Nectar Sugar Limits Larval Growth of Solitary Bees (Hymenoptera: Megachilidae)

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ABSTRACT The bottom-up effects of plant food quality and quantity can affect the growth, survival, and reproduction of herbivores. The larvae of solitary bee pollinators, consumers of nectar and pollen, are also herbivores. Although pollen quantity and quality are known to be important for larval growth, little is known about how nectar quality limits solitary bee performance. By adding different levels of nectar sugar directly to solitary bee provisions in the subalpine of Colorado, we tested the degree to which larval performance (development time, mass, and survival) was limited by nectar sugar. We found that larval growth increased with nectar sugar addition, with the highest larval mass in the high nectar-sugar addition treatment (50% honey solution). The shortest larval development time was observed in the low nectar-sugar addition treatment (25% honey solution). Neither low nor high nectar-sugar addition affected larval survival. This study suggests that, in addition to pollen, nectar-sugar concentration can limit solitary bee larval growth and development, and nectar should be considered more explicitly as a currency governing foraging decisions related to producing optimally sized offspring. The availability and sugar content of nectar may scale up to affect bee fitness, population dynamics, and plant–pollinator mutualisms.

KEY WORDS *Hoplitis*, *Megachile*, *Osmia*, pollinator performance, resource limitation

The quality and quantity of food resources are known to have dramatic effects on higher trophic levels, affecting individual performance, population size, and species interactions (Hunter and Price 1992, Bukovinszky et al. 2008). A wealth of studies have tested the bottom-up effects of food quality and quantity on foliar herbivores and secondary consumers (Stiling and Rossi 1997, Forkner and Hunter 2000, Stiling and Moon 2005), with foliage quality typically enhancing herbivore performance (reviewed in Awmack and Leather 2002). In particular, host plant quality has been shown to increase the growth, survival, and reproduction of insect herbivores (Mattson 1980, Scribner and Slansky 1981, Hemmi and Jormalainen 2002, Chen et al. 2004). Some pollinators are herbivores that limit their diet to nectar and pollen (Williams 2003, Praz et al. 2008). The effects of nectar and pollen quality on pollinator consumers, however, are not well understood. Pollen quality, in particular protein content, is important for bee colony growth and individual larval growth and development (McCaughey et al. 1980, Schmidt et al. 1987, Genissel et al. 2002, Roulston and Cane 2002); however, pollen quality is often difficult for pollinators to detect while foraging (Roulston et al. 2000, but see Robertson et al. 1999). A growing body of evidence indicates that some insect pollinators, such as honey bees and butterflies, prefer nectar with higher amino acid content, which may enhance their fecundity as adults (Alm et al. 1990, Mevi-Schutz and Erhardt 2005). Here, we used solitary bee pollinators that use nectar and pollen to provision their offspring to test how nectar sugar quality affected larval performance.

Solitary bees vary in growth and reproduction based on resource availability. For example, adult solitary bees vary in body size, which is influenced by their larval pollen provision size and can vary seasonally with floral nectar and pollen resources (Kim and Thorp 2001). Subsequently, larger adult female solitary bees produce more and larger eggs than smaller females (Tengo and Baur 1993, Kim 1997). In addition, when available floral resources are enhanced, for example, through potted flowering plants in flight cages, brood cell production rate can increase (Goodell 2003). Moreover, more and heavier *Megachile apicalis* offspring are produced when floral resources are increased (Kim 1999). Larger offspring often have higher survival and fecundity through territory defense, nest usurpation and mating opportunities (Tepedino and Torchio 1994, Alcock 1995, Kim 1997, Roulston and Cane 2002, but see Bosch and Vicens 2006).

Variation in nectar resources across the landscape is common (Zimmerman 1981, Marden 1984, Rathcke 1992), and solitary bees can detect nectar-rewarding flowers based on visual and olfactory cues (Nuttman et al. 2006, Howell and Alarcon 2007). For example,

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invasive plant species can drive variation in nectar, in some cases increasing its availability at the landscape level (Chittka and Schürkens 2001, Schürkens and Chittka 2001, Brown et al. 2002, Ghazoul 2002). Abiotic environmental conditions, such as soil nutrient enrichment, can also affect the quality and quantity of floral rewards and patterns of pollinator visitation (Campbell and Halama 1993, Munoz et al. 2005, Burkle 2008). In particular, nutrient enrichment can increase the amino acid and sugar concentrations of nectar (Petanidou et al. 1999, Gardener and Gillman 2001), suggesting pathways by which soil nutrients could scale up to affect solitary bee larval performance.

Here, by adding nectar sugar to solitary bee larval provisions, we tested the degree to which larval performance was nectar limited. This study was conducted in the subalpine of western North America, where nectar may limit the abundance and reproduction of bumble bees (Bowers 1985) and hummingbirds (Montgomerie and Gass 1981) in some years. We focused on testing nectar-sugar limitation of larval performance in solitary bees in the Megachilidae because they are common floral visitors in the subalpine and other systems (Eickwort et al. 1996, Price and Waser 1998, Blionis and Vokou 2001, Alston et al. 2007). Moreover, solitary bees are commonly used in feeding trials, and some species are affected by pollen quantity and quality at the larval stage (Williams 2003, Praz et al. 2008). This study provides insight to the potential for nectar sugar limitation of solitary bee survival, growth, and reproduction, an important topic given the significance of solitary bees as pollinators and of the threatened status of some bee pollinators worldwide (NRC 2007, Williams and Kremen 2007).

Materials and Methods

Study System

This study was conducted in the summer of 2007 near the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Gunnison County, CO (elevation, 2,900 m). This area is characterized by large, open subalpine meadows dominated by wildflowers and bordered by aspen-fir forests. In the meadows surrounding the RMBL, solitary bees make up 25% of pollinator visits to wildflowers (Burkle 2008). We focused on bees in the genera *Megachile, Hoplitis,* and *Osmia* (Hymenoptera: Megachilidae). These mason and leafcutter bees lay a single egg on each provision of pollen and nectar and use a variety of materials, including mud, leaf material, and pebbles, to partition their offspring (Michener 2000). Only 12% of nesting tubes contained provisions with a single pollen species (mean pollen species richness ± SE = 2.70 ± 0.07; range 1–8; $N = 297$ artificial nesting tubes sampled in 2004; L.A.B., unpublished data). The mass of provisions ranges from 26.8 to 420.4 mg (mean ± SE = 171.9 ± 2.7 mg; $N = 462$ provisions; this study). Larvae in the genera *Megachile, Hoplitis,* and *Osmia* typically have five larval instars and reach pupation in 3 wk (Torchio 1989). Around the RMBL, adults provision a mean ± SE of 5.69 ± 0.23 offspring per completed nesting tube (2004, $N = 256$ artificial nesting tubes; L.A.B., unpublished data). Female eggs are typically provisioned on larger pollen provisions at the back of the tube, whereas males are provisioned on smaller pollen provisions near the tube opening (Torchio 1989).

Field and Laboratory Methods

Nesting Blocks. We used 30 solitary bee pine nesting blocks (20 by 18 by 4 cm), each with 20 evenly spaced 1.25 cm diameter holes, 15 cm deep. We lined each hole with cardboard guard tubes and paper liners (Knox Cellars, Bellingham, WA) and placed all nesting blocks in the field on or near existing dead wood (e.g., fallen trees, old wooden structures). Female solitary bees naturally provisioned their offspring in the nesting blocks throughout the summer. Filled or partially filled tubes were removed from the nesting blocks every 4–7 d and brought into the laboratory.

In this study, we were unable to successfully rear the majority of offspring to adults in the laboratory; thus, we could not identify larvae to species. Instead, our understanding of taxonomic distinctions was restricted to nesting habits. For all tubes, we recorded nesting material (leaves, mud, and/or pebbles) and construction (single divisions of leaves, mud, or pebbles between cells, entire provision and egg wrapped in leaves). Hereafter, we refer to nesting material and construction as nesting habit. This nesting habit information, along with accompanying differences in provision size, allowed us to differentiate two categories of bees: larger provisions partitioned with walls of leaves, mud, and/or pebbles (in the genera *Megachile, Hoplitis,* and *Osmia*) and smaller provisions enclosed with the egg wrapped inside a cylinder constructed of leaf pieces (in the genus *Megachile;* Michener 2000). Based on recent collections of Megachilidae around the RMBL, *Hoplitis* is represented by at least 3 species, *Megachile* by at least 7 species, and *Osmia* by at least 15 species (*Appendix 1*).

Each egg or larva, along with its provision, was transferred to a plastic well (cryogenic tube 10 mm wide cut to a height of 12 mm; Perfector Scientific Cryo-Store, Atascadero, CA) and weighed to the nearest 0.01 mg. Larvae that were seen visually feeding on their provision were excluded from the study. Whether the larvae were females or males was assessed by their location within the tube and their relative provision size by weight. To ensure that there were no systematic biases in pollen species among nectar treatments (described below), two small pollen samples from each provision were stained in basic fuchsin (Kearns and Inouye 1993) and identified to species under a compound microscope using a pollen reference collection. The entire slide was scanned, one representative field of view was chosen randomly, and the proportion of each pollen species was determined. We assigned nectar treatments across pollen species to eliminate systematic biases.

Nectar Treatments. The eggs or larvae were randomly assigned to one of four treatments: control (no addition), water addition (10 μl), low nectar-sugar addition (10 μl of 25% honey water), or high nectar-sugar addition (10 μl of 50% honey water). The water addition treatment controlled for any effects associated with additional moisture addition. We added 10 μl of liquid because it is the volume roughly equivalent to the amount of nectar that could be collected from 100 flowers in this system (Waser 1978, Zimmerman 1986). Honey water concentrations of 25 and 50% were chosen to reflect low and high nectar-sugar concentrations of flowers commonly found in the field, respectively (Waser 1978, Pleasants 1983). Although we used offspring with provisions of different sizes, we maintained equal volumes of nectar in treatments, and we addressed potential interactions between provision size or nesting habit and nectar treatment statistically (see Predictions and Data Analyses). We used local, high elevation Colorado honey (Ambrosia Honey, Parachute, CO) for the honey water solutions. We added honey water, rather than sugar water, to bee provisions to provide a food containing other natural nectar components (Baker 1977); hereafter, we refer to the low and high honey-water solutions as nectar sugar. We assumed that each nesting tube was provisioned by one adult female solitary bee (Tepedino and Torchio 1982); thus, when possible, we divided nectar treatments within sex within each tube to control for maternal effects. However, there were only 4.81 ± 0.33 (SE) eggs and/or nonfeeding larval offspring per nesting tube present at the time of collection ($N = 96$ artificial nesting tubes). Therefore, there were typically not enough eggs and/or nonfeeding larvae to block nectar treatment by tube in the statistical analyses (see below); we would have needed four females and four males per tube. All nectar treatments were added to the provisions with an Eppendorf pipetter (Hamburg, Germany) before larvae began feeding. For the larvae wrapped in leaf cylinders, we temporarily removed the leaf cap at the top of the cylinder, delivered the nectar treatment onto the provision, and replaced the leaf cap. We treated a total of 450 larvae, with 113 control, 117 water addition, 110 low nectar-sugar addition, and 110 high nectar-sugar addition larvae.

Larval Performance. We estimated larval performance as larval development time, larval mass just before pupation (wet and dry mass), and survival. All offspring were allowed to develop in a dark growth room at 21–25°C. We monitored the larvae daily and measured their larval development time as the duration between the date of first feeding to the date of initial cocoon spinning. For bees that encased their provisions in leaves, we were not able to observe the spinning date and did not measure their development time. After 5 mo of simulated winter diapause at 4°C, we measured larval survival and the wet mass (to the nearest 0.0001 mg) of larvae that survived. Larvae were dried at 20°C and reweighed for dry mass.

Predictions and Data Analyses. We predicted that nectar-sugar addition would reduce larval development time by providing access to energy-rich food, as has been shown in other Hymenoptera, such as Ichneumonid wasps (Winkler et al. 2006), and would increase larval mass and the probability of survival relative to the control treatment (Haggstrom and Larsson 1995). We also predicted that high nectar-sugar addition would have the greatest benefits on larval performance and low nectar-sugar addition would have intermediate benefits relative to the control. Finally, we expected that there would be no difference in bee performance between the control and the water addition treatments, assuming that liquid addition has no effect on larval performance.

We tested the effects of nectar treatment and nesting habit on larval development time and larval mass with initial provision mass included as a covariate using planned linear contrasts. We used a separate linear contrast for larval development time and larval mass. The planned linear contrasts allowed us to partition the analysis of covariance (ANCOVA) sum of squares to test our prediction that the high nectar-sugar addition would produce the greatest effects on measures of larval performance and the low nectar-sugar addition would produce intermediate effects, relative to both the control and water addition treatments. Each planned linear contrast also tested our prediction that larval performance would not differ between the control and water addition treatments. We included provision mass as a covariate in these analyses, instead of estimates of larval sex, because provision mass was measured with certainty and should be correlated with larval sex (with female provisions being larger than male provisions; Torchio 1989). To test the effects of nectar treatment on larval survival, we used multiple logistic regression with initial provision mass and nesting habit as covariates. We used a separate test for each component of bee performance because development time could not be recorded for all larvae (see Larval Performance), and mortality during development removed some larvae ($N = 82$ individuals) from the analyses. We tested for interactions between nesting habit or provision size and nectar treatment in each analysis because we expected an interaction based on the relative amount of sugar added to provisions of different sizes; however, we found no significant interactions ($P > 0.05$ in all cases), suggesting that nectar treatment had similar effects on bees across provision sizes and nesting habits. Therefore, we report the results without interaction terms in the models. In addition, because we collected offspring throughout the summer, there may have been interactions between the date that a tube was filled and larval development time or between date and nectar treatment; we tested for these interactions and again found no significant interactions ($P > 0.05$ in all cases). Thus, we did not include interactions with date in the models. The planned linear contrasts and logistic regressions were conducted using JMP 4.0. We report least squared means because of unbalanced sample sizes among nectar treatments.

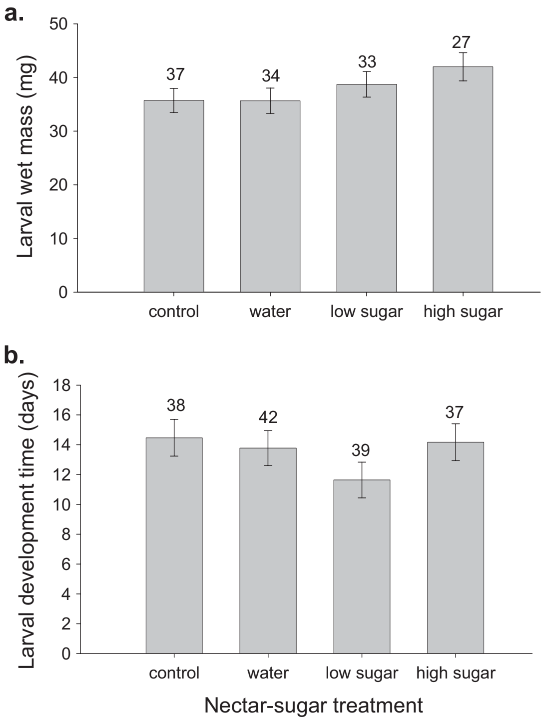

Fig. 1. (a) Larval wet mass increased with nectar-sugar addition, but (b) low nectar-sugar addition resulted in a decrease in development time. Error bars are ±SE for least-squared means. Sample sizes for each treatment are indicated above the error bars.

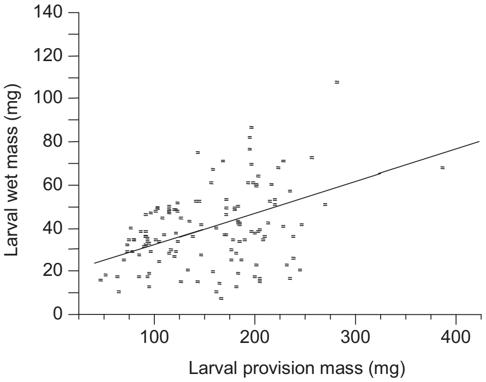

Fig. 2. The effects of provision mass on larval wet mass across all nectar treatments and all species. Larval mass = 17.3 + 0.15 × provision mass.

Results

Nectar treatment affected components of larval performance. Larval wet mass increased with nectar-sugar addition (Fig. 1a; $F = 4.37$; df = 1,125; $P = 0.039$), with 18% larger larvae in the high nectar-sugar addition treatment compared with the control. Larval dry mass showed the same positive pattern with nectar-sugar addition (F = 5.50; df = 1,125; P = 0.021). Contrary to our prediction, larval development time did not decrease with nectar-sugar addition (Fig. 1b; $F = 0.42$; df = 1,150; $P = 0.52$). Instead, we found that larvae developed 24% faster in the low nectar-sugar addition treatment compared with the control. Larval survival was not affected by nectar-sugar treatments ($\chi^2 = 1.32$; $P = 0.72$). Overall, survival to the final larval instar was 35% in the control treatment (N = 40 individuals), 34% in the low nectar addition treatment ($N = 37$ individuals), 31% in the water treatment (N = 36 individuals), and 29% in the high nectar addition treatment (N = 32 individuals).

In general, across nectar treatments, provision mass positively affected larval mass (Fig. 2; $r^2 = 0.23$; $N = 131$; $P < 0.0001$) but not larval development time ($r^2 = 0.015$; N = 156; P = 0.13). In addition, larval wet mass (t = 3.2; df = 129; P = 0.0016), dry mass (t = 11.08; df = 129; $P = 0.0011$), development time ($t = 4.8$; df = 154; $P < 0.0001$), and survival (χ^2 = 51.7; $P < 0.0001$) differed between the two nesting habits (Table 1). Larval wet and dry mass were 32 and 34% greater, respectively, for larvae with mud and leaf partitions compared with wrapped in leaf cylinders. Moreover, development time was 59% longer and survival was 32% higher for larvae with mud and leaf partitions compared with wrapped in leaf cylinders (Table 1). Both provision mass and nesting habit explained a significant amount of the variance in larval mass and development time in all contrasts ($P < 0.0003$ in all cases). Nesting habit explained a significant amount of the variance in survival (χ^2 = 44.93, N = 450, $P <$ 0.0001), whereas provision mass did not (χ^2 = 0.91, N = 450, P = 0.34).

Discussion

The performance of herbivores can be strongly affected by the quality and quantity of plant food resources (Awmack and Leather 2002). Such bottom-up effects can scale up through ecological communities, influencing the abundance of individuals and species interactions (Hunter and Price 1992, Bukovinszky et al. 2008). Pollinators, such as solitary bees, are herbivores, feeding on nectar and pollen, and their preference and performance as adults may be affected by the quality and quantity of floral resources they received as larvae. Pollen is known to be important for solitary bee larval growth (Roulston and Cane 2002, Williams 2003), and although solitary bee adults and larvae

Table 1. Means ± SE of larval wet and dry mass, development time, and survival of solitary bee larvae between two nesting habits: mud and leaf partitions or provisions and larvae wrapped in leaves

	Nesting habit	
	Mud and leaves	Wrapped in leaves
Larval wet mass (mg)	44.7 ± 2.1 (81)	33.9 ± 2.6 (50)
Larval dry mass (mg)	21.7 ± 1.1 (81)	16.2 ± 1.0 (50)
Development time (d)	16.8 ± 0.8 (96)	10.6 ± 1.0 (60)
Survival (%)	51.4% (94)	19.1% (51)

Sample size for each treatment is given in parentheses.

consume nectar, little is known about the degree to which nectar quality limits larval growth. By adding simulated nectar solutions (i.e., honey water) with different sugar concentrations to provisions, we tested nectar-sugar limitation of larval performance. Larval mass increased with nectar-sugar concentration, a signal evident after controlling for provision size and nesting habit. In addition, larvae receiving intermediate levels of nectar sugar showed the fastest development times. Thus, in addition to pollen, nectar can also limit solitary bee larval growth, and nectar quality and availability may have important implications for plant–pollinator mutualisms.

Nectar-sugar addition had a positive effect on larval mass, an effect that may subsequently increase adult mass and fecundity (Roulston and Cane 2002). In their preference for nectar with a high sugar concentration during foraging (Waller 1972, Bolten and Feinsinger 1978, Corbet 1978), bees may benefit their larval offspring through this selective foraging. Although some female solitary bees can alter the sugar concentration of nectar they collect through dehydration (Wittmann and Scholz 1989), given competition for floral rewards and time constraints, it may be more energetically profitable for adult bees to forage on concentrated nectar (Heinrich 1975, Roubik and Buchmann 1984). Thus, through adult foraging preferences, plant species that produce nectar with higher sugar concentration may disproportionately contribute to the growth of solitary bee offspring. Interestingly, high nectar-sugar addition did not decrease larval development time; larvae in the low nectar-sugar addition treatment had the shortest development times (measured as the amount of time from first larval feeding to cocoon spinning). It was surprising that low nectar-sugar addition reduced larval development time but that high nectar-sugar addition did not. One potential explanation for this result is that larvae in the high nectar-sugar addition treatment exhibited an extended feeding, growing, and development period. Thus, it is possible that at high nectar-sugar levels, the energy provided by the additional sugar was allocated to growth, whereas at low nectar-sugar addition levels, the energy may not have been enough to substantially increase body mass and was instead allocated to a rapid development time (Chown and Nicolson 2004). More detailed observations of larval development and additional experiments manipulating nectar sugar across more nectar-sugar levels are needed to assess the validity of this explanation.

Three caveats are important in the interpretation of the results. First, larvae were reared in a controlled laboratory setting in the absence of predation and parasitism, such as by birds, parasitic bees, or other parasites (Munster-Swendsen and Calabuig 2000, Goodell 2003, Wcislo et al. 2004). In the field, faster development time may decrease the amount of time larvae are vulnerable to predation and parasitism, possibly enhancing their survival. For example, faster-growing leaf beetles have been shown to have higher survival in the presence of predation relative to slower-growing leaf beetles (Haggstrom and Larsson 1995). Thus, rearing larvae in the field under different nectar-sugar diets may show indirect effects of nectar addition on larval growth and survival through changes in parasitism and predation, providing a more complete understanding of the effects of nectar on solitary bee performance. The second caveat is that the identity of solitary bee species was not determined in this study. Thus, the exact nature of species-specific differences in performance remains unknown. Independent of nectar treatments, provision mass, and nesting habit often influenced larval performance measures, reinforcing the importance of pollen availability for solitary bee reproduction and the possibility of species-specific differences in performance and life-history characters. Mud and leaf nesters (Megachile, Hoplitis, and Osmia) were larger, took longer to develop, and had higher survival than those that constructed a leaf cylinder to envelop each offspring (Megachile). The lack of interaction between nesting habit or provision size and nectar treatment may indicate that the metabolic rates of smaller versus larger bees differ as well, with smaller bees having higher metabolic rates (Bosch and Vicens 2002) and burning more of the added nectar-sugar during growth and development compared with larger bees. It is also possible that there are physiological restrictions to maximum larval growth rate such that bees, irrespective of their size, could not respond to increased nectar sugar after an initial increase in growth. Third, our nectar treatment involved the addition of honey water, so we cannot fully determine that the effect we observed was caused by sugar only or some other honey component. However, given that honey is composed primarily of sugar, it is likely that the main effects we observed occurred through the sugar addition.

This study is in agreement with work showing that nectar sugar is important to solitary bees and other pollinators. Honey bees select inflorescences that provide them with more nectar sugar (Higginson et al. 2006) and can change their foraging behavior to maximize their rate of nectar sugar (energy) intake (Dedej and Delaplane 2005). The overwintering survival of honey bee colonies can depend on the size of their honey reserves (Seeley and Visscher 1985). Furthermore, honey bee colonies foraging in the field in an area of sparse floral resources that were also provided with a daily concentrated sugar solution had higher drone production compared with unfed colonies, indicating that energy is a limiting resource for some aspects of colony reproduction (Seeley and Mikheyev 2003). The growth, survival, and reproduction of bumble bee colonies are also likely limited by the rate of energy gain (Bowers 1985). One recent study has shown that nectar addition can increase larval performance of *Osmia lignaria* (Elliott et al. 2008). Nectar resources and their quality may be more important for the growth and reproduction of individuals and populations than previously appreciated.

Investigating which factors limit the growth and reproduction of species is fundamental to understanding their distribution and species interactions and becomes more important when species, or the ecosystem services they provide, are threatened (Kremen et al. 2007). Solitary bees and other pollinators may be declining worldwide (NRC 2007); yet, many basic aspects of solitary bee natural history are unknown. In particular, the main factors limiting the reproductive success of solitary bees and their relative importance are not fully understood (Morato and Martins 2006) but likely include nest sites and materials as well as food resources (Gathmann and Tscharntke 2002, Steffan-Dewenter and Schiele 2008). Only recently have ecologists begun to study the influence of floral rewards on solitary bee reproduction and not just foraging patterns in the field (Kim 1999, Kim and Thorp 2001, Goodell 2003). Here, we conclude that nectar-sugar resources, in addition to pollen, are important for larval growth and development of solitary bees. Explicit consideration of nectar as a food currency influencing bee foraging decisions will improve our understanding of production of optimally sized offspring. Although the magnitude of effect of nectar sugar on bee body size increase is likely more limited compared with pollen, it is noteworthy that the signature of nectar sugar alone is evident. Further work is necessary to determine how nectar quality and availability in the field influence larval performance and how these factors may scale up to affect adult bee fitness, bee abundance, and plant–pollinator mutualisms. Including the effects of floral rewards on pollinator reproduction can provide a more comprehensive understanding of how environmental change may affect species, their interactions, and the ecosystem services they provide.

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References Cited

Alcock, J. 1995. Persistent size variation in the anthophorine bee *Centris pallida* (Apidae) despite a large male mating advantage. Ecol. Entomol. 20: 1–4.

Alm, J., T. E. Ohnmeiss, J. Lanza, and L. Vriesenga. 1990. Preference of cabbage white butterflies and honey bees for nectar that contains amino acids. Oecologia (Berl.) 84: 53–57.

Alston, D. G., V. J. Tepedino, B. A. Bradley, T. R. Toler, T. L. Griswold, and S. M. Messinger. 2007. Effects of the insecticide phosmet on solitary bee foraging and nesting in orchards of Capitol Reef National Park, Utah. Environ. Entomol. 36: 811–816.

Awmack, C. S., and S. R. Leather. 2002. Host plant quality and fecundity in herbivorous insects. Annu. Rev. Entomol. 47: 817–844.

Baker, H. G. 1977. Non-sugar chemical consituents of nectar. Apidologie 8: 349–356.

Blionis, G. J., and D. Vokou. 2001. Pollination ecology of Campanula species on Mt Olympos, Greece. Ecography 24: 287–297.

Bolten, A. B., and P. Feinsinger. 1978. Why do hummingbird flowers secrete dilute nectar. Biotropica 10: 307–309.

Bosch, J., and N. Vicens. 2002. Body size as an estimator of production costs in a solitary bee. Ecol. Entomol. 27: 129–137.

Bosch, J., and N. Vicens. 2006. Relationship between body size, provisioning rate, longevity and reproductive success in females of the solitary bee *Osmia cornuta.* Behav. Ecol. Sociobiol. 60: 26–33.

Bowers, M. A. 1985. Bumble bee colonization, extinction, and reproduction in subalpine meadows in northeastern Utah. Ecology 66: 914–927.

Brown, B. J., R. J. Mitchell, and S. A. Graham. 2002. Competition for pollination between an invasive species and a native congener. Ecology 83: 2328–2336.

Bukovinszky, T., F.J.F. van Veen, Y. Jongema, and M. Dicke. 2008. Direct and indirect effects of resource quality on food web structure. Science 319: 804–807.

Burkle, L. A. 2008. Bottom-up effects of nutrient enrichment on plants, pollinators, and their interactions. PhD dissertation, Dartmouth College, Hanover, NH.

Campbell, D. R., and K. J. Halama. 1993. Resource and pollen limitations to lifetime seed production in a natural plant population. Ecology 74: 1043–1051.

Chen, Y. Z., L. Lin, C. W. Wang, C. C. Yeh, and S. Y. Hwang. 2004. Response of two *Pieris* (Lepidoptera: Pieridae) species to fertilization of a host plant. Zool. Stud. 43: 778–786.

Chittka, L., and S. Schürkens. 2001. Successful invasion of a floral market. Nature (Lond.) 411: 653.

Chown, S. L., and S. W. Nicolson. 2004. Insect physiological ecology: mechanisms and patterns. Oxford University Press, Oxford, United Kingdom.

Corbet, S. A. 1978. A bee's view of nectar. Bee World 59: 25–32.

Dedej, S., and K. Delaplane. 2005. Net energetic advantage drives honey bees (*Apis mellifera* L) to nectar larceny in *Vaccinium ashei* Reade. Behav. Ecol. Sociobiol. 57: 398–403.

Eickwort, G. C., J. M. Eickwort, J. Gordon, and M. A. Eickwort. 1996. Solitary behavior in a high altitude population of the social sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). Behav. Ecol. Sociobiol. 38: 227–233.

Elliott, S. E., R. E. Irwin, L. S. Adler, and N. M. Williams. 2008. The nectar alkaloid, gelsemine, does not affect offspring performance of a native solitary bee, *Osmia lignaria* (Megachilidae). Ecol. Entomol. 33: 298–304.

Forkner, R. E., and M. D. Hunter. 2000. What goes up must come down? Nutrient addition and predation pressure on oak herbivores. Ecology 81: 1588–1600.

Gardener, M. C., and M. P. Gillman. 2001. The effects of soil fertilizer on amino acids in the floral nectar of corncockle, *Agrostemma githago* (Caryophyllaceae). Oikos 92: 101–106.

Gathmann, A., and T. Tscharntke. 2002. Foraging ranges of solitary bees. J. Anim. Ecol. 71: 757–764.

Genissel, A., P. Aupinel, C. Bressac, J.-N. Tasei, and C. Chevrier. 2002. Influence of pollen origin on performance of *Bombus terrestris* micro-colonies. Entomol. Exp. Appl. 104: 329–336.

Ghazoul, J. 2002. Flowers at the front line of invasion? Ecol. Entomol. 27: 638–640.

Goodell, K. 2003. Food availability affects *Osmia pumila* (Hymenoptera: Megachilidae) foraging, reproduction, and brood parasitism. Oecologia (Berl.) 134: 518–527.

Haggstrom, H., and S. Larsson. 1995. Slow larval growth on a suboptimal willow results in high predation mortality in the leaf beetle *Galerucella lineola.* Oecologia (Berl.) 104: 308–315.

Heinrich, B. 1975. Energetics of pollination. Annu. Rev. Ecol. Syst. 6: 139–170.

Hemmi, A., and V. Jormalainen. 2002. Nutrient enhancement increases performance of a marine herbivore via quality of its food alga. Ecology 83: 1052–1064.

Higginson, A. D., F. S. Gilbert, and C. J. Barnard. 2006. Morphological correlates of nectar production used by honeybees. Ecol. Entomol. 31: 269–276.

Howell, A. D., and R. Alarcon. 2007. *Osmia* bees (Hymenoptera: Megachilidae) can detect nectar-rewarding flowers using olfactory cues. Anim. Behav. 74: 199–205.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73: 724–732.

SAS Institute. 2001. JMP, version 4.0. SAS Institute, Cary, NC.

Kearns, C. A., and D. W. Inouye. 1993. Techniques for pollination biologists. University Press of Colorado, Boulder, CO.

Kim, J. Y. 1997. Female size and fitness in the leaf-cutter bee *Megachile apicalis.* Ecol. Entomol. 22: 275–282.

Kim, J. Y. 1999. Influence of resource level on maternal investment in a leaf-cutter bee (Hymenoptera: Megachilidae). Behav. Ecol. 10: 552–556.

Kim, J. Y., and R. W. Thorp. 2001. Maternal investment and size-number trade-off in a bee, *Megachile apicalis,* in seasonal environments. Oecologia (Berl.) 126: 451–456.

Kremen, C., N. M. Williams, M. A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, L. Packer, S. G. Potts, T. Roulston, I. Steffan-Dewenter, et al. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecol. Lett. 10: 299–314.

Marden, J. H. 1984. Intrapopulation variation in nectar secretion in *Impatiens capensis.* Oecologia (Berl.) 63: 418–422.

Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. Annu. Rev. Ecol. Syst. 11: 119–161.

McCaughey, W. F., M. Gilliam, and L. N. Standifer. 1980. Amino acids and protein adequacy for honey bees of pollens from desert plants and other floral sources. Apidologie 11: 75–86.

Mevi-Schutz, J., and A. Erhardt. 2005. Amino acids in nectar enhance butterfly fecundity: a long-awaited link. Am. Nat. 165: 411–419.

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

Montgomerie, R. D., and C. L. Gass. 1981. Energy limitation of hummingbird populations in tropical and temperate communities. Oecologia (Berl.) 50: 162–165.

Morato, E. F., and R. P. Martins. 2006. An overview of the proximate factors affecting the nesting behavior of solitary wasps and bees (Hymenoptera: Aculeata) in preexisting cavities in wood. Neotrop. Entomol. 35: 285–298.

Munoz, A., C. Celedon-Neghme, L. Cavieres, and M. Arroyo. 2005. Bottom-up effects of nutrient availability on flower production, pollinator visitation, and seed output in a high-Andean shrub. Oecologia (Berl.) 143: 126–135.

Munster-Swendsen, M., and I. Calabuig. 2000. Interaction between the solitary bee *Chelostoma florisomne* and its nest parasite *Sapyga clavicornis*— empty cells reduce the impact of parasites. Ecol. Entomol. 25: 63–70.

[NRC] National Research Council. 2007. Status of pollinators in North America. National Academies Press, Washington, DC.

Nuttman, C. V., F. M. Semida, S. Zalat, and P. G. Willmer. 2006. Visual cues and foraging choices: bee visits to floral colour phases in *Alkanna orientalis* (Boraginaceae). Biol. J. Linn. Soc. 87: 427–435.

O'Toole, C., and A. Raw. 1991. Bees of the world. Blanford Press, London, United Kingdom.

Petanidou, T., V. Goethals, and E. Smets. 1999. The effect of nutrient and water availability on nectar secretion and nectar structure of the dominant *Labiatae* species of Phrygana. Syst. Geog. Plants 68: 233–244.

Pleasants, J. M. 1983. Nectar production patterns in *Ipomopsis aggregata* (Polemoniaceae). Am. J. Bot. 70: 1468–1475.

Praz, C. J., A. Muller, and S. Dorn. 2008. Specialized bees fail to develop on non-host pollen: do plants chemically protect their pollen? Ecology 89: 795–804.

Price, M. V., and N. M. Waser. 1998. Effects of experimental warming on plant reproductive phenology in a subalpine meadow. Ecology 79: 1261–1271.

Rathcke, B. J. 1992. Nectar distribution, pollinator behavior, and plant reproductive success. *In* M. D. Hunter, I. Ohgushi, and P. W. Price (eds.), Effects of resource distribution on plant-animal interactions. Academic, New York.

Robertson, A., C. Mountjoy, B. Faulkner, M. Roberts, and M. Macnair. 1999. Bumble bee selection of *Mimulus guttatus* flowers: the effects of pollen quality and reward depletion. Ecology 80: 2594–2606.

Roubik, D. W., and S. L. Buchmann. 1984. Nectar selection by *Melipona* and *Apis mellifera* (Hymenoptera: Apidae) and the ecology of nectar intake by bee colonies in a tropical forest. Oecologia (Berl.) 61: 1–10.

Roulston, T. H., and J. H. Cane. 2002. The effect of pollen protein concentration on body size in the sweat bee *Lasioglossum zephyrum* (Hymenoptera: Apiformes). Evol. Ecol. 16: 49–65.

Roulston, T. H., J. H. Cane, and S. L. Buchmann. 2000. What governs the protein content of pollen grains: pollinator preferences, pollen-pistil interactions, or phylogeny? Ecol. Monogr. 70: 617–643.

Schmidt, J. O., S. C. Thoenes, and M. D. Levin. 1987. Survival of honey bees, *Apis mellifera* (Hymenoptera: Apidae), fed various pollen sources. Ann. Entomol. Soc. Am. 80: 176–183.

Schürkens, S., and L. Chittka. 2001. The significance of the invasive crucifer species *Bunias orientalis* (Brassicaceae) as a nectar source for central European insects. Entomol. Gen. 25: 115–120.

Scribner, J. M., and F. Slansky. 1981. The nutritional ecology of immature insects. Annu. Rev. Entomol. 26: 183–221.

Seeley, T. D., and P. K. Visscher. 1985. Survival of honey bees in cold climates: the critical timing of colony growth and reproduction. Ecol. Entomol. 10: 81–88.

Seeley, T. D., and A. S. Mikheyev. 2003. Reproductive decisions by honey bee colonies: tuning investment in male production in relation to success in energy acquisition. Insect. Soc. 50: 134–138.

Steffan-Dewenter, I., and S. Schiele. 2008. Do resources or natural enemies drive bee population dynamics in fragmented habitats? Ecology 89: 1375–1387.

Stiling, P., and A. M. Rossi. 1997. Experimental manipulations of top-down and bottom-up factors in a tri-trophic system. Ecology 78: 1602–1606.

Stiling, P., and D. C. Moon. 2005. Quality or quantity: the direct and indirect effects of host plants on herbivores and their natural enemies. Oecologia (Berl.) 142: 413–420.

Tengo, J., and B. Baur. 1993. Number and size of oocytes in relation to body size and time of day in the kleptoparasitic bee *Nomada lathburiana* (Hymenoptera: Anthophoridae). Entomol. Gen. 18: 19–24.

Tepedino, V. J., and P. F. Torchio. 1982. Phenotypic variability in nesting success among *Osmia lignaria propinqua* females in a glasshouse environment (Hymenoptera: Megachilidae). Ecol. Entomol. 7: 453–462.

Tepedino, V. J., and P. F. Torchio. 1994. Founding and usurping: Equally efficient paths to nesting success in *Osmia lignaria propinqua* (Hymenoptera: Megachilidae). Ann. Entomol. Soc. Am. 87: 946–953.

Torchio, P. F. 1989. In-nest biologies and development of immature stages of three *Osmia* species (Hymenoptera: Megachilidae). Ann. Entomol. Soc. Am. 82: 599–615.

Waller, G. D. 1972. Evaluating responses of honey bees to sugar solutions using an artificial flower feeder. Ann. Entom. Soc. Am. 65: 857–862.

Waser, N. M. 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. Ecology 59: 934–944.

Wcislo, W. T., L. Arneson, K. Roesch, V. Gonzalez, A. Smith, and H. Fernandez. 2004. The evolution of nocturnal behaviour in sweat bees, Megalopta genalis and *M. ecuadoria* (Hymenoptera: Halictidae): an escape from competitors and enemies? Biol. J. Linn. Soc. 83: 377–387.

Williams, N. M. 2003. Use of novel pollen species by specialist and generalist solitary bees (Hymenoptera: Megachilidae). Oecologia (Berl.) 134: 228–237.

Williams, N. M., and C. Kremen. 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. Ecol. Appl. 17: 910–921.

Winkler, K., F. Wackers, G. Bukovinszkine-Kiss, and J. van Lenteren. 2006. Sugar resources are vital for *Diadegma semiclausum* fecundity under field conditions. Basic Appl. Ecol. 7: 133–140.

Wittmann, D., and E. Scholz. 1989. Nectar dehydration by male carpenter bees as preparation for mating flights. Behav. Ecol. Sociobiol. 25: 387–391.

Zimmerman, M. 1981. Patchiness in the dispersion of nectar resources—probable causes. Oecologia (Berl.) 49: 154–157.

Zimmerman, M. 1986. Reproduction in *Polemonium:* patterns and implications of floral nectar production and standing crops. Am. J. Bot. 73: 1405–1415.

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Appendix

List of species in the Megachilidae in three genera, *Hoplitis, Megachile,* and *Osmia*, potentially used in this study and found around the Rocky Mountain Biological Laboratory, CO (R.E.I., unpublished data). Bees in the genus *Hoplitis* are known to create nest partitions from leaves and pebbles, *Megachile* from mud, leaves, and leaf cylinders, and *Osmia* from mud, leaves, and pebbles (O'Toole and Raw 1991, Michener 2000).

Hoplitis albifrons argentifrons
Hoplitis fulgita fulgita
Hoplitis robusta
Megachile frigida
Megachile inermis
Megachile melanophaea
Megachile montivaga
Megachile perihirta
Megachile pugnata
Megachile relativa
Osmia albolateralis
Osmia bucephala
Osmia coloradensis
Osmia ednae
Osmia giliarum
Osmia grindeliae
Osmia longula
Osmia montana montana
Osmia nanula
Osmia nigrifrons
Osmia paradisica
Osmia penstemonis
Osmia proxima
Osmia subaustralis
Osmia tristella