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A trade-off between the frequency and duration of bumblebee visits to flowers

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Abstract Pollinator behavior influences plant reproduction in many ways. A traditional measure of pollination, the number of visits received, may be a poor predictor of plant reproductive success, particularly when there are trade-offs between visit quantity and components of visit quality. For example, the duration of pollinator visits may be negatively correlated with the number of visits received by a flower. We tested for a trade-off between the number of bumblebee visits and the duration of those visits in an experimental population of snapdragons (*Antirrhinum majus*: Scrophulariaceae). The duration of a bumblebee visit to a flower increased significantly with the time interval since the flower had last been visited. Over the lifetime of a flower the correlation between the total number and average duration of visits received by a flower was weakly negative. However, at the whole-plant level the correlation was positive: plants whose flowers received more visits also received visits of longer duration. Factors affecting the relationship between quantity and duration of pollinator visits to flowers also were investigated. Two factors weakened the negative dependence of average visit duration on number of visits received by individual snapdragon flowers: (1) the correlation between the total number of visits to a flower and the average interval between visits was only −0.53, as visits to individual flowers were not very evenly spaced over time, and (2) newly opened flowers received fewer and shorter visits than older flowers. Comparing whole plants, nectar production per flower varied dramatically across individuals, a probable explanation for the positive correlation between visit number and average duration per flower observed at the plant level. The potential for a trade-off between these two components of pollinator service exists when visit duration depends on reward quantity; whether the trade-off is realized will depend on variation in nectar production and on whether pollinators forage systematically.

Key words Bumblebees · Foraging behavior · Nectar volume · Pollination

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Introduction

Reproductive success in animal-pollinated plants is rarely a simple function of the number of pollinator visits a plant receives. This means that researchers studying pollinator-mediated selection on plant traits are not safe in assuming that visit quantity is an accurate predictor of pollination success. For one thing, pollinators vary widely in the quality of pollen transfer services they provide (Young 1988; Stanton et al. 1991; Wilson and Thomson 1991). Furthermore, there may be trade-offs between the number of visits received and the quality of those visits. In particular, the average length of time a pollinator spends in a flower, which can affect the amount of pollen received and/or exported (Thomson 1986; Harder 1990; Young and Stanton 1990; Thostesen and Olesen 1996; Wilson and Thomson 1996), may be negatively correlated with the number of visits the flower receives. For example, in an experimental array of yellow-flowered and red-flowered snapdragon (*Antirrhinum majus*: Scrophulariaceae) plants, yellow flowers received more bumblebee visits on average than red ones (1.8 per day per yellow flower vs 0.5 per day per red flower, $t = 311$, $P < 0.0001$), but the visits to yellow flowers were

shorter (3.6 s to yellow flowers vs 11.2 s to red, $t = 588$, $P < 0.0001$; K.N. Jones, J.S. Reithel, and R. Irwin, unpublished work). Depending on which aspect of pollinator behavior (number or duration of visits) was more important for plant reproductive success, either color morph could have had a selective advantage in this case.

For pollinators whose behavior is driven by energetic considerations (Heinrich 1975), one might expect the number and duration of visits to a flower to be negatively correlated. In flowers that continually secrete nectar, the length of time since a flower was last visited should predict the amount of nectar it contains (standing crop). If pollinators spend longer amounts of time in flowers with more nectar (e.g., Hodges and Wolf 1981; Zimmerman 1983; Galen and Plowright 1985), then the time a pollinator spends in a flower should increase with the length of time since the flower was last visited. On average, therefore, flowers visited more frequently should have lower standing crops of nectar and thus receive visits of shorter duration than less frequently visited flowers (Fig. 1).

We were able to evaluate these expectations by observing all pollinator visits to an experimental population of snapdragon plants over 18 days, keeping track of each flower individually. At the level of individual flower visits, we tested whether the duration of a pollinator visit was correlated with the time interval since the flower was previously visited. Then, shifting the focus to total visitation over a flower's lifetime, we asked whether the number of pollinator visits and the average duration of visits received by a flower were correlated, as a negative correlation would indicate a trade-off between these two components of pollinator service. Finally, we tested whether such a trade-off existed at the whole-plant level, i.e., whether plants that received greater numbers of visits per flower received visits of shorter average duration.

These hypotheses have several underlying assumptions whose violation would complicate this intuitive scenario. First, the duration of pollinator visits to a flower must depend on nectar quantity. Second, nectar must be replenished steadily after depletion. Secretion may be stimulated by depletion so that more frequently visited flowers have higher total nectar production (Corbet 1978; Pyke 1991), or nectar may be reabsorbed by undervisited flowers (Corbet 1978; Burquez and Corbet 1991; Nicolson 1995). Third, in order for the whole visit history of a flower to be the relevant scale on which to test for trade-offs, nectar secretion and pollinator visit rates must be reasonably constant over the flower's lifetime. If nectar production rates vary over the blooming period of a flower, then there may be trade-offs within subsets of the flower's lifespan during which secretion is relatively constant; however, these may not be manifest on the scale of a flower's lifetime if flowers spend different amounts of time in the different phases (for example, depending on the weather conditions during the blooming period). Flowers of different ages have different nectar production rates in some species (Pyke 1978; Devlin and Stephenson 1985; Burquez and Corbet 1991), but not in others (Pleasants 1983; Marden 1984). Any of the above factors could decouple visit duration from the time interval between visits. Also, the strength of the correlation between the number of visits received and the average interval between visits will depend on how evenly spaced visits are over a flower's lifetime. Flowers visited by systematic foragers that return to plants at regular intervals (Kadmon 1992; Thomson 1996) should experience the strongest trade-off between the number of visits they receive and the average duration of those visits. Finally, if some plants have higher rates of nectar secretion than others, flowers on the more productive plants may have greater standing crops of nectar and so receive both more visits and longer visits than flowers on other plants (Fig. 1), potentially overriding a flower-level trade-off.

We addressed these supporting issues by asking the following questions:

1. Does adding nectar to snapdragon flowers increase pollinator visit duration?
2. Is nectar secreted continually in snapdragon flowers, so that standing crop is correlated with time interval since the last visit?
3. Does the frequency of nectar removal affect secretion rates?
4. Does visit frequency or duration vary with flower age?
5. Are visits to a flower regularly spaced, so that there is a tight correlation between the number of visits received and the average interval between visits?
6. Is there significant variation between plants in nectar secretion rate?

The results of experiments on each of these supporting questions are discussed in relation to the two main hypotheses concerning the correlations between visit duration, time interval between visits, and number of visits received per flower.

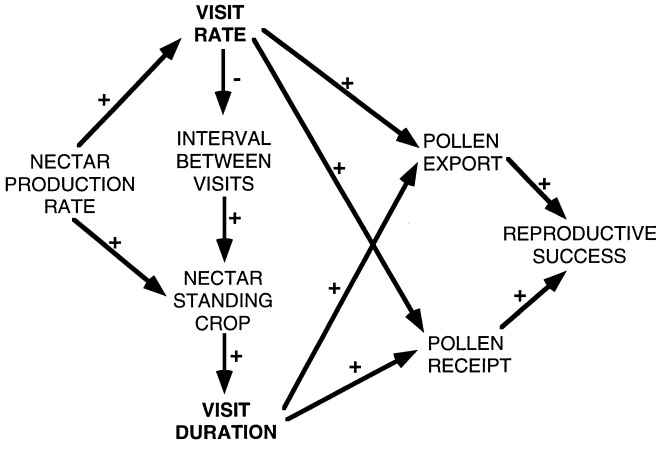

Fig. 1 Path diagram outlining the hypothesized relationship between pollinator visit rate and average visit duration per flower, with probable implications of these two components of pollinator service for plant reproductive success

Methods

Study organisms and location

Antirrhinum majus L. is an excellent model organism for studies of pollinator-mediated selection on floral traits. The genetics of many aspects of floral design, such as symmetry and color patterning, are well-studied in this species (e.g., Luo et al. 1991; Martin et al. 1991). In its native Mediterranean habitat and in our experimental populations it is pollinated primarily by bumblebees (K. Jones, personal observation), whose methodical behavior is readily quantifiable. *A. majus* flowers are hermaphroditic and protandrous. Anthers dehisce on the 1st day that the corolla becomes accessible to pollinators and the stigma becomes receptive on the 3rd or 4th day. Individual flowers remain open for 5–15 days, with a lack of pollination extending the bloom time (K.N. Jones and J.S. Reithel, unpublished work). Plants in our field experiments averaged 3.6 flowers open at a time on a single inflorescence.

This study is part of a long-term project examining selection by pollinators on a single-locus flower color polymorphism in snapdragon. We observed pollinator visits to experimental arrays of potted yellow- and white-flowered offspring from crosses between two *A. majus* strains (*incolorata*-19 and *sulfurea*-57, provided courtesy of R. Carpenter, John Innes Institute, Norwich, Norfolk, UK). Flower color did not affect aspects of bee behavior relevant to this study; therefore data from both morphs were combined for analysis.

Arrays were placed in subalpine meadows at the Rocky Mountain Biological Laboratory (RMBL), elevation 2900 m, in Gunnison County, Colorado, United States (107°W, 39°N), where they were visited by freely foraging bumblebees, primarily *Bombus appositus* workers, with a small percentage of visits ($< 1\%$ in the array used to test the two main hypotheses) from *B. flavifrons* and *B. californicus*. To the best of our knowledge, there were no snapdragon plants within a 5-km radius of the site prior to our introduction of the experimental arrays, so the bees most likely were inexperienced with snapdragons. Plants were watered sufficiently to ensure that nectar production was not limited by water availability.

Intensive pollinator observations

From 11 to 28 July 1995, we observed all pollinator visits to an array of 36 potted plants, obtaining for each flower a record of the number and spacing of visits, and the duration of most visits. Two observers moved around the outside of the array to keep each bee in clear view, from 0900 until 1700 hours daily. When the plants were not being observed, during rainstorms and overnight, they were covered to prevent visitation; bees generally were not foraging in the surrounding meadow during these times. The time interval between visits was assigned a maximum value of 12 h, since relatively little nectar is produced overnight in snapdragons (C. Prenot, unpublished work). We defined flower visit duration as the time between the entrance of a bee's head into the corolla tube, after the two corolla lips were pried apart, and the reappearance of her head as she backed out of the flower. Visit duration was recorded for as many of the flower visits as possible (71% of 1545 visits).

Nectar addition experiment

Three experimental populations were placed in meadows around the RMBL. They were staggered in time and separated by at least 2 km of blooming wildflowers favored by bumblebees, so it was unlikely that the same bees visited more than one experimental population. In previous experiments at the same locations, bees were marked with powdered fluorescent dye; never did we see a bee from one location at any of the others. Each population had 48 potted plants, 36 white-flowered and 12 yellow-flowered (Hardy-Weinberg proportions of this single-locus polymorphism) randomly distributed in a regularly spaced array.

In two of the populations, each open yellow flower had an extra 10 μl of 30% sucrose solution pipetted into the throat of the corolla, where nectar accumulates, at 0900 and 1300 hours daily. This amount of additional nectar is more than the typical standing crop, but less than the average total nectar production of a snapdragon flower (see Results). In the third population there were no nectar additions. Populations were randomly assigned as nectar addition or control sites.

Each population remained in place for two weeks, and was observed in 3- to 4-h periods between 0830 and 1700 hours, for a total of 224 h of field observations: 26 June–10 July (control population), 1–15 July (experimental population 1), and 16–30 July (experimental population 2) 1997. The movements of individual bees were recorded on audio tape for as long as they remained in the array.

Nectar secretion measurements

Nectar production per flower was examined in a separate set of 12 snapdragon plants housed in a mesh exclosure to prevent pollinator visits. There were three treatments applied to four plants each, two white-flowered and two yellow-flowered: nectar extraction twice a day (morning and afternoon, separated by 4-h intervals), once daily in the morning, or every other day in the morning. All open flowers on each plant had their nectar extracted at the appropriate intervals between 0900 and 1700 hours from 30 July through 3 August 1997. Nectar was removed and measured with 10-μl glass capillary tubes (Drummond Scientific). These plants also were watered regularly as needed. The two flower colors did not differ in total nectar production over the 4-day period (white: 11.34 μl ± 6.22, yellow: 11.38 μl ± 9.17; $P > 0.9$); therefore data from the two color morphs were combined for analysis.

Data analyses

Nonparametric analyses were used for all tests involving the time since last visit, because those data did not approximate a normal distribution. Individual visit duration data were natural-log transformed to meet the assumptions of parametric analyses, and nectar volume data (totals per flower) were square-root transformed. Data expressed as averages over a flower's lifetime or over all flowers per plant did not require transformation for parametric tests. Data analyses were performed using StatView 4.1 (Abacus Concepts 1994).

The hypothesis that there was no correlation between visit duration and the time since the flower was last visited was tested with a Spearman rank correlation analysis, corrected for ties in the data, with each flower visit as the unit of observation. Whether visit duration per flower differed between yellow-flowered (nectar-enhanced in some arrays) and white-flowered plants was analyzed separately for each array, using a *t*-test with plant as the unit of observation (visit durations per flower were averaged over all flowers per plant to give a mean value of flower visit duration for each plant). Nectar standing crop for the plants screened from pollinators was compared to the time interval since nectar was last removed (4, 24, or 48 h) using a Spearman rank correlation analysis, corrected for ties. An ANOVA tested whether the frequency of nectar removal (treatment) affected the total volume of nectar produced by the flowers over the 4-day sampling period, with the individual plants nested within treatment so that we could also test for variation among plants in nectar production per flower.

We addressed the second main hypothesis, regarding the potential trade-off between number of visits received over a flower's lifetime and the average duration of those visits, in two ways. Because individual plants varied in overall vigor, number of flowers open at a time, and probably nectar production rates (see Results) and other components of pollinator attraction, we expressed the data for each flower as residuals, having subtracted the

mean value for each plant from the flower-level values. Controlling for plant-level effects in this way, we tested for a correlation between the visit number residuals and the average visit duration residuals at the level of individual flowers. Also, we tested the number of visits per flower and the average visit duration per flower for a correlation at the whole-plant level, by averaging flower means over all flowers on a plant (mean number of flowers per plant = 5.9). Similarly, we tested for correlations between the number of visits and the average time interval between visits to a flower, at both the individual flower (residuals from plant means) and whole-plant levels.

To determine whether the spacing of pollinator visits to a flower was regular, random or clumped, we used a Wilcoxon signed rank test to analyze whether the coefficient of variation (standard deviation: mean ratio) in time interval between visits was greater than one for half of the flowers, and less than one for half, which would be the random expectation if visits were independent of each other (Possingham 1989; Kadmon 1992). A flower with at least five visits received was chosen randomly to represent each plant in the analysis.

To test whether variance in visit duration could be explained by flower age, we used a one-way ANOVA, followed by Fisher's protected least significant difference post hoc analysis to test for differences between pairs of floral age groups. We also tested whether visit frequency varied with flower age, by randomly choosing two days of pollinator observations (20 and 24 July) and tallying the number of visits to flowers in age categories of 1–8 days. Since we knew the age in days of all flowers in the array, we could compare the observed numbers to expectations based on the frequency of each age class on those days of observation, using a chi-squared test with 7 *df*.

Table 1 Adding nectar to flowers increased the duration of pollinator visits to individual flowers. In the experimental populations, all yellow flowers had extra nectar added twice a day. No flowers received extra nectar in the control population. Sample sizes for each population were 12 yellow-flowered plants and 36 white-flowered plants. Mean visit durations for all flowers on a plant were averaged for each replicate. Visit durations are listed below as the mean ± SE over all replicates per flower color

Population	Visit duration			
	Yellow flowers	White flowers	*t*	*P*
Control	4.28 ± 0.48	4.26 ± 0.28	0.004	0.997
Experimental 1	8.46 ± 0.86	5.17 ± 0.94	3.930	0.0003
Experimental 2	12.29 ± 0.99	6.13 ± 0.63	4.931	< 0.0001

Table 2 Total nectar per flower does not depend on frequency of nectar removal (treatment) but does vary over individual plants (nested within treatment). Model $R^2 = 0.374$

Source	*df*	SS	*F*	*P*
Treatment	2	3.965	0.406	0.6779
Plant (treatment)	9	43.938	5.188	0.0001
Residual	58	54.583		

Results

In the test of the first main hypothesis, the time a bee spent in a flower was positively correlated with the length of time since the flower was previously visited ($r_s = 0.383$, $n = 1090$ flower visits, $P < 0.0001$). Bumblebees spent an average of 4.9 s (SD = 4.2) in a flower, and the average interval between visits to an individual flower was 7.7 h (SD = 5.4).

The addition of extra "nectar" to yellow flowers significantly increased the duration of bee visits to those flowers, compared to unmanipulated white flowers, whereas in the array where neither flower color was augmented, visit duration did not differ between colors (Table 1). Thus, visit duration was sensitive to reward quantity.

Nectar production measurements showed that nectar was secreted continually, so that there was a significant correlation between time interval since previous draining and standing crop ($r_s = 0.696$, $n = 12$ plants, $P = 0.021$). Total nectar production per flower did not depend on frequency of nectar removal, but did vary significantly across individual plants (Table 2). Total volume of nectar produced over the 4 days of observation averaged 11.36 µl per flower (SD = 7.99).

In the test of the second main hypothesis, at the level of individual flowers over their lifetimes, the correlation between the residuals (adjusted for plant means) of the number of visits received and the average duration of those visits was weakly negative ($r = -0.163$, $n = 214$ flowers, $P = 0.017$; Fig. 2A). In contrast, at the whole-plant level, the correlation between average number of visits received per flower and average visit duration per flower was significantly positive ($r = 0.386$, $n = 36$ plants, $P = 0.019$; Fig. 2B).

The correlation between the number of visits received per flower and the average time interval between those visits was significantly negative at both the individual flower (residuals from plant means, $r = -0.532$, $n = 228$ flowers, $P < 0.0001$) and whole-plant ($r = -0.534$, $n = 36$ plants, $P = 0.0008$) levels. These values were further from a perfect negative correlation than we had expected. Visits to individual flowers were less regularly spaced than reported in previous studies of systematic pollinator foraging (Possingham 1989; Kadmon 1992). The coefficient of variation for visit interval was 0.70 overall, and the mean interval exceeded the standard deviation for more flowers than expected if the visits were independent [Wilcoxon signed rank test, $n = 36$ flowers (one per plant), $P = 0.005$], indicating that visits were regularly spaced. However, we had standardized the overnight interval to 12 h and used this as the maximum value for time between visits, which would constrain the standard deviation even more than the mean interval and thus result in an artificially low coefficient of variation. Therefore we repeated the test for intervals within days only (leaving out overnight intervals). For this subset of the data, the coefficient of variation was 1.24, and the mean interval exceeded the standard deviation for fewer flowers than expected for random visit intervals ($n = 36$, $P = 0.012$). Thus, visits to flowers within a day were clumped in time. The coefficients of variation for individual flowers ranged from 0.77–2.94 for visit intervals of less than 12 h.

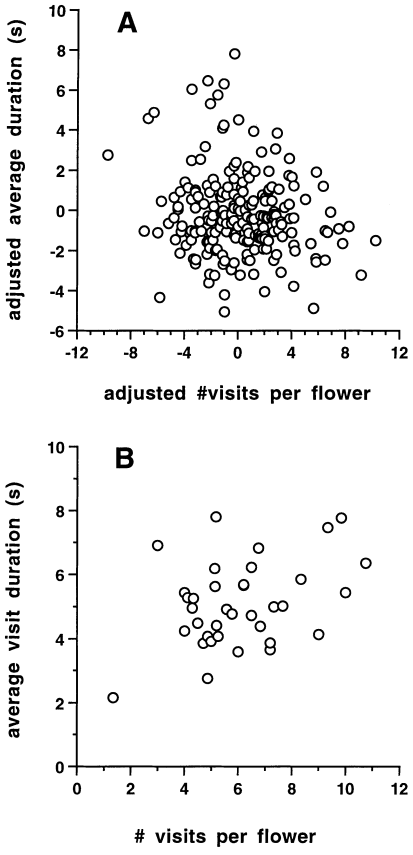

Fig. 2A,B A trade-off between number of visits received and the average duration of those visits was found at the level of individual flowers, but not for whole plants. **A** Data for individual flowers ($n = 214$), expressed as residuals after the mean value for each plant was subtracted from the flower-level data, to control for plant-level effects (hence *adjusted* on the axis labels). Significant negative correlation: $r = -0.163$, $P = 0.017$. **B** Significant positive correlation at the plant level ($r = 0.386$, $P = 0.019$). Each data point represents a single plant whose data per flower have been averaged across all flowers on the plant ($n = 36$ plants)

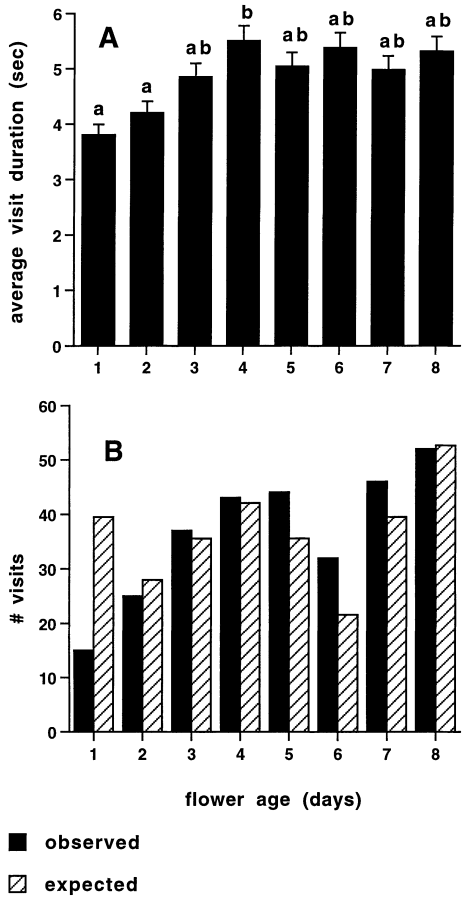

Fig. 3A,B Visit duration and frequency both vary with flower age. **A** 1- and 2-day-old flowers received shorter visits than 4-day-old flowers (Fisher's PLSD, $P < 0.05$, indicated by the different *letters* above the *bars*). **B** Observed and expected values for number of visits to flowers of different ages on 20 and 24 July 1995 ($\chi^2 = 23.7$, $df = 7$, $P < 0.005$)

Both visit duration and number of visits varied with flower age: 1- and 2-day-old flowers received shorter visits than did 4-day-old flowers (Fisher's PLSD: 1-day-old < 4-day-old, $P = 0.0253$; 2-day-old < 4-day-old, $P = 0.0113$; Fig. 3A). The observed numbers of visits did not match the expected numbers of visits to flowers of different ages, as 1-day-old flowers received fewer visits than expected, and 5-, 6- and 7-day-old flowers received more visits than expected based on their frequencies in the population ($\chi^2 = 23.7$, $df = 7$, $P < 0.005$; Fig. 3B).

Discussion

The number of pollinator visits may not be a good predictor of the pollination success of a flower or plant (Stanton et al. 1991; Wilson and Thomson 1991). Our results illustrate the interdependence between visit quantity and duration, a component of visit quality. We found that the length of time that a bumblebee spent in a snapdragon flower increased with the elapsed time since the flower was last visited. A simple causal explanation for this observation is that the flowers that built up a greater standing crop of nectar received longer visits, because it took the bees longer to imbibe more nectar. Experimental nectar addition increased visit duration, supporting this explanation. Also, we showed that nectar standing crop increased with the elapsed time since a snapdragon flower was drained by hand, on a time scale relevant to the time intervals between visits experienced by the plants in the field population. A similar correlation between visit duration and time interval since previous visit should exist for any plant-pollinator interaction in which: (1) the time a pollinator spends in a flower depends on the nectar standing crop, (2) a visit typically drains a flower of most of its nectar (not always the case; Zimmerman 1983), and (3) the flowers replenish nectar steadily after being visited.

However, this correlation was found at the level of individual flower visits, and many factors affect its extrapolation to the level of the total visit histories of flowers, let alone whole plants or phenotypes. Indeed, we found only a very weak negative correlation between the total number of pollinator visits and the average duration of visits received by snapdragon flowers over their lifetimes. At the level of whole plants, flowers on some plants received both more visits and longer visits than those on other plants, so that there was a significant *positive* correlation between these two components of pollinator service at the plant level.

In order for the correlation between visit duration and elapsed time since last visit to translate into a trade-off between the number of visits and average duration of visits to a flower, there must be a reasonably tight negative correlation between the number of visits and the average interval between visits to a flower, so that the fewer visits a flower receives the longer the average time interval between visits will be. Differences between flowers in the spacing of visits weaken the correlation between the number of visits and average interval between visits to flowers. For example, if a flower receives a total of ten visits, and all are within a single morning, the average interval between visits will be lower than for a flower that receives a greater number of visits scattered more evenly over several days. Snapdragon flowers in our experimental population experienced a much greater range of variance in visit intervals (CV ranged from 0.77 to 2.94) than flowers in other studies with pollinators that foraged systematically (CV ranges from 0.4 to 1.0, Possingham 1989; and 0.44 to 0.79, Kadmon 1992).

The overall correlation between number of visits to a flower and the average interval between them was –0.53 for the snapdragons, a fairly weak link between visit number and average duration. In this case the strength of the correlation between visit duration and interval between visits at the level of individual visits would be cut nearly in half to generate an expected correlation between the total number of visits to a flower and their average duration. Indeed, the negative correlation between total number of visits received and average duration for snapdragon flowers was −0.163, approximately half as strong as the correlation between visit duration and time interval since last visit at the individual visit level ($r_s = 0.383$). We predict that plant populations experiencing systematic foraging, for example by traplining bumblebees (Thomson 1996), will have a stronger trade-off between the number and average duration of visits than those whose pollinators have more random visit patterns, other factors being equal.

The large range of variance in visit intervals indicates that some snapdragon flowers were foraged much more systematically (lower CV, i.e., visits were more regularly spaced) than others. A probable cause of this variation, compared to that found in other studies, is the relatively long time scale of the study, 18 days of continuous pollinator observations. The days varied considerably in the number of pollinator visits to the experimental plants, from 0 to 130 per day (mean = 43.9 plant visits per day, $SD = 43.2$). Weather is notoriously variable in the Rocky Mountains in July; 6 of the 18 days had at least one rainstorm, and there were hard frosts on several of the nights. It seems reasonable that pollinators could be more systematic during sunny weather; their visits would be necessarily more irregular on inclement days. Thus the regularity of visits to a flower probably depended at least in part on which days it was open during the observation period, and the weather it experienced over its lifetime.

Other factors that would affect the strength of the trade-off for a plant population include several aspects of nectar production. If plants can adjust rates of nectar production so that frequently visited flowers are replenished more quickly than others, or if nectar is resorbed by less-visited flowers, then a correlation between number and duration of visits would be reduced. We found no effect of nectar removal frequency on total nectar production per snapdragon flower, but such effects have been observed in other species (Raw 1953; Pleasants 1983; Zimmerman and Pyke 1986; Burquez and Corbet 1991; Nicolson 1995).

If plants within a population vary widely in nectar production rates, then those which replenish nectar more rapidly may receive both more visits and longer visits than those with lower rates of secretion (Cohen and Shmida 1993). The result would be a positive correlation between these variables that may reduce or override a trade-off at the level of whole plants. The volume of nectar produced per day over a 4-day period varied ten-fold among snapdragon flowers, with a significant portion of the variance (36%) between individual plants. Nectar production probably experiences stabilizing selection in most natural populations (Cohen and Shmida 1993), whereas our laboratory-cultured snapdragons had gone through several generations without selection on nectar characteristics. On the other hand, our experimental plants were kept in identical pots with the same potting soil and watering schedule, so they probably had less environmentally-driven variation in nectar production rates (Corbet 1990; Jakobsen and Kristjansson 1994; Herrera 1995) than would be found in a field population. Nectar levels varied at least three-fold between nearby plants in field populations of *Ipomopsis aggregata* (Polemoniaceae), and such variation is probably not unusual since nectar production is often correlated with other components of morphology such as flower size (Mitchell 1993). Whatever the cause, the extreme variation in nectar production rates among our snapdragon plants likely was of primary importance in reversing the expected negative correlation between the number and average duration of visits to flowers at the whole-plant level.

It is also possible that plants vary nectar production with flower age, so that flowers at a critical stage of stigma receptivity, for example, could encourage longer pollinator visits by having larger nectar standing crops. Snapdragon flowers that were 4 days old received the longest visits, significantly longer than 1- and 2-day-old flowers, and older flowers received more visits than the youngest ones. When outcross pollen was hand-applied to stigmas of snapdragon flowers of different ages in a greenhouse experiment, flowers that were 4 or 5 days old at the time of pollination produced twice as much seed mass as those that were 1, 2, or 3 days old (K.N. Jones and J.S. Reithel, unpublished work). Preliminary data indicated that nectar production was relatively slow on the 1st and 2nd days after a flower opened, then increased on the 3rd day. It appears that snapdragons experience variation in pollinator visitation as nectar secretion changes over the life of a flower, similar to *Phacelia tanacetifolia* (Williams 1997) and *Alstroemeria aurea* (Aizen and Basilio 1998).

For plants in which the importance of a pollinator visit varies over the life of a flower, it probably is more relevant to ask whether visit number and duration are negatively correlated within the time intervals most critical for reproductive success, rather than over the entire lifespan of a flower. For example, in protandrous species the first few visits are likely to be especially important for donation of viable pollen, since pollen viability generally declines with time since anther dehiscence (Thomson and Thomson 1992), whereas visits prior to stigma receptivity may be of little benefit to seed production. If on a longer visit a greater fraction of the pollen carried by a pollinator is deposited on a stigma, then a long visit when the stigma has just become receptive may result in greater opportunities for selection among pollen donors than several short visits in which only the most recently acquired pollen (probably from near neighbors) is removed from the pollinator's body. Especially if pollinator visits are regularly spaced within the critical time intervals, there may well be a trade-off between the number of visits during those times and the duration of those important visits.

To summarize, two parameters widely used in estimates of pollinator-mediated selection on floral traits, the number of visits received and the duration of those visits, are not independent of each other. However, a correlation between visit duration and the time interval since the previous visit may not be extrapolated to a trade-off between number and average duration of visits, unless nectar secretion is fairly uniform across plants and pollinator visits are regularly spaced.

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