The energy cost of bee pollination for *Pontederia cordata* (Pontederiaceae)

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Summary

Each day during flowering a *Pontederia cordata* (Pontederiaceae) inflorescence produces 10–40 uniovulate flowers which open for only 8 h. In favourable weather, specialist (*Melissodes apicata*) and generalist bees (*Bombus* spp.) visited this plant so intensively that they removed 95% of the pollen produced by midday. From flower opening until the end of pollen availability, *P. cordata* flowers produced nectar with an energy content of 0.82 ± 0.084 J (mean$\pm$SE). During the subsequent 4 h that the flowers remained open they produced an additional 0.63 ± 0.184 J of nectar energy. Therefore these flowers expended 45.1% (median) more energy on nectar production than was necessary to ensure pollen dispersal. This apparently extra cost of animal pollination could be selectively advantageous if it maintains the attention of generalist pollinators that do not depend on *Pontederia cordata* or if it provides a bet-hedging mechanism to promote pollination in weather that is unfavourable to pollinator activity. Regardless of whether this post-pollination nectar is advantageous, its production probably involves little physiological expense as nectar comprises only 3% of the energy content of each *Pontederia cordata* flower. This small investment contrasts with findings for *Asclepias syriaca*, which expends up to 33% of its daily photosynthetic production during flowering on nectar. Regression analysis of the relation between 'per flower' nectar production and inflorescence size for 27 species indicates that *A. syriaca* produces an unusually large amount of nectar, whereas *Pontederia cordata* produces the amount expected given its flower production. Hence nectar production by most bee-pollinated plants probably involves little energetic cost.

Key-words: Bombus spp., generalist pollinators, *Melissodes apicata*, nectar, pollination energetics, specialist pollinators

Introduction

Animal-pollinated plants that do not rely on deceit to attract pollinators must provide pollinators with some inducement to move between conspecifics while incidentally carrying pollen. To serve this purpose, the flowers of most animal-pollinated angiosperms produce nutritive rewards with high energy content, such as nectar or floral oils (reviewed by Simpson & Neff 1983). As abiotically pollinated plants do not produce these rewards, energy expended in their production constitutes part of the cost of animal pollination. If pollinator rewards involve a large physiological expense (Pleasants & Chaplin 1983; Southwick 1984), then this cost could affect the allocation of resources to floral structures or future reproduction (Pyke 1991) and thereby constrain floral evolution.

Pontederia cordata L. (Pontederiaceae) appears to pay an inordinately large cost of animal pollination. This emergent, aquatic, perennial plant ranges from southern Canada to northern Argentina (Lowden 1973). Each day during the flowering period, inflorescences produce 10–40 tubular flowers which bloom for 6–8 h before wilting (Wolfe & Barrett 1987). Observations of northern populations suggest that this species requires pollinators only for the first few hours of flowering, because: (1) a diverse pollinator fauna actively visits its flowers (Wolfe & Barrett 1988); (2) pollen tubes reach the ovary within 2 h of pollination (Wolfe 1985; Anderson & Barrett 1986); and (3) each flower contains only one ovule. Surprisingly, even though fertilization occurs quickly, *Pontederia cordata* flowers produce nectar until they wilt (Wolfe & Barrett 1987). These flowers therefore

produce much more nectar than is necessary to ensure pollination.

The apparent over-production of nectar in *Pontederia cordata* could be retained evolutionarily for at least three mutually compatible reasons. First, extended nectar production may maintain the attention of generalist pollinators which do not depend on *Pontederia cordata*. Second, longer periods of nectar production may be a necessary bet-hedging strategy to ensure pollination because pollinator abundance varies unpredictably between and within seasons (Wolfe & Barrett 1988). Finally, if nectar production by *Pontederia cordata* involves little physiological cost, then extended nectar production need not compromise allocation of energy to other functions.

In this paper, we present the results of two studies which assess these explanations for the seemingly excessive cost of animal pollination paid by *Pontederia cordata*. During one study we examined the within-day dynamics of nectar production, pollinator abundance and pollen removal to quantify nectar production before and after the completion of pollination. We also measured the energy content of *Pontederia cordata* flowers, so that the energy expended on nectar could be considered relative to the cost of flower production. During the other study we evaluated the need for bet-hedging by recording the effects of between-day variation in daily temperature (and presumably pollinator abundance) on fruit production.

Materials and methods

NECTAR PRODUCTION AND POLLEN REMOVAL

Pontederia cordata is tristylous, so that typical populations include three morphs which differ in the positioning of the stigma and the two anther levels. To facilitate collection of nectar and pollen from the same flower (see below) we measured nectar production and pollen removal only from short-styled plants. Wolfe & Barrett (1987) found that the morphs produced equivalent amounts of nectar, so that this restriction should not affect general conclusions concerning the cost of nectar production in this species.

We measured nectar production throughout the flowering periods of 27 and 28 July 1990 in a large, contiguous population of *Pontederia cordata* in a channel between Opinicon and Hart Lakes, Ontario, Canada (44° 32′N, 76° 20′W). Both days had similar weather (maximum temperatures, 31·9 and 32·0°C; minimum temperatures, 18·8 and 19·2°C; minimum relative humidities, 41·2 and 48·7%), except for some cloudiness during midday on 28 July. Because of the proximity of the study area to a hill which obscured the rising sun, the roughly linear study area was gradually exposed to full sunlight during 30 min

each morning, resulting in a parallel progression of anthesis.

On both days, we sampled two adjacent inflorescences (<0·5 m apart) at each of 10 sites, which were separated by at least 2 m. One inflorescence of each pair was covered with a fine-mesh bag before anthesis to exclude pollinators. These bagged inflorescences provide estimates of accumulated nectar production, whereas the adjacent exposed inflorescence provided an estimate of standing crop. At the end of the first sampling day, the bagged inflorescence was uncovered and the bag was placed on the previously exposed inflorescence of the next sampling day.

Each sampling day included six sampling cycles. To start each cycle we observed a stand of 137 flowering ramets (4·25×4·25 m) for 5 min and counted all pollinators. We then visited each site in turn and sampled nectar from one flower on each of the bagged and exposed inflorescences. Nectar was withdrawn from the flower with small wicks of filter paper, which were then impaled on a pin to be dried and stored. The constricted base of *Pontederia cordata* flowers necessitated destructive sampling to ensure complete extraction of nectar. Each cycle required approximately 80 min to complete and six cycles were conducted between flower opening and wilting. The total carbohydrate content of the sampled nectar was later assayed as described by McKenna & Thomson (1988).

To measure the amount of pollen remaining in visited flowers, we collected the anthers of the exposed flowers that were sampled for nectar between 09.45 and 13.45 h (pollen collection preceded nectar collection). The corolla and stamens were cut below the mid-level anthers and placed in a vial with 70% ethanol. All of the pollen collected was later counted under a compound microscope.

ENERGY CONTENT OF FLOWERS

To estimate the structural energy in *Pontederia cordata* flowers we collected 18 samples of five flowers each. Six samples were collected for each of the three floral morphs (long-styled, mid-styled and short-styled). Half of the samples for each morph involved flowers from which the nectar had been removed with filter paper wicks. Each sample was placed in an aluminium foil envelope and dried to a constant mass at 60°C. The dried samples were then subjected to microbomb calorimetry (Phillipson 1964).

DAILY VARIATION IN SEED PRODUCTION

To investigate the daily variation in fruit set by *Pontederia cordata* flowers, a cohort of 23 randomly chosen inflorescences, which included all three morphs, was sampled in a population at Paugh Lake,

Ontario, Canada (45° 35′N, 77° 45′W) from 4 to 19 August 1982. All inflorescences commenced flowering on the same day and terminated flowering by 19 August. Each day all open flowers were counted and marked at the corolla base with paint. Developing infructescences were bagged at the end of the flowering period to facilitate collection of fruit approximately 6 weeks later. Of the 2053 fruits produced, 165 (8·0%) lost their paint marks and their flowering day could not be identified. Weather data for the observation period were obtained for Barry's Bay, Ontario (11 km south of Paugh Lake) from the Atmospheric Environment Service of Environment Canada.

The proportion of flowers setting fruit (p) was statistically analysed by multiple regression after logistic transformation {log odds=$\log_e[p/(1-p)]$: Neter, Wasserman & Kutner 1985}. Because the variance of a proportion (or its log odds) depends on the size of the proportion, we employed a weighted regression which weighted each observation by the inverse of the expected variance [$Np(1-p)$; where N is the number of flowers on which the proportion was based]. Based on the resulting regression statistics, the predicted proportion of flowers setting fruit is given by $p = e^{a+\Sigma bX}/[1+e^{a+\Sigma bX}]$, where a is the intercept and ΣbX is the sum of the products of the independent variables and their respective partial regression coefficients.

Results

POLLINATORS AND POLLEN REMOVAL

During the study period, *P. cordata* primarily received visits from *Melissodes apicata* Lovell and Cockerell (Hymenoptera, Anthophoridae) and workers of several bumble-bee species (in order of decreasing abundance, *Bombus vagans* Smith >*Bombus impatiens* Cresson>*Bombus griseocollis* (Degeer)>*Bombus borealis* Kirby=*Bombus fervidus* (Fabricus)=*Bombus pennyslvanicus* (Degeer)). Throughout its range, *Melissodes apicata* collects only *Pontederia cordata* pollen (Mitchell 1962). This species dominated the pollinator fauna during the morning; however, it stopped foraging by 13.30h (Fig. 1). In contrast, the generalist bumble-bees began collecting nectar from *Pontederia cordata* before the flowers had opened, and continued at relatively stable numbers until the flowers wilted at 16.30h (Fig. 1). Less common visitors included an unidentified skipper (Lepidoptera, Hesperiidae), *Hemaris diffinus* (Boisduval) (Lepidoptera, Sphingidae), *Dufourea novae-angliae* (Robertson) (Hymenoptera, Halictidae) and an unidentified leaf-cutter bee (Hymenoptera, Megachilidae, *Megachile* sp.).

At our study area, short-styled flowers produced an average ($\pm$SD) of 12650$\pm$1815 pollen grains
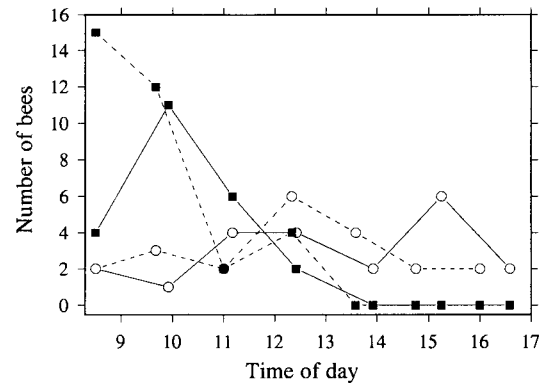

Fig. 1. Abundance of *Melissodes apicata* (■) and bumble-bees (○) observed feeding from 137 *Pontederia cordata* inflorescences during 5-min observation periods on 27 (——) and 28 (- - -) July 1990.

(n =44; L.D. Harder & S.C.H. Barrett, unpublished data). This number declined rapidly during both sampling days (Fig. 2), so that by noon most flowers contained less than 5% of their original pollen. Hence, pollen dispersal was essentially complete by midday, when *Melissoides apicata* stopped foraging. An analysis of covariance comparing pollen standing crop (log-transformed) at the 10 sampling sites, with time of day as the covariate, indicated a general tendency for plants that first experienced full sunlight to contain less pollen at any time after anthesis than later-sunlit plants (overall site effect, $F_{9,9}$ =9·58, $P<0.005$; linear location trend, $F_{1,9}$=23·17, $P<0.005$).

NECTAR PRODUCTION AND FLORAL ENERGY CONTENT

Bagged *Pontederia cordata* flowers accumulated nectar throughout the day (Fig. 3, upper data). Because the variance in cumulative nectar content also increased with time, we log-transformed sugar content before conducting a two-factor (date and site) analysis of covariance with log(time) and log(time)^2 as covariates. This analysis indicates a sigmoidal
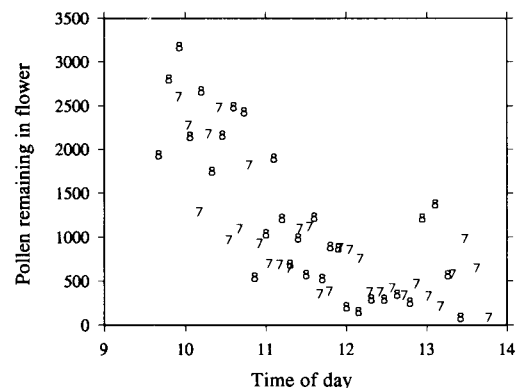

Fig. 2. Number of pollen grains in short-styled *Pontederia cordata* flowers during 27 (7) and 28 (8) July 1990. Anther dehiscence began at approximately 08.45h.
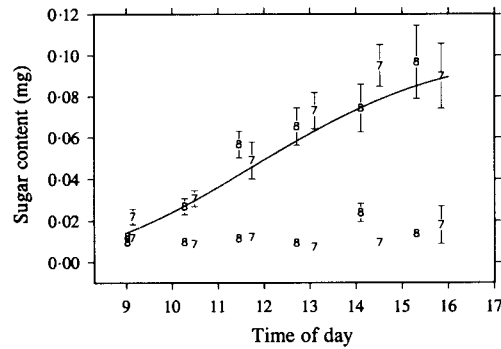
Fig. 3. Changes in mean (±SE; $n=10$) cumulative nectar production (upper data) and nectar standing crop (lower data) during 27 (7) and 28 (8) July 1990. The curve is the back-transformed prediction from a quadratic regression based on log-transformed data.

relation between sugar content and time, with secretion rate increasing slightly during the morning and then declining near the end of the flowering period [linear log(time) effect, $F_{1,96}=9\cdot77$, $P<0\cdot005$; quadratic log(time) effect, $F_{1,96}=7\cdot26$, $P<0\cdot01$, $R^2=0\cdot660$]. In addition, mean sugar content varied significantly between sites ($F_{9,96}=2\cdot00$, $P<0\cdot05$), with the plants that first experienced full sunlight generally containing more sugar (linear location trend, $F_{1,96}=17\cdot37$, $P<0\cdot001$). Nectar production did not differ significantly between the two sampling days ($F_{1,96}=0\cdot62$, $P>0\cdot25$), nor did the site effect depend on sampling date (date×site interaction, $F_{9,96}=1\cdot01$, $P>0\cdot25$).

Because little pollen remained in flowers by midday, nectar production during the afternoon exceeded the energy expenditure necessary to facilitate pollen dispersal. On average, nectar collected during the sampling cycle that ended at 12.25h contained 0·82J of energy, whereas that collected during the last cycle of the day contained a significantly greater 1·44J (Table 1; $F_{1,9}=9\cdot06$, $P<0\cdot025$, based on the time effect from a three-factor ANOVA in which the effects of site and date and all interactions were not significant). Hence, *Pontederia cordata* flowers produced nectar with an average energy content of 0·63J after pollen dispersal was complete. This extra production constitutes a median of 45·1% of the daily energy expenditure on nectar.

An average (±SD) *Pontederia cordata* flower had a dry mass of 2·3±0·18mg (based on 18 samples of five flowers) and an energy content of 43·83±3·114J

Table 1. Cumulative nectar production (mean±SE) by *Pontederia cordata* flowers ($n=20$)

Period	Sugar content (mg)	Energy content (J)
Anthesis to 12.25h	0·05±0·005	0·82±0·084
Anthesis to 16.30h	0·09±0·012	1·44±0·180
12.25h to 16.30h	0·04±0·012	0·63±0·184

(based on 15 samples). Neither flower mass, nor energy content depended significantly on floral morph or whether the nectar was removed before processing (based on two-factor ANOVA, $P>0\cdot1$ in all cases). Our inability to alter floral energy content by removing nectar simply reflects the small overall expenditure on nectar. The total nectar production by a *Pontederia cordata* flower contained an average of 1·44J, which is 3·3% of the total energy invested in a flower. In contrast, total floral energy, largely a function of flower size, had a coefficient of variation of 7·1%.

Pollinator foraging maintained a relatively constant nectar standing crop in *Pontederia cordata* flowers (Fig. 3, lower data). During the last daily sampling cycles, exposed flowers contained an average (±SE) of 0·24±0·070J of nectar energy. Therefore, if exposed flowers secreted nectar at the same rate as bagged flowers, then pollinators removed about 83% of the total nectar production.

DAILY VARIATION IN SEED PRODUCTION

At Paugh Lake during 1982, fruit set by *Pontederia cordata* flowers varied between 25·6 and 78·5%, depending on flowering date. A weighted multiple regression based on logistically transformed proportional fruit set ($R^2=0\cdot617$, $n=15$) indicated that fruit set declined steadily during the observed flowering period ($b_{date}=-0\cdot077$, $s_b=0\cdot031$, $t=2\cdot52$, $P<0\cdot05$), probably because of increasing resource depletion. During this period, daily temperatures fluctuated considerably (Fig. 4a) and fruit set generally increased with the maximum temperature on the day of flowering (Fig. 4b; $b_{temperature}=0\cdot080$, $s_b=0\cdot033$, $t=2\cdot47$, $P<0\cdot05$). Flowering date and maximum temperature were not significantly correlated ($r=-0\cdot045$, $P>0\cdot75$).

Discussion

Two aspects of nectar production warrant comment before we discuss the central results of our study. First, estimates of a species' cumulative nectar production can depend on whether flowers are sampled once at the end of a prescribed secretion period, or repeatedly during that period. The effect of repeated sampling apparently differs between species as both increased (Cruden, Hermann & Peterson 1983; Corbet & Delfosse 1984; Pyke 1991) and decreased (McDade & Kinsman 1980; Corbet & Wilmer 1981) cumulative nectar production have been reported. Unfortunately, floral morphology precluded repeated sampling of *Pontederia cordata* nectar. Consequently, our measured cumulative nectar production may not exactly reflect cumulative nectar production by flowers subject to repeated pollinator visits. This caution is probably more pertinent to discussion of absolute nectar production, than to
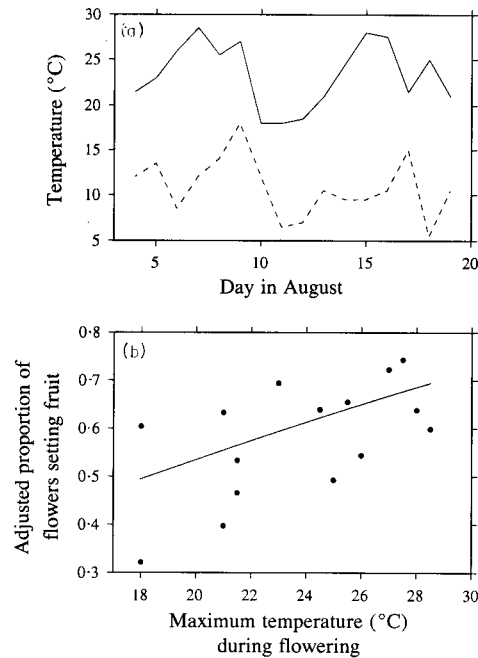
Fig. 4. Variation in (a) daily temperatures (———, maximum temperatures; - - -, minimum temperatures) and (b) the proportion of *Pontederia cordata* flowers setting fruit at Paugh Lake, Ontario, during 1982. Panel (b) relates proportional fruit set to the maximum temperature on the date of flowering. Each plotted point is the sum of the mean proportional fruit set and the residual from a regression of proportional fruit set (logistically transformed) against date. This adjustment allows illustration of the observations in isolation from the effect of flowering date.

comparisons of production at different times of the day.

The second feature that deserves comment involves the observed influence of location on nectar production and pollination. A significant portion of the between-site variation in nectar production and pollen availability could be attributed to the order in which sites became sunlit each morning. In particular, sites that first experienced full sunlight produced more nectar and contained less pollen by any specific time of day. Because these site effects did not interact significantly with time of day, they probably resulted from differences in the initiation of nectar production and pollen removal, rather than differences in rates.

These results indicate that full insolation promotes pollen dispersal, probably because it speeds anther dehiscence and bees prefer to feed in sunlit situations (see Beattie 1971). Such an influence could affect the general pattern of pollen flow, with pollen from longer-illuminated areas having a greater likelihood of reaching stigmas of newly exposed plants. If early arrival of pollen promotes successful fertilization (Marshall & Ellstrand 1985; Epperson & Clegg 1987), as is likely for a plant with uniovulate, 1-day flowers, then repeatable local environmental effects such as those observed here could strongly influence a plant's paternal success.

THE COST OF MAINTAINING GENERALIST POLLINATORS

If nectar production constitutes an energetic cost of animal pollination, then *Pontederia cordata* apparently pays a higher cost ($\approx 45\%$ more) than is necessary to ensure pollen dispersal during a given day with favourable environmental conditions. However, the necessary cost of animal pollination may vary depending on the types of pollinators that visit a particular species. Many plants support both generalist pollinators, which feed on many species, and specialist pollinators, which feed from a single genus or species, often because of physiological requirements.[1] If a plant species relied solely on specialists for pollen dispersal, then nectar would only have to be produced as long as pollen was available because the pollinators must return to the same species on subsequent days. In contrast, generalist pollinators, such as bumble-bees, generally choose the most rewarding plants (reviewed by Plowright & Laverty 1984). If a chosen species stops producing nectar at midday, generalist pollinators will switch to species that produce nectar throughout the day, perhaps reducing the likelihood of returning to the first species on the next morning. As a result, plants that expend extra energy to produce nectar after pollination is complete may more successfully maintain the services of generalist pollinators. Obviously, this concern is only relevant to plants that produce flowers that open relatively synchronously and last for 1 day, a trait which is more common in tropical species than in temperate species (Primack 1985).

HEDGING AGAINST UNCERTAIN CONDITIONS

We measured pollen removal and nectar production under conditions amenable to insect activity. This activity resulted in consumption of 83% of a flower's nectar production, a harvesting level well within the range observed by Heinrich (1976) for 25 plant species. However, *Pontederia cordata* flowers for about 2 months in eastern Ontario (Price & Barrett 1982), during a period with variable weather (Fig. 4a). Fruit production also varies during this period, partly in response to variation in atmospheric conditions during flowering (Fig. 4b). We interpret this relation of fruit set to weather as a reflection of daily variation in visitation rates which influenced the probability of pollination. Pollinator activity varies considerably with existing meteorological conditions (Szabo & Smith 1972; Käpylä 1974; Teräs 1976a, 1985) producing corresponding variation in fruit set (Teräs 1976b; Thomson 1985; Devlin & Stephenson 1987).

[1]Characterization as generalist or specialist refers to diet diversity and bears no connotation of a species' effectiveness at dispersing pollen (see Schemske 1983).
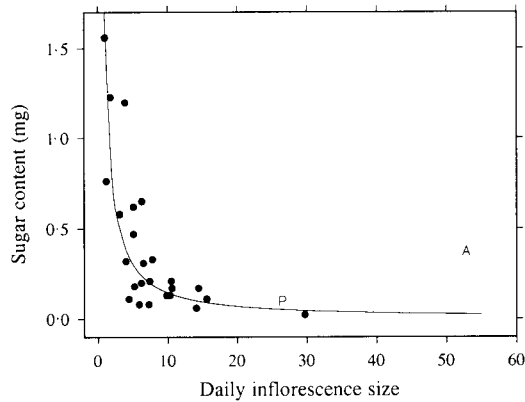
Fig. 5. Relation between 12-h nectar production (*S*) and daily inflorescence size (*I* for 27 plant species, including *Pontederia cordata* (P) and *Asclepias syriaca* (A). Estimation of the prediction line, $S = 1.693\,I^{-1.070}$ ($r^2 = 0.648$; based on log-transformed data), did not involve *A. syriaca* or *Pontederia cordata*. The data were obtained from this study (*Pontederia cordata*), Harder & Cruzan (1990; nine legume species and eight ericad species) and T. M. Laverty & L. D. Harder (unpublished data; nine species, including *A. syriaca,* from diverse families, collected on Amherst Island, Ontario, Canada).

Maintenance of a flower's attractiveness throughout its life could clearly buffer plants against the uncertain frequency of pollinator visits. Continued nectar production would ensure that flowers received the maximum possible visitation on days unfavourable to pollinator activity. The same production pattern on more favourable days would not detract from pollen dispersal and would only bear negative consequences if production of extra nectar reduced resources available for other functions.

IS NECTAR PRODUCTION EXPENSIVE?

From the plant's perspective, the ecological and evolutionary consequences of producing more nectar than is necessary for pollen dispersal will depend on the accrued cost and the extent to which paying that cost competes with other demands on limited resources. *Pontederia cordata* expends rather little energy on nectar relative to the cost of producing each 1-day flower ($\approx 3\%$). In contrast, two studies of milkweeds (*Asclepias* spp.) have revealed large energy investments in nectar production. Pleasants & Chaplin (1983) reported that the nectar produced during the life of an *A. quadrifolia* flower represented about 30% of the energy devoted to a flower. Similarly, Southwick (1984) reported that about 33% of the photosynthate assimilated by *A. syriaca* plants during flowering was invested in nectar production. Because milkweed flowers bloom for several days (*A. quadrifolia*, 3–4 days, Pleasants & Chaplin 1983; *A. syriaca*, 3–5 days, Willson & Bertin 1979), nectar production represents a large proportion of the flowering costs for these species. Overall, this energy

expenditure accounted for 3–4% of a milkweed's energy budget during the entire growing season (Pleasants & Chaplin 1983; Southwick 1984).

To determine whether *Asclepias* or *Pontederia cordata* is more representative of bee-pollinated angiosperms, we compared the 'per flower' nectar production for 27 species, including *Pontederia cordata* and *A. syriaca* (Fig. 5). Because nectar production per flower generally varies inversely with the number of open flowers on an inflorescence (Harder & Cruzan 1990), we first regressed 12-h sugar production against inflorescence size for all species except *Pontederia cordata* and *A. syriaca*. We then used the calculated regression equation to estimate sugar production for species that produced as many flowers per day as *Pontederia cordata* and *A. syriaca*. Based on this analysis, a species that produces as many flowers per inflorescence per day as *A. syriaca* should produce 0.024 mg of sugar per flower (lower SE = 0.017 mg, upper SE = 0.035 mg; based on log-transformed data). Instead, this species produces 0.37 mg, a 15-fold excess difference. Clearly, *A. syriaca* produces considerably more nectar per flower than expected, probably because its intricate pollination mechanism (Macior 1965) requires long pollinator visits to promote pollinia removal and insertion. In contrast, *Pontederia cordata* produces an amount of nectar (mean±SE = 0.093±0.012 mg) only slightly greater than that expected for angiosperms with similar inflorescence sizes (0.051 mg, lower SE = 0.039 mg, upper SE = 0.067 mg; Fig. 5).

These results imply that nectar production represents a minor component of the energy expended on flowering for most bee-pollinated angiosperms. Indeed, the actual physiological cost of nectar production to a plant may be negligible as flowers are photosynthetically active (Bazzaz, Carlson & Harper 1979; Werk & Ehleringer 1983) and Williams, Koch & Mooney (1985) reported that *Diplacus aurantiacus* (Scrophulariaceae) flowers produce sufficient photosynthate to support autonomously their own nectar production. Such self-support of nectar production may explain the unresponsiveness of nectar production by *Polemonium folioissimum* (Polemoniaceae) to removal of 50% of a plant's leaves (Zimmerman & Pyke 1988). In contrast, similar experiments with *A. quadrifolia* (Pleasants & Chaplin 1983) resulted in a 31% reduction in nectar production. As long as nectar production has a small impact on the energy budgets of plants, seemingly extravagant patterns of nectar production could be sustained evolutionarily, especially if such patterns enable ancillary benefits, such as maintaining generalist pollinators or hedging against environmental uncertainty.

Our proposal that nectar production involves little net cost contradicts Pyke's (1991) recent demonstration that three-fold stimulation of nectar production significantly reduced seed production by *Blandfordia nobilis* (Liliaceae). Removal of nectar

from flowers of this species stimulates further production. Pyke liberally pollinated all flowers on both control and stimulated plants and counted subsequent seed production. Like most bird-pollinated plants, *Blandfordia nobilis* produces much more nectar per flower (mean±SE=23·3±2·6 mg for 4-day production by stimulated flowers) than bee-pollinated species (see Fig. 5; Cruden *et al.* 1983). As a result, nectar production may involve greater physiological costs for bird-pollinated species. Perhaps more importantly, Pyke reported that pollen receipt chronically limits seed production by *Blandfordia nobilis*, so that his saturation pollination of all flowers probably resulted in unusual demands for photosynthate by the fruit developing from initial flowers. The observed cost of nectar production is therefore a reasonable outcome, given that experimental plants experienced extra costs of both nectar production and seed production. Whether nectar production constitutes a cost for *Blandfordia nobilis* under natural pollination regimes remains to be demonstrated.

At the outset, we characterized nectar production as part of the cost of animal pollination. Production of large, showy flowers to attract pollinators may represent such a cost (although see Primack & Hall 1990) and nectar production is generally correlated with the allocation of resources to sexual reproduction (Spira 1980; Sutherland & Vickery 1988). However, our results suggest that nectar production represents a rather small cost of animal pollination, particularly if it is largely supported by floral photosynthesis. This conclusion contradicts Heinrich & Raven's (1972) suggestion that 'a flower must provide sufficient reward to attract foragers, but it must limit this reward so that the animals will go on to visit other plants of the same species' (p. 602).

Heinrich and Raven's upper limit on nectar production may have little evolutionary significance if Bell (1985) is correct in concluding that '. . . the flower is primarily a male organ, in the sense that the bulk of allocation to secondary floral structures is designed to procure the export of pollen . . .' (p. 223; see also Lloyd 1984). This perspective fosters an altered view of the evolution of nectar secretion rates. In particular, Harder & Thomson (1989) suggested that pollen export would be maximized if individual pollinators removed little pollen and plants instead used all available visitors to disperse pollen. Pollen removal generally increases with the duration of a visit (Harder & Thomson 1989; Harder 1990) and visit duration increases with a flower's nectar volume (Montgomerie 1984; Martinez del Rio & Eguiarte 1987; Cartar & Dill 1990). As a result, a plant's total pollen dispersal should be maximized if pollinators find little nectar in flowers, leading to short visits and restricted pollen removal. Hence, nectar production rates should be evolutionarily minimized as long as attractiveness to pollinators is

maintained. Such a process would lead to a small cost of nectar production.

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