *I. aggregata* can be challenging as observable pollinator visits to flowers are infrequent. For example, Campbell et al. (1991) observed average pollinator visitation rates to *I. aggregata* of only 0.1 visits per flower per hour during *peak* visitation times (usually dawn and dusk for hummingbird-pollinated species). Therefore, understanding the relationship between pollinator visitation and pollen receipt may provide a useful tool for estimating pollinator visitation in this system.

We hypothesized that increased pollinator visitation would increase pollen receipt across natural variation in floral morphology and pollinator visitation levels. Thus, in addition to quantifying pollinator visitation rate and pollen receipt on flowers of *I. aggregata*, we measured natural variation in floral and plant characters known to be important to pollinator visitation and/or pollen receipt (Campbell, 1989a; Wolf and Hainsworth, 1990). We then dissected the effects of natural variation in floral and plant characters on pollen receipt by looking at pollinator visitation rate vs. pollinator efficiency. Specifically, we asked (1) To what degree does increased pollinator visitation per flower increase pollen deposition? and (2) What is the relative importance of natural variation in floral and plant characters to pollen deposition through changes in pollinator visitation and pollinator efficiency? Finally, because increased pollinator visitation per flower may also result in increased geitonogamy in unemasculated plants, we also counted all of the fruits and seeds produced per plant, and asked (3) Do changes in pollinator visitation and pollen deposition translate into changes in female plant reproductive success (total seeds produced)?

MATERIALS AND METHODS

Study system—*Ipomopsis aggregata* (scarlet gilia; Polemoniaceae) is a montane herb native to the western United States and to areas surrounding the Rocky Mountain Biological Laboratory in Colorado, USA (RMBL; latitude 38°959′ N, longitude 106°989′ W, altitude 2900 m), where this study was conducted. *Ipomopsis aggregata* lives as a vegetative rosette for 2–10 yr until it accumulates enough resources to bolt, flower once, then die (Waser and Price, 1989). Upon bolting, the plant produces a stalk of scarlet, trumpet-shaped flowers (number of flowers produced = 84 ± 66 flowers, mean ± 1 SD; Campbell, 1989b). Each plant flowers for 4–8 wk. The individual hermaphroditic flowers last for 3–5 d. Flowers are protandrous, but the temporal separation between anthers and stigmas may be incomplete (Waser and Price, 1991). *Ipomopsis aggregata* are primarily self-incompatible (Waser and Price, 1991). Male- and female-phase flowers occur on the same plant at the same time. Flowers produce nectar in both male and female phases, initiating nectar production as buds begin to elongate (Pleasants, 1983). Individual plants vary in plant and floral morphological characters within and among populations, including variation in plant height, corolla length and width, and floral display size (Campbell, 1989a, b). Broad-tailed hummingbirds [*Selasphorus platycercus* Swainson (Trochilidae)] and rufous hummingbirds (*S. rufus* Gmelin) are the most common pollinators of *I. aggregata* around the RMBL (Waser, 1978).

Field procedures—We randomly marked 40 flowering *I. aggregata* with similar flowering phenologies on a south-facing slope in a population with approximately 200 flowering *I. aggregata*. We measured plant height to the nearest 0.1 cm at the onset of flowering and randomly chose one flower per plant and measured corolla length (from the base of the calyx to the floral opening) and corolla width (at the opening of the corolla tube) to the nearest 0.1 mm using digital calipers. Measures of corolla length and width are highly repeatable across flowers within *I. aggregata* plants (Campbell et al., 1991; Wolf and Campbell, 1995); therefore, measuring one flower per plant should

provide a reliable estimate of corolla length and width. We also counted the number of open flowers per plant twice a week as an estimate of the size of the floral display. We measured plant height, corolla length and width, and floral display because these characters affect pollinator visitation rate and/or pollinator efficiency in this system (Campbell, 1989a, b, 1991).

From 27 June to 20 July 2001, 5 d per wk, we observed hummingbird foraging behavior from approximately 0530 until 0900, when hummingbirds foraged most actively in this population (E. C. Engel and R. E. Irwin, personal observation). Because the population was relatively small (approximately 10 × 10 m in area), we could observe all study plants at once for pollinator visits. For each observation period, we recorded the number of times each plant was visited and the number of flowers probed per plant visit. We conducted a total of 57 h of observations.

Biweekly, we collected stigmas from 50% of the flowers in the female phase on each plant to quantify the number of pollen grains received as a function of hummingbird visitation. We squashed stigmas in basic fuchsin dye and counted the number of conspecific and heterospecific pollen grains using a compound microscope (Kearns and Inouye, 1993). We counted pollen grains on a total of 825 stigmas.

Once plants senesced, we collected all of the fruit capsules to assess the relationship between pollen receipt and seed production per plant. We counted the number of seeds in each seed-bearing fruit.

Data analysis—For each plant, we calculated hummingbird visitation rate as (number of times the plant was visited per observation period) × (mean percentage of flowers probed per plant visit per observation period), averaged across the flowering season (square-root transformed). For each plant, this measure represents hummingbird visitation rate on a per-flower basis averaged across observation periods. Because we only observed pollinator visits once per day, hereafter we refer to this variable as visitation rate per observation period or simply visitation rate. We calculated mean pollen receipt per stigma per plant as the mean number of *I. aggregata* pollen grains received per stigma collected for each plant, averaged across the flowering season. Because very few heterospecific pollen grains were found on the stigmas, we did not include heterospecific pollen receipt in the analyses. We did not compare visitation rate and pollen receipt on a weekly basis because we were primarily interested in the seasonal relationship between pollinator visitation rate and pollen receipt. Initially, we fit linear and quadratic terms for the relationship between visitation rate and pollen receipt. A significant quadratic term might indicate that at the upper bound of visitation rate, pollen receipt would not increase because the stigma is limited in size. We found no evidence for nonlinearity in the relationship and further dissected the linear relationship between visitation rate and pollen receipt below.

We used path analysis (Wright, 1921, 1934; Li, 1975) combined with structural equation modeling (SEM; reviewed in Mitchell, 1992, 1993) to examine the fit of four competing a priori hypotheses exploring the relationship between pollinator visitation rate and pollen receipt (Fig. 1). Path analysis allows for the examination of multiple relationships among variables, both direct and indirect, using a set of a priori hypotheses and allows for the estimation and comparison of effect sizes (Kingsolver and Schemske, 1991; Mitchell, 1992, 1993). One caveat about path analysis is that it identifies correlations among variables, not the causal nature of such links (Kingsolver and Schemske, 1991; Mitchell, 1992; Petraitis et al., 1996). In the path diagrams (Fig. 1), the effect of natural variation in floral characters on pollinator efficiency are *direct effects* on pollen receipt, whereas the effect of natural variation in plant and floral characters on pollinator attraction are *indirect effects* on pollen receipt mediated through pollinator visitation rate.

In Model A (Fig. 1), corolla length and/or width affect pollen receipt directly through changes in pollinator efficiency (Campbell, 1989a) and indirectly through changes in attractiveness to pollinators (Campbell et al., 1991). We include plant height in all models as a proxy for the attractiveness of plants to pollinators. Plant height and mean floral display size are positively and significantly correlated ($r = 0.45$, $N = 40$, $P = 0.004$); therefore, plant height captures both the size of the floral display and the height at which those flowers are advertised to pollinators. Plant height is unlikely to directly influence pollen receipt; therefore, no direct path is drawn between plant height and pollen receipt. However, plant height may have indirect effects on pollen receipt through increased plant attraction to pollinators (Wolf and Hainsworth, 1990). Finally, pollinator visitation rate directly influences pollen receipt (Mitchell and Waser, 1992), and plant and floral traits are intercorrelated as a result of both genetic and environmental factors (Campbell, 1996). Model B is nested within Model A (Fig. 1), with the indirect effects of corolla length and width on pollen receipt mediated through pollinator visitation rate constrained to zero, but all other paths remain identical. We include this second competing model because corolla length and width may have no indirect effects on pollen receipt through changes in pollinator attraction. For example, Campbell et al. (1991) found that corolla width had no effect on pollinator visitation rate once nectar production and corolla length were controlled for. However, corolla length and width may still have direct effects on pollen receipt through changes in pollinator efficiency. If we find evidence support-

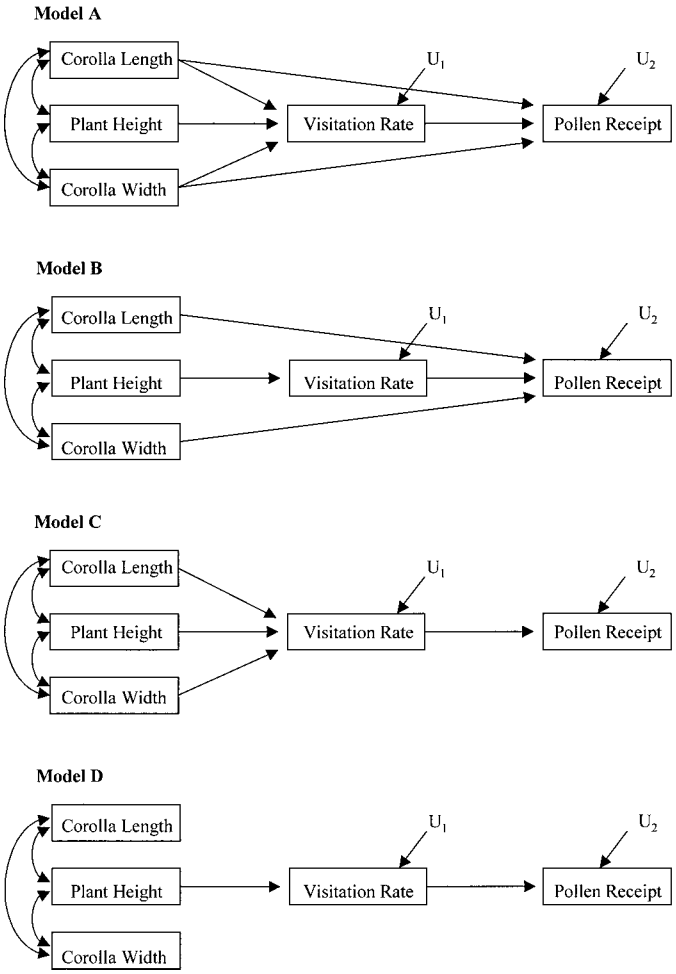

Fig. 1. Four hypothesized path diagrams of the direct and indirect effects that determine pollinator visitation rate and pollen receipt. In Model A, corolla length and width have direct effects on pollen receipt and indirect effects on pollen receipt mediated through changes in pollinator visitation rate. Plant height has a direct effect on visitation rate and an indirect effect on pollen receipt through visitation rate, and visitation rate directly influences pollen receipt. Model B is nested within Model A, with the indirect effects of corolla length and width on pollen receipt through visitation rate constrained to zero. Model C is nested within Model A, with the direct effects of corolla length and width on pollen receipt constrained to zero. Model D is nested within the above models, with the direct and indirect effects of corolla length and width on pollen receipt constrained to zero. In all models, double-headed arrows indicate correlations among variables, and there is unexplained variation $[(1 - R^2)^{0.5}]$ associated with the measurement of pollinator visitation rate (U_1) and pollen receipt (U_2).

TABLE 1. Observed correlations among morphological characters, visitation rate, and pollen receipt below the diagonal.

Character	Plant height	Corolla length	Corolla width	Visitation rate	Pollen receipt
Plant height	1.00				
Corolla length	0.24	1.00			
Corolla width	0.16	0.10	1.00		
Visitation rate	0.49	0.08	−0.01	1.00	
Pollen receipt	0.43	−0.19	0.18	0.52	1.00

TABLE 2. A comparison of alternative path diagrams (Fig. 1) using structural equation modeling. Nonsignificant χ^2 values suggest that the models do not deviate significantly from the observed data. AIC is Akaike's information criterion. Models that minimize AIC provide the most reliable fit to the observed data.

Model	χ^2	df	P	AIC
A	3.41	1	0.0649	1.4076
B	3.92	3	0.2700	−2.0781
C	8.88	3	0.0309	2.8811
D	9.39	5	0.0943	−0.6046

ing Models A or B, then pollen receipt is dually determined by pollinator visitation rate and pollinator efficiency, suggesting that visitation rate may not be a reliable indicator of pollen receipt alone. Model C is nested within Model A (Fig. 1), with the direct effects of corolla length and width on pollen receipt constrained to zero, but all other paths remain identical. We included this third model because corolla length and width may have no direct effect on pollinator efficiency at depositing pollen but may have indirect effects on pollen receipt mediated through changes in visitation rate. Finally, in Model D (Fig. 1), which is nested within the Models above, both the direct and indirect effects of corolla length and width on pollen receipt are constrained to zero. If we find evidence for Models C or D, this would suggest that visitation rate is directly and solely linked to pollen receipt because corolla length and width have no significant effect on pollinator efficiency at depositing pollen.

We used SEM to test statistically which competing hypothesis, Model A, B, C, or D (Fig. 1), provided the most appropriate fit to the observed data (Hayduk, 1987; Loehlin, 1987; Mitchell, 1992, 1993). Structural equation modeling tests among models using a goodness-of-fit statistic that approximates a χ^2 distribution with df = the difference between the number of observed correlations and the number of coefficients. A nonsignificant χ^2 value indicates no significant difference between the expected and observed correlation matrices; therefore, the model provides an appropriate fit to the observed data. We also report Akaike's information criterion (AIC); the model that minimizes AIC provides the most parsimonious fit to the data. For the four competing path models, we used PROC CALIS in SAS (METHOD = ML) to calculate AICs, goodness-of-fit statistics, and significance values (SAS, version 8.02). Petraitis et al. (1996) recommend a sample size of 5–20 times larger than the number of estimated paths in the competing path models. With a sample size of 40 plants (Fig. 1), our sample size is within the acceptable range, albeit on the low side, to conduct SEM. In addition, to screen for collinearity among corolla length, corolla width, and plant height, we calculated variance inflation factors (hereafter referred to as VIFs; VIF option in PROC REG). Correlations among variables inflate VIFs and cause a loss of precision in the path analysis. In all cases, the VIFs were less than 1.1; therefore, it is unlikely that collinearity had a strong impact on the results (Myers, 1990).

For the path diagram that provided the most appropriate fit to the observed data, we calculated direct and indirect effects and significance values using PROC CALIS. Direct effects represent standardized partial regression coefficients (p, path coefficients). Indirect effects represent the portion of variation jointly determined by the independent and transmitter variables on the dependent variable.

Finally, to ensure that changes in visitation rate and pollen receipt translated into differences in plant reproduction, as has been shown previously for *I. aggregata* (e.g., Campbell and Halama, 1993), we examined the relationship between pollen receipt and total seed production per plant. We found no evidence that the relationship between pollen receipt and seed set per plant was nonlinear; we report results from linear regression only using PROC REG.

RESULTS

Over the season, we recorded 79 hummingbird-foraging bouts consisting of 270 visits to plants and 1069 visits to flowers. On any given day, less than 50% of the available plants and flowers were visited by foraging hummingbirds. Mean visitation rate ranged from 0.05 to 7.11 with a mean ± 1 SE of 1.49 ± 0.24. Stigmas received a range of 9–183 pollen grains with a mean ± 1 SE of 72.39 ± 6.39 pollen grains. We found positive correlations among corolla length, corolla width, and plant height (Table 1); however, these correlations were not statistically significant ($P > 0.05$ in all cases).

Using SEM, we found that the correlation matrix for Model C (Fig. 1) deviated significantly from the observed correlation matrix (Table 2); therefore, Model C did not provide a reliable fit to the observed data. The correlation matrices for Models A, B, and D did not differ significantly from the observed correlation matrix (Table 2), suggesting that the observed data fit all three models. To further compare the relative fit of the three nested models to the observed data, we took the difference in their goodness-of-fit statistics and degrees of freedom (Mitchell, 1993). We found a nonsignificant difference between Models A and B ($\chi^2 = 0.5$, df = 2, $P = 0.8$). Because Model B was simpler than Model A and had a lower AIC value than Model A, we retained Model B based on the principle of parsimony and because the model that minimizes AIC provides the most reliable fit to the observed data (Table 2). We then compared Model B to Model D and found a marginally significant decrease in fit for Model D compared to Model B ($\chi^2 = 5.5$, df = 2, $P = 0.05$). In addition, Model B had a lower AIC value than Model D, suggesting that Model B provided the most reliable fit to the observed data.

In Model B (Fig. 2), pollinator visitation rate, measured as the number of times plants were visited multiplied by the mean percentage of flowers probed per visit, had a direct, positive, linear effect on pollen receipt (Table 3; Fig. 2). As per-flower visitation rate increased, pollen receipt per stigma increased significantly (Fig. 3). Plant height had a direct positive effect on pollinator visitation rate (Table 3; Fig. 2). Taller plants experienced significantly higher visitation rates. In addition, plant height had an indirect effect on pollen receipt mediated through pollinator visitation rate (Table 3). Corolla length had a weak negative direct effect on pollen receipt (Table 3; Fig. 2). The negative effect of increasing corolla length on pollen receipt was marginally significant at $P = 0.06$ (Table 3). Corolla width had a weak, positive nonsignificant effect on pollen receipt (Table 3; Fig. 2). Of the direct pathways examined, visitation rate had the strongest direct effect on pollen receipt (Fig. 2).

Finally, changes in pollinator visitation and subsequent pollen receipt translated into an effect on plant reproduction. Plants with increased stigma pollen loads produced more total seeds (regression equation: total seeds = 1.44(pollen receipt per stigma) + 118.41; $r^2 = 0.25$; $F_{1,38} = 12.77$, $P = 0.001$).

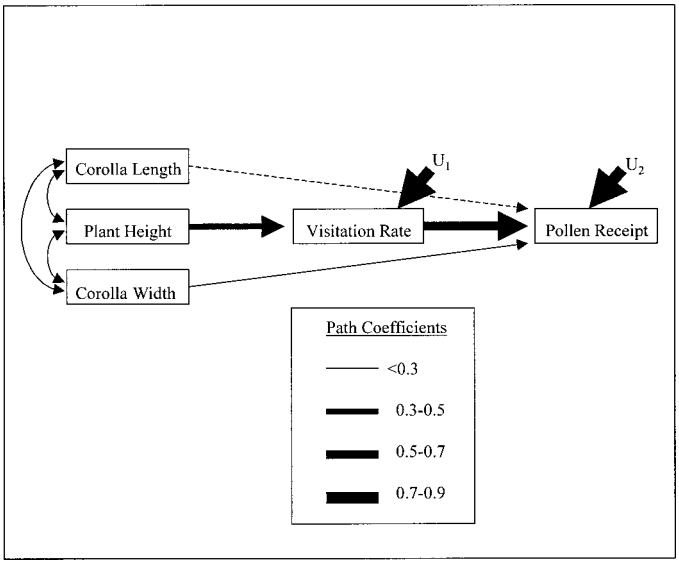

Fig. 2. Best-fit path diagram showing the direct and indirect effects determining pollinator visitation rate and pollen receipt. Positive effects are indicated by solid lines and negative effects by dashed lines. The width of the arrow represents the magnitude of the standardized path coefficients listed in legend. See Table 2 for exact path values and significance levels.

DISCUSSION

We hypothesized that pollen receipt should provide a reliable estimate of pollinator visitation, assuming that any pollen that was deposited on the stigma must have been put there by a pollinator, and increased pollinator visitation resulted in increased pollen receipt by stigmas. We found that of the measured variables, pollinator visitation rate to *I. aggregata* had the strongest direct, positive effect on pollen receipt. Therefore, pollen receipt may serve as a proxy for hummingbird pollinator visitation to flowers of *I. aggregata*. This result mirrors previous work by A. K. Brody (University of Vermont, unpublished data) showing a positive correlation between pollinator visitation and pollen receipt in emasculated flowers of *I. aggregata* ($r = 0.44$, $N = 20$, $P < 0.05$). Our work extends these results by linking pollinator visitation rate and pollen receipt to unemasculated flowers while statistically controlling for floral morphology. Pollinator visitation rate represents the number of times plants were visited multiplied by the mean percentage of flowers probed per visit. Both components of visitation rate were positively correlated ($r = 0.47$, $N = 40$, $P = 0.002$), suggesting that number of plant visits and proportion of flowers probed per visit may be related to the increase in pollen receipt.

That we found a positive link between visitation rate and pollen receipt suggests that a variety of mechanisms associated with autodeposition of pollen (i.e., temporal overlap within flowers between pollen dehiscing anthers and receptive stigmas) did not overwhelm the positive relationship. Moreover, increased visitation rate and pollen receipt were also associated with increased seed production. Because *I. aggregata* is self-incompatible, this increase in seed production suggests that the majority of pollen deposited on stigmas was outcrossed pollen deposited by pollinators and was not self-pollen deposition. The relationship between visitation rate and pollen receipt was linear, suggesting that pollen receipt did not show a decelerating relationship with increased pollinator visitation (Galen and Stanton, 1989). Visitation rate to *I. aggregata* flowers is low (Campbell et al., 1991); therefore, pollinator visitation rates and subsequent pollen deposition levels may only rarely be high enough to result in stigma saturation. Whether the strong relationship between visitation rate and pollen receipt is common in other hummingbird-pollinated plant systems with low pollinator visitation rates remains to be tested. For plant–pollinator systems with high pollinator visitation rates and/or diverse pollinator assemblages, the relationship between number of floral visits and pollen receipt may not have such clear patterns.

We hypothesized that the link between pollinator visitation and pollen receipt may not hold if pollen receipt was also a function of pollinator efficiency, especially for species such as *I. aggregata* in which floral morphology varies. Our results only partially supported this hypothesis. Model B (Fig. 2) provided the most appropriate fit to the observed data, suggesting that pollen receipt was jointly determined by pollinator visitation rate and pollinator efficiency. In this case, pollinator efficiency was measured as the direct effect of floral morphology on pollen receipt. However, corolla length and width had only weak, nonsignificant effects on pollen receipt, indi-

TABLE 3. Direct, indirect, and total effects of plant and floral characters and pollinator visitation rate on pollen receipt for Model B (Fig. 2). Direct effects are path coefficients (standardized partial regression coefficients).

Variable	Visit rate			Pollen receipt		
	DE	IE	TE	DE	IE	TE
Height	0.49**	—	0.49	−0.25*	0.27	0.27
Corolla length	—	—	—	—	—	−0.25
Corolla width	—	—	—	0.21	—	0.21
Visit rate	—	—	—	0.54**	—	0.54
R^2		0.24			0.36	

Note: DE = direct effects; IE = indirect effects; TE = total effects. * $P = 0.06$; ** $P < 0.001$.

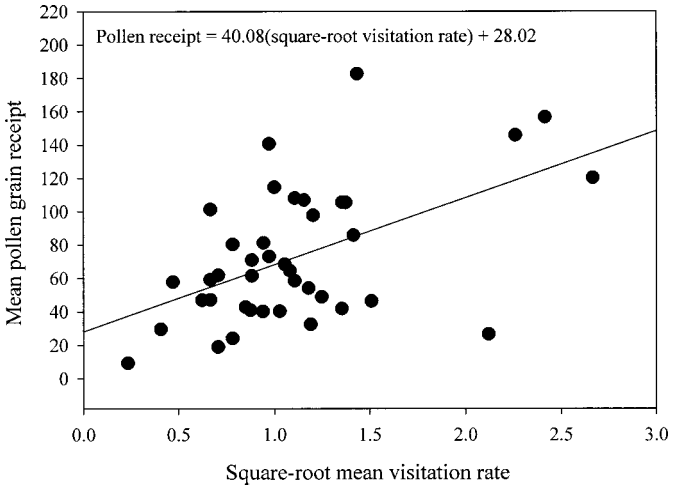

Fig. 3. Positive relationship between mean pollinator visitation rate and mean pollen receipt ($P < 0.001$). Each point represents the mean per-flower estimate for one plant ($N = 40$ plants) for pollinator visitation rate and pollen receipt. Pollinator visitation rate was calculated as (number of plant visits) × (mean percent of flowers probed per visit), square-root transformed to meet assumptions of normality.

cating that natural variation in these two morphological characters only marginally affected pollinator efficiency. The strongest direct positive effect on pollen receipt in this study was pollinator visitation rate.

That corolla length and width had only weak effects on pollinator efficiency mirrors previous studies with *I. aggregata*. Campbell (1989a) found only a weak relationship between pollen receipt by flowers of *I. aggregata* and corolla length and width. While floral shape (e.g., corolla length, corolla width) is thought to reflect, at least in part, selection through increased pollinator efficiency (e.g., Nilsson, 1988; Schemske and Horvitz, 1989), a surprising number of studies have not found a relationship between corolla shape and pollinator efficiency at depositing pollen on the stigmas of flowers (e.g., Murcia, 1990; Young and Stanton, 1990; Wilson, 1995; Wilson and Thomson, 1996). Corolla shape may reflect selection through male function (e.g., pollen removal, pollen export) more so than female function (Young and Stanton, 1990; Campbell et al., 1991; Connor et al., 1995). We did not estimate the effect of corolla length and width on pollen export in this study. However, if pollen export is strongly affected by corolla shape, this effect may help explain the high levels of phenotypic variation in these characters in natural populations (Campbell, 1991), especially if the strength of selection on floral morphology through male function varies from year to year.

One caveat about interpretation of our results is that path analysis is conditional upon which variables are included in the models, and the addition of other variables could change the magnitude and significance of the path coefficients in this study (Mitchell, 1993). We included corolla length, corolla width, and plant height in the path models because these characters have been shown in previous studies to at least marginally affect pollinator visitation rate and/or pollinator efficiency in *I. aggregata* (Campbell, 1989a; Wolf and Hainsworth, 1990; Campbell et al., 1991). However, other characters, such as stigma exsertion, nectar production rate, and flowering date, also affect pollinator visitation and/or pollen receipt (e.g., Campbell, 1989a; Mitchell, 1992), and we cannot rule out the importance of these characters in this system. Given these limitations, with our simple model we were still able to account for 24% of the variation in pollinator visitation rate and 36% of the variation in pollen receipt. More studies are needed to quantify the general relationship between pollinator visitation rate and pollen receipt across varying floral morphology and pollinator efficiency to test the generality of the positive link between pollinator visitation rate and pollen receipt.

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