Pollen removal and deposition by pollen- and nectar-collecting specialist and generalist bee visitors to *Iliamna bakeri* (Malvaceae)

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Abstract—Up to 60% of the bee species of a region are oligolectic; they collect pollen only from a closely related group of plants though nectar-collecting choices are often broader. Bee specialists are expected to be superior to generalists in gathering pollen from their host plants and perhaps in transferring pollen to host stigmas. We used the oligolege *Diadasia nitidifrons* and its pollen-host *Iliamna bakeri* to ask if specialists 1) were more efficient than generalists as pollen-collectors; 2) deposited more pollen on stigmas than generalists; and 3) if pollen-collectors removed and deposited more pollen than did nectar-collectors. We found support for the first and third hypotheses. *Diadasia* pollen- and nectar-collectors removed more pollen per flower-visit than did their primary generalist competitors (*Agapostemon* spp.). The superior pollen-gathering efficiency of *Diadasia* exceeded differences that might be attributed to size: although *Agapostemon* females are, on average, 12.5% smaller than *Diadasia* females, pollen-collecting *Agapostemon* left 22.9% more pollen in flowers than did *Diadasia*. We found no difference between taxa in time spent foraging on a single flower. *Diadasia* and *Agapostemon* pollen-collectors deposited significantly more pollen on *I. bakeri* stigmas than did nectar-collectors; there was no difference between taxa in pollen deposition. *Diadasia* was superior to generalists as a pollinator in two ways: *Diadasia* was 1) a more reliable presence in *I. bakeri* populations; and 2) always most abundant at *I. bakeri* flowers. The association between *D. nitidifrons* and *I. bakeri* appears to be another example of a highly specialised bee affiliated with an unspecialised host-plant.

Keywords: *Pollen removal, Pollen deposition, Specialization, Oligolecty, Iliamna, Diadasia*

INTRODUCTION

Oligolecty describes an inherent preference by all members of a bee population or species for the pollen of a circumscribed taxon of plants (Minckley & Roulston 2006). Up to 60% of the bee species of a region may be oligolectic (Minckley & Roulston 2006). Why this fraction is so large has intrigued bee biologists and pollination ecologists for at least a century (Robertson 1914). The commonest explanation for oligolecty is related to one advanced by Darwin (1876) for flower constancy (Cane & Sipes 2006; Raine & Chittka 2007). Darwin thought that individuals that restricted their visits to a few closely related plants would learn from frequent use to collect pollen from those flowers more effectively than their generalist competitors. Over time, at least some of those learned foraging behaviors are presumed to have become instinctive.

Pollen is the main source of amino acids, protein, lipids, and starch that female bees supply to their progeny (Roulston & Cane 2000); nectar, by contrast, is primarily an energy source and is commonly collected from both the pollen host and various other species (Robertson 1914; Linsley 1958; Eickwort & Ginsberg 1980; Wcislo & Cane 1996). More efficient collection of specific host-plant pollen by female oligoleges than by polyleges is likely to be strongly selected for at least two reasons: 1) pollen is more likely to be a limiting trophic resource because, unlike nectar, it is not replenished within flowers (e.g., Percival 1955; Linsley 1978; Minckley et al. 1994; Schlindwein et al. 2005; Larsson 2005; Larsson & Franzén 2007; Carvalho & Schlindwein 2011); and 2) only host-plant pollen is available to oligoleges but polyleges forage on a variety of different floral species with diverse morphologies and resource dispensing mechanisms.

While there is some evidence to support the hypothesis that specialists are superior to generalists in collection of pollen grains/unit time from their host plants (e.g., Strickler 1979; Cane & Payne 1988; Laverty & Plowright 1988; Thostesen & Olsen 1996; Larsson 2005; reviewed in Minckley & Roulston 2006), not all studies concur (Harder & Barrett 1993; Castellanos et al. 2003). Thus, our first objective was to compare the pollen-collecting ability of a specialist, the mallow oligolege *Diadasia nitidifrons* Cockerell (Arneson 2004; Arneson et al. 2004; Sipes & Tepedino 2005) on its host plant, *Iliamna bakeri* (Jepson)

Wiggins (Malvaceae), with that of its generalist bee competitors.

Plant species such as *I. bakeri* that have been "adopted" by a specialised pollinator such as *D. nitidifrons* may, in turn, begin to adapt to or coevolve with those pollinators, particularly when their presence at the flowers is as reliable as is that of *D. nitidifrons* (Arneson et al. 2004). However, because *I. bakeri*, with its large, open flowers, and easily accessible pollen and nectar, is also an attractive prospect for generalised visitors, there may be little selective pressure to co-evolve with a specialist pollinator. Alternatively, floral adaptations can sometimes be quite subtle and unexpected (Armbruster 2006), and specialists may sometimes be superior to generalists as pollinators of host flowers (Thomson 2003; Williams & Thomson 2003; Fenster et al. 2004; Minckley & Roulston 2006) though sometimes they are not (Tepedino 1981; Sampson & Cane 2000; Mayfield et al. 2001; Castellanos et al. 2003; Larsson 2005). Thus, our second objective was to determine whether visits by *D. nitidifrons* to *I. bakeri* flowers result in more fruit or seed than visits by generalists.

Differences in the behaviour of pollen and nectar collectors on flowers may also lead to differences in pollen removal, deposition, or the likelihood of contact with reproductive parts (Tepedino & Parker 1982; Wilson & Thomson 1991; Williams & Thomson 2003; Castellanos et al. 2003; McIntosh 2005). For example, simple preferences for flowers in the male stage by pollen collectors may lead to ineffective pollination even by specialists (Tepedino & Parker 1982). Therefore, our third objective was to compare pollen removal and deposition between nectar and pollen foragers.

MATERIALS AND METHODS

Study plant

I. bakeri is a globally rare though locally abundant, short-lived (≤ 10 yr), fire-following mallow limited to the volcanic soils of high-elevation arid shrublands and open forests of northeast California and southeast Oregon, USA (Wooley 2000). Flowers are large and open, are open throughout the day, last for approximately 24 hrs, and produce between 16 and 18 stigmas and about 140 stamens (range 116-160; Arneson et al. 2004). Flowers are hermaphroditic and protandrous; male and female phases each last up to 12 hrs.

Over 85% of anthers are fully dehisced by the time the flower is one-third open, and bees are common visitors at these early stages when pollen and nectar are readily obtainable (Arneson 2004). Thus, pollen can be depleted quickly if visitors are abundant. The styles gradually emerge from the malvaceous column after anther dehiscence. By the time the styles extend above the column, the central most anthers have begun to reflex away from the column thus making minimal contact with stigmatic surfaces (Arneson 2004).

Arneson (2004) found that most *I. bakeri* plants are self-incompatible and that fruit and viable seed production requires pollinators. Hand-pollination experiments showed

limited fruit and seed production from geitonogamous treatments and no fruit production from autogamy. Outcrossing treatments yielded significantly higher fruit set than did geitonogamy treatments.

Pollen Remaining

Single-visit experiments were used to estimate the number of pollen grains removed from virgin flowers. From 9 – 25 July 2003, budded inflorescences on 10 *I. bakeri* plants at the Clark Valley Road population in NE California (see Arneson et al. 2004 for details) were bagged (10 × 10 × 30 cm) with white bridal veil material (mesh 1 mm²) to exclude visitors. When flowers displayed receptive stigmas, bags were removed and the target flower was allowed one bee visit and then immediately rebagged. Stigmas were judged receptive when they had extended above the column and appeared moist under 10× magnification.

A visit was defined as an actual landing upon the flower followed by an obvious attempt to gather pollen and/or nectar. We sight-identified generalist and specialist flower-visitors to the lowest taxonomic level possible. Subsequent identification of collected specimens revealed generalists to be four species of bumblebees (Apidae: mostly *Bombus vosnesenskii* Radoszkowski, but also *B. centralis* Cresson, *B. huntii* Greene, *B. melanopygus* Nylander) and two species of green sweat bees (Halictidae: mostly *Agapostemon angelicus* Cockerell/*A. texanus* Cresson, but also *A. femoratus* Crawford). We noted whether foragers collected nectar, pollen or both. "Pollen" and "both" categories were subsequently combined because the time spent collecting nectar following pollen collection was always brief, usually lasting only a few seconds. As we had no control over the identity or abundance of visitors, we had to settle for the visits that occurred. Therefore, our sample sizes are unequal and, in some cases, small.

Unvisited control flowers selected for pollen counts were immediately adjacent to single-visit flowers and in the same bag. Depending on availability, the number of control flowers varied from 2 to 6 per plant (median = 3.5, N = 39 total flowers), and the number of visited flowers varied from 1 - 25 per plant (median = 8.5, N = 102 total flowers). There was no indication that the unequal numbers of control and visited flowers per plant biased our results; for example, control flowers from a plant with one experimental flower produced approximately the same number of pollen grains as did those from a plant with 25 experimental flowers (mean ± SE (# flowers): plants with one flower visited = 24,930 ± 9,981 (2); plants with 25 flowers visited = 25,568 ± 5,182 (5)).

We used pollen remaining in unvisited controls and in single-visited flowers as our dependent variable. The day after single-visit flowers and control flowers closed, whole corollas were detached from the pedicel, placed individually in glass vials, and stored in the freezer to prevent fungal infestation. Pollen grains remaining, including those that had fallen into the corolla or been dislodged from the anthers, were counted in the lab two months later.

All remaining pollen grains were removed from stamens and petals in each flower via sonication in filtered ethanol,

then counted using a HIAC Royco 8-channel particle counter (Model 8000A). *I. bakeri* pollen grains are approximately 50 microns in diameter and were distinguished, by size, from all particles less than 40 or greater than 60 microns in diameter. Flowers that became infested with fungal mycelia were discarded because pollen grains could not be dis-aggregated.

Strickler (1979) proposed that a comparison of pollen-removal efficiency among bee species should incorporate adjustments for size differences and for the average duration of individual flower visits. We used body volume as our size metric using the formula for a cylinder (volume $=\pi r^2 h$; where r = distance between the wing bases (tegulae) and h = body length (abdomen unteloscoped)). Body size has been shown to be a reasonable substitute for offspring provision size (Strickler 1979; Müller et al. 2006; Neff 2008). We measured the inter-tegular distance and body length of 15 females each of *D. nitidifrons*, *B. vosnesenskii* (workers), and *A. angelicus/A. texanus*, computed volume for each individual, and averaged over individuals. Duration of most individual single-flower visits was recorded with a stop-watch. Precise time was recorded for visits ≤ 60 seconds; for longer visits (97% of visits) we rounded up or down to the nearest half minute.

Pollinator Quality

We used the number of pollen grains deposited on *I. bakeri* stigmas as our metric of pollinator quality. We estimated pollen deposition for single bee visits to an unbagged, virgin flower using the same flowers used to measure pollen removal. Five of the 16-18 stigmas were chosen for pollen grain counts from a distance at which presence of pollen grains could not be distinguished by the unaided eye (6–9 dm). We selected the central-most stigma and one each near the periphery in the four compass directions (N, S, E, W). Pollen grains on each stigma were counted under 10× magnification in the field. We used the average number of pollen grains on the five stigmas for each flower as an estimate both of pollinator quality and also to compare with fruit set and seed number. Fruit capsules were collected approximately 3-4 weeks later when mature, returned to the lab, recorded and dried, and seeds were counted.

Statistical Analyses

The number of pollen grains in control flowers was compared to the number of pollen grains remaining in single-visited flowers for five visitor groups using a one-way ANOVA in a completely randomised design; Dunnett's test was used to control Type I error for multiple comparisons of the control group to each visitor group. There were five visitor groups: *Diadasia* (specialist) pollen and nectar collectors, *Agapostemon* (generalist) pollen and nectar collectors, and *Bombus* (generalist) nectar collectors.

Differences due to species (generalist versus specialist) and purpose (nectar versus pollen) on number of remaining pollen grains were assessed using a two-way factorial ANOVA in a completely randomised design. As *Bombus*

workers did not "intentionally" collect pollen, they were excluded from this analysis.

Differences in number of remaining pollen grains among the three nectar-feeding groups (generalist, specialist, and *Bombus*) were assessed using a one-way ANOVA in a completely randomised design. Post-hoc multiple comparisons among the three groups were controlled for Type I error using the Tukey-Kramer method.

Differences in visit duration by species (generalist versus specialist) and purpose (nectar versus pollen) were assessed using a two-way factorial ANOVA in a completely randomised design. Because *Bombus* visit durations were clearly shorter than those of other bee species and because *Bombus* data had only two unique values, no statistical comparisons with this visitor group were made. To elucidate the nature of interaction between species and purpose, we compared simple effects (i.e., generalists to specialists for each level of purpose, and nectar to pollen for each level of species); reported *P* values are unadjusted.

We used similar two-way and one-way ANOVAs to analyse number of pollen grains deposited in single visits. A two-sample t-test was used to compare the number of pollen grains deposited on flowers that set fruit with those that aborted.

To better meet assumptions of normality and homogeneity of variance, number of remaining pollen grains and number of deposited pollen grains were square-root transformed, and visit duration was log-transformed prior to analysis. Data calculations were made using the GLIMMIX procedure in SAS/STAT 13.2 in the SAS System for Windows 9.4 (TS1M2).

RESULTS

Iliamna bakeri flowers were visited by bee taxa that differed in size and in purpose. *Agapostemon* females were smallest (volume mean ± SE = 99.1 ± 8.2 mm³) and actively collected pollen in 20 of 30 (67%) visits; *Diadasia nitidifrons* females were larger (volume mean ± SE = 111.5 ± 7.2 mm³) and collected pollen during 26 of 38 (68%) visits; *Bombus vosnesenskii* workers (volume mean ± SE = 590.4 ± 79.5 mm³) were over five times *Diadasia*'s size and removed pollen only passively as they actively collected nectar. Pollen-collecting visitors of both *Diadasia* and *Agapostemon* tended to accumulate more pollen on body parts as they scrambled around and across the multi-stamen flowers whereas nectar collectors remained stationary for longer periods on flowers while 'drinking.'

Pollen Remaining

Pollen remaining in flowers differed among control and visitor groups ($F_{5,112} = 14.4$, $P < 0.001$; Fig. 1A). Pairwise mean comparisons showed significantly more pollen remained in control flowers than in flowers visited by *Diadasia* and *Agapostemon* pollen collectors (DP, AP; $P < 0.001$) or by *Diadasia* and *Bombus* nectar collectors ($P = 0.002$ and < 0.001, respectively) but not in *Agapostemon* nectar collectors ($P = 0.545$).
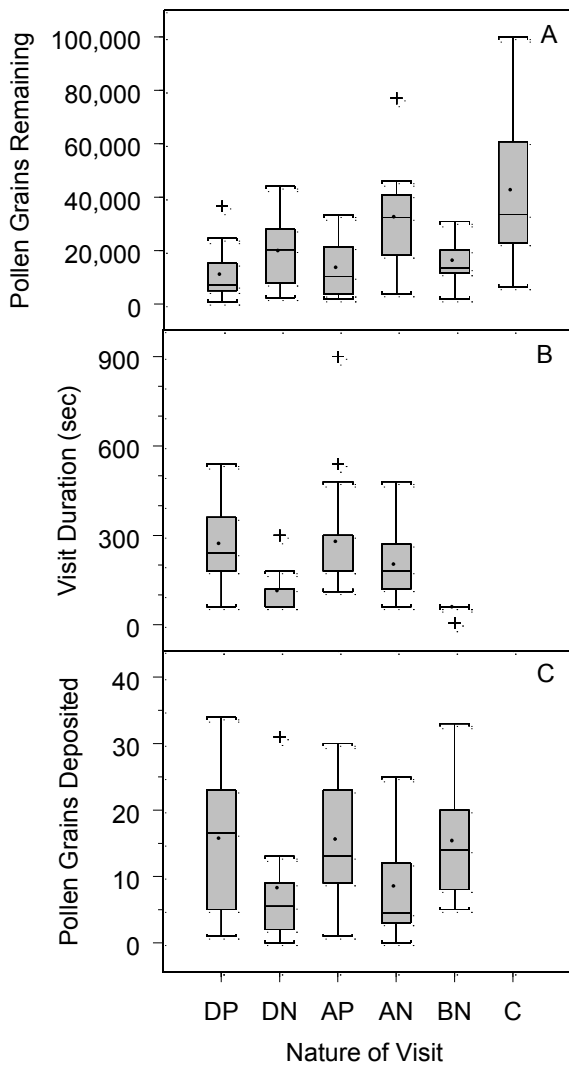
FIGURE 1. Box plots of results of single bee-visits to previously unvisited *Iliamna bakeri* flowers: A) number of pollen grains remaining; B) the duration of single flower-visits; C) the number of pollen grains deposited on stigmas. Shown are means (circles), maximum and minimum values, 25th and 75th percentiles, and outliers (+). Abbreviations: D (*Diadasia* – specialist), A (*Agapostemon* – generalist), B (*Bombus* – generalist), P (pollen-collectors), N (nectar-collectors), C (Control). Sample sizes: DP (26), DN (12), AP (20), AN (10), BN (11), C (39).

A two-factor analysis of pollen remaining showed that flowers visited by pollen-collectors had significantly less pollen remaining than those visited by nectar collectors ($F_{1,64}$ = 14.82, $P < 0.001$) and that flowers visited by *Diadasia* had fewer pollen grains remaining than those visited by *Agapostemon* ($F_{1,64}$ = 3.63, $P = 0.061$). The interaction term did not approach significance ($F_{1,64}$ =1.06, $P = 0.308$). There was no difference in pollen remaining among the three nectar-collecting taxa ($F_{2,30}$ = 2.35, $P = 0.113$).

We also incorporated a measure of visit duration into our assessment of foraging efficiency (Fig. 1B). The comparison of visit duration between specialist (*Diadasia*) and generalist (*Agapostemon*) by purpose (nectar vs. pollen-collection) yielded a significant interaction ($F_{1,82}$ = 6.36, $P = 0.014$). While there was no evidence of a difference between specialist and generalist pollen collectors ($P = 0.832$), specialist nectar-collectors foraged more rapidly than did generalist nectar-collectors ($P = 0.004$). Specialist and generalist nectar-collectors also foraged more rapidly than did their pollen-collecting counterparts (P < 0.001; 0.063, respectively).

Pollinator Quality

We found no difference in pollen deposition between specialist (*Diadasia*) and generalist (*Agapostemon*) ($F_{1,85}$ = 0.12, $P = 0.729$; Fig. 1C). Pollen foragers deposited more pollen on stigmas than did nectar foragers ($F_{1,85}$ = 15.23, $P < 0.001$). There was no evidence of interaction ($F_{1,85}$ = 0.03, $P = 0.870$). A one-way ANOVA showed differences in pollen deposition among nectar collectors ($F_{2,40}$ = 3.93, $P = 0.028$): *Bombus* workers deposited more pollen on *Iliamna* stigmas than did *Diadasia* ($P = 0.029$) or *Agapostemon* ($P = 0.095$) nectar collectors. *Diadasia* and *Agapostemon* nectar collectors were not shown to be different ($P = 0.948$).

Overall, only 11 of 101 singly-visited flowers (10.9%) set fruit. Fruit-set was below 25% for all bee-purpose categories. Fruit set was too low to support comparisons between generalists and specialists or nectar and pollen collectors in fruit set. The 11 flowers that set fruit did not receive more pollen grains per stigmatic surface (mean = 15.3, S.E. = 2.9, $N = 11$) than did those flowers which did not set fruit (mean = 12.8, SE = 1.0, $N = 90$; $t_{99} = 0.82$, $P = 0.41$). Clearly, flowers must be visited more than once to realise the 70% level of fruit set reported by Arneson et al. (2004) for this population.

DISCUSSION

Recently, several enduring hypotheses of melittologists and pollination biologists have been questioned: 1) that specialist bees remove more pollen per flower visit from their preferred host plants than do generalist bees (Minckley & Roulston 2006); 2) that specialists deposit more pollen per flower visit to their host plants than do generalists and are thus better pollinators (Tepedino 1981; Thomson 2003; Williams & Thomson 2003; Franzén & Larsson 2009); and 3) that pollen-collecting bees collect and deposit more pollen per visit than do nectar-collectors (Williams & Thomson 2003). We found tentative support for the first and third hypotheses but not the second.

Specialist *Diadasia* foragers, whether collecting pollen or nectar, left fewer pollen grains in *I. bakeri* flowers after a single visit, i.e., they collected more pollen than did their generalist *Agapostemon* counterparts. Not only did *Diadasia* females collect more pollen than *Agapostemon* in an average visit but they collected disproportionately more as a percentage of body size. *Agapostemon* females are 12.5% smaller than *Diadasia* females but *Agapostemon* pollen-collectors left 22.9% more pollen grains in flowers (12,687) than did their specialist counterparts (10,322). The difference in amount of pollen left by nectar-collectors was even more dissimilar: *Agapostemon*-visited flowers averaged 65.6% more pollen grains remaining than did *Diadasia*-visited flowers (31,701 versus 19,134 respectively). Because

body size and provision size tend to be positively correlated (Muller et al. 2006, Neff 2008), this suggests that *Diadasia* collected a greater proportion of each larval provision on each flower visit than did *Agapostemon*. Thus, the specialist *D. nitidifrons* appears to be superior to *Agapostemon* as a forager on *I. bakeri*, especially when size is factored in. However, this interpretation should be viewed with caution for several reasons: 1) the large variation in the number of pollen grains produced in unvisited flowers, and remaining in single-visited flowers (Fig. 1A); 2) our inability to measure the size of individual foragers, and thus to statistically test the effects of size on pollen extraction differences; 3) potential complications arising from different proportions of pollen in the provisions of different bee taxa (Neff 2008); 4) our estimates of pollen removal are indicative only of freshly opened, unvisited flowers (see below).

The addition of time measures to our comparison of foraging efficiency (Strickler 1979) gave no reason to alter our assessment of *Diadasia* as a superior gatherer of *Iliamna* pollen. In removing greater numbers of pollen grains (Fig. 1B), *Diadasia* foragers did not use significantly more time/flower than did *Agapostemon* foragers. Or, stated differently, *Agapostemon* foragers did not gain equivalence with *Diadasia* in pollen-harvesting efficiency by foraging faster on individual flowers. Additional time savings are likely to accrue to *Diadasia* foragers from their propensity to nest near their host plants. *Diadasia* species such as *D. nitidifrons* (personal observations) and several others (Schlising 1972; Neff et al. 1982; Ordway 1984, 1987) that nest near their host plants, likely enjoy a competitive advantage over generalists in accessing resources and also save time and expend less energy in doing so (Eickwort & Ginsberg 1980; Gathmann & Tscharntke 2002; Franzén et al. 2009). In contrast, generalists are not under any selective pressure to nest closer to *Iliamna* populations than to other plant species from which they forage. Indeed, we were unable to compare travel times amongst bee taxa because only *D. nitidifrons* nests were evident near *Iliamna* populations. The incorporation of travel time to resource patches would likely show significant time-saving for *Diadasia*.

A final complicating factor in this and related studies of foraging efficiency is that, to standardise our conditions, we were forced to time visits to virgin flowers with copious pollen. Thus, our estimates of visit duration are indicative of freshly opened, unvisited flowers and are of much longer duration than visits to previously visited, pollen- and nectar-exploited flowers (Arneson 2004). We conclude that measuring the time factor in foraging efficiency studies will require much more careful gathering and integration of data on flower-visit time, total foraging-trip time, and travel time at different times during the day, all against amounts of pollen and/or nectar removed, to reach convincing conclusions on the overall role of time in floral resource collection efficiency.

Our tentative results on pollen removal are in agreement with the few other studies that have compared specialist and generalist bees. In her pioneering study, Strickler (1979) found that, when adjusted for size and flower-handling time, the specialist bee, *Hoplitis anthocopoides*, removed more

pollen per *Echium vulgare* flower than did four species of generalists. Harder & Barrett (1993) compared two generalist *Bombus* species with the much smaller solitary specialist, *Melissodes apicata*, on the tristylous floral host *Pontederia cordata*. Although they did not report *M. apicata* to be a more efficient pollen harvester, when adjustment is made for the large differences in body size between bee species (*M. apicata* is 50-65% smaller than the bumblebees), *M. apicata* becomes a far more efficient pollen harvester than either of the generalists. Thostesen & Olesen (1996) and Larsson (2005) also showed that specialist bees removed a larger quantity of pollen than did generalists.

We found no indication that *D. nitidifrons* was superior to generalists as a pollinator when number of pollen grains deposited on receptive stigmas was used as the criterion of pollination success (Fig. 1C). Other comparisons of pollen deposition between specialist and generalist bees are few. Thostesen & Olesen (1996) showed that only the specialist bumblebee *B. consobrinus* deposited pollen on host plant stigmas and was therefore superior to generalists as a pollinator. While not examining pollen deposition directly, McIntosh (2005) found that visits by specialists (species of *Diadasia*) were more effective than generalists at producing seeds of *Ferocactus*. Studies by Tepedino (1981) and Larsson (2005) illustrate how subtle and misleading simple comparisons of pollen deposition can be (reviewed in Ne'eman et al. 2010). Tepedino (1981) found that while the specialist bee *Peponapis pruinosa* deposited 33% more pollen grains on squash stigmas than did the generalist honeybee, honeybees improved their pollination value by preferring pistillate flowers while squash bees preferred staminate flowers. Similarly, Larsson (2005) found that the specialist bee, *Andrena hattorfiana*, deposited more pollen on stigmas of its host plant than did generalists but that it visited fewer stigma-presenting flowers and more pollen-presenting flowers than did generalists. Larsson (2005) concluded that *A. hattorfiana* was actually an inferior pollinator. Thus, the value of specialist bees to plant species with open flowers varies with the bee-plant association.

Other factors are at least as important in evaluating pollinator value as the number of pollen grains deposited per flower visit. Indeed, the total number of pollen grains deposited can be a misleading index of pollinator value (e.g., Cane & Schiffhauer 2003; Ne'eman et al. 2010), especially for mostly self-incompatible species like *I. bakeri* where geitonogamous pollinations are less effective than outcrossing at producing seeds. Arneson (2004) found that *Diadasia* typically visited only one flower per inflorescence before moving to other inflorescences on the same, or other, plants while generalists tended to visit multiple *Iliamna* flowers per inflorescence. One *Diadasia* visit/inflorescence is likely to translate to more inter-plant movements, and therefore more potential pollinating visits than by generalists which were more likely to move pollen between flowers within plants, thereby effecting unproductive selfing. Because of this likely difference in movement patterns between visitor types, *D. nitidifrons* visits are probably more effective at achieving pollinations on a per visit basis.

D. nitidifrons confers other advantages as a pollinator of its host plant: predictability of occurrence and numerical dominance. In their review, Vazquez et al. (2005) concluded that visitation frequency was the most valuable pollinator attribute to a plant. Arneson et al. (2004) found *D. nitidifrons* visiting *I. bakeri* flowers in all nine populations observed in northern California including those that were only two years old and > 25 km from the nearest *Iliamna* population, demonstrating high colonization potential. In addition, Tepedino (unpublished) found nesting populations of *D. nitidifrons* and high visitation rates to *Iliamna longisepala* (Torrey) Wiggins flowers at all nine sites surveyed in south central Washington, USA; *D. nitidifrons* was almost always the most abundant species visiting *Iliamna* flowers. Arneson et al. (2004) showed that at five of six *I. bakeri* sites studied most intensively, *D. nitidifrons* accounted for at least 60% of all *I. bakeri* visits and that high visitation rates were typically associated with high fruit production. Thus, the most important attribute of *D. nitidifrons* as a pollinator of *I. bakeri* may be its fidelity.

We found clear support for the third hypothesis, that pollen collectors removed and deposited more pollen per visit than did nectar collectors (Figs. 1A, C). This contrasts with some other studies which have shown that pollen collectors removed more pollen from flowers than did nectar collectors but that there was no difference in pollen deposition (e.g., Freitas & Paxton 1998; Thomson & Goodell 2001; Williams & Thomson 2003; Castellanos et al. 2003; Young et al. 2007). Pollen collectors sometimes deposited less pollen than nectar collectors (Thomson & Thomson 1992; Young et al. 2007) and sometimes more (Williams & Thomson 2003). In a related study, McIntosh (2005) found no difference in seed production by *Ferocactus* species with many stamens and open flowers between native bee collectors of nectar versus pollen.

The association between *D. nitidifrons* and *Iliamna* species appears to follow a general pattern for solitary bees and their host plants delimited by Waser et al. (1996), Wcislo & Cane (1996), and Minckley & Roulston (2006). First, oligolectic bees seem to become allied with host plants that are widespread, abundant, iteroparous, and have reliable and easily-exploited blooms. *Iliamna* species have all these characteristics except they are not widespread (indeed, *I. bakeri* and several congeners are globally rare). However, *Iliamna* species are usually locally abundant and predictable in that they are primary successional species that follow frequent fires (Wooley 2000, Arneson et al. 2004). A second emerging characteristic is that while the bee member of the association is highly specialised, the plant taxon is less so (Minckley & Roulston 2006). Indeed, *I. bakeri*, with ample patronage by both specialist and generalist bees, is not specialised in its pollinator requirements.

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