

Selim Dedej · Keith S. Delaplane

## Net energetic advantage drives honey bees (*Apis mellifera* L) to nectar larceny in *Vaccinium ashei* Reade

Received: 30 March 2004 / Revised: 3 August 2004 / Accepted: 5 September 2004 / Published online: 6 November 2004  
© Springer-Verlag 2004

**Abstract** Carpenter bees (*Xylocopa* spp.) act as primary nectar thieves in rabbiteye blueberry (*Vaccinium ashei* Reade), piercing corollas laterally to imbibe nectar at basal nectaries. Honey bees (*Apis mellifera* L) learn to visit these perforations and thus become secondary nectar thieves. We tested the hypothesis that honey bees make this behavioral switch in response to an energetic advantage realized by nectar-robbing flower visits. Nectar volume and sugar quantity were higher in intact than perforated flowers, but bees (robbers) visiting perforated flowers were able to extract a higher percentage of available nectar and sugar so that absolute amount of sugar (mg) removed by one bee visit is the same for each flower type. However, because perforated flowers facilitate higher rates of bee flower visitation and the same or higher rates of nectar ingestion, they are rendered more profitable than intact flowers in temporal terms. Accordingly, net energy (J) gain per second flower handling time was higher for robbers on most days sampled. We conclude that the majority evidence indicates an energetic advantage for honey bees that engage in secondary nectar thievery in *V. ashei*.

**Keywords** *Apis mellifera* · *Xylocopa virginica* · *Vaccinium ashei* · Nectar larceny · Foraging

### Introduction

Some flowers have morphological features that impede access by certain taxa of nectarivores, including bees. One example of this is rabbiteye blueberry, *Vaccinium ashei* Reade, a bush-type species native to the southeastern

United States where it is cultured commercially. The *V. ashei* flower has a long tubular corolla with basal nectaries relatively inaccessible to those short-tongued bees ordinarily restricted to gaining access at the aperture. In the case of *V. ashei* in the southeastern United States, however, there is an interesting syndrome of primary and secondary nectar thievery. The native short-tongued carpenter bee, *Xylocopa virginica* L, gains access to *V. ashei* nectar by imbibing it through perforations it makes with its maxillary galeae in the lateral walls of the corolla, an example of primary nectar thievery (Faegri and Van der Pijl 1979). The exotic, short-tongued honey bee, *Apis mellifera* L, subsequently visits these perforations and becomes a secondary thief (Delaplane and Mayer 2000). The effects of nectar larceny on plant reproduction are variable. Even though the removal of floral nectar can decrease the standing crop and change sugar concentration of nectar available to other pollinators (Pleasant 1983), its effects on plant reproduction range from benign (Maloof 2001) to damaging (Inouye 1983; Maloof and Inouye 2000; Irwin et al. 2001; Dedej and Delaplane 2004).

In the local syndrome described above, *A. mellifera* is incapable of perforating the *V. ashei* corolla and learns to transition from aperture visits (legitimate) to lateral visits (larceny) only after *X. virginica* becomes active in the orchard. Dedej and Delaplane (2004) showed that this transition from legitimate to robbing flower visits is rapid, going from initial lows to near-fixation at 95% within 4–6 days of 21–22 observed. The most plausible explanation for this rapid behavioral transition is an energetic advantage realized by nectar-robbing flower visits. This study was designed to test this hypothesis.

Communicated by R. Page

S. Dedej · K. S. Delaplane (✉)  
Department of Entomology,  
University of Georgia,  
Athens, GA 30602, USA  
e-mail: ksd@uga.edu  
Tel.: +1-706-5422816  
Fax: +1-706-5423872

### Methods

#### General

The study was conducted during spring 2003 at a mature 15-year-old plantation of *V. ashei* at the Horticulture Farm of the University of Georgia, Oconee County, Ga. (33°50'N, 83°26'W). Anthesis at

this site lasts from shortly after mid-March to mid-April, and quantity of sucrose per flower averages 1.095 mg (range 0.05–4.56) and tends to increase in a flower up to 4 days post-anthesis (Dedej 2004).

Nectar was extracted without excising flowers, using calibrated 1- 5- $\mu$ l disposable pipettes (Fischer Scientific, Pittsburgh, Pa.) (Corbet 2003); nectar volume was measured to the nearest 0.1  $\mu$ l. Sugar concentration was measured as % Brix (grams sucrose per 100 g solution) (Corbet 2003) using a hand-held refractometer model MT-098 (Taipei, Taiwan) with range 0–80% Brix and accuracy to the nearest 0.5%. The Brix percentage was temperature-corrected using the correction table provided by the manufacturer. The quantity of sucrose per sample (mg) was calculated by multiplying volume of nectar $\times$ temperature-corrected % Brix $\times$ the sucrose density values after Dafni (1992, p 148).

Nectar standing crop in intact and *X. virginica*-perforated flowers and quantity of nectar removed by honey bees per *V. ashei* flower visit

With the intention of calculating how much energy honey bees gain during legitimate or robbing flower visits, we measured nectar standing crop ( $\mu$ l) in unvisited flowers (before bee visitation on that day) ( $n=299$ ) and in flowers after one visit by a honey bee ( $n=275$ ) on each of 6 days (28 and 29 March and 1, 2, 4, and 14 April). These measures were taken for both perforated and intact flowers. The rare occasions when a bee visited a perforated flower legitimately (at the aperture) were excluded from the data set, so that for Tables 1 and 2, "intact" flower=legitimate visits and "perforated" flower=robbing. Nectar standing crop in unvisited flowers was measured early in the morning before bees started visiting flowers (28 and 29 March) or later using cages (1.8 $\times$ 1.8 $\times$ 1.8 m frames covered with Lumite screen; Bioquip, Calif.) to exclude large insects. After measuring nectar standing crop in unvisited flowers (in both perforated and intact flowers), the screen of the cage was removed and honey bees were allowed to visit flowers freely. Once a flower was observed to be visited by a honey bee, the flower was immediately excised, sealed in a plastic container, and its nectar standing crop measured within 1 h. Each day, from 20 to 25 flowers were sampled for each flower class: unvisited/perforated, unvisited/intact, visited/perforated, visited/intact); from these data we were able to derive average daily nectar standing crop (Table 1), average daily volume ( $\mu$ l) of nectar or quantity of sugar (mg) (S) ingested by one honey bee per flower visited, as well as percentage of available nectar ( $\mu$ l), percentage of available sugar (mg), and absolute amount of sugar (mg) removed by one bee visit. Nectar ingestion rate for both legitimate and robbing foragers was calculated as the average volume ( $\mu$ l) of nectar per flower for a particular day divided by handling time (seconds, see *H* below).

The effects of flower type (intact or perforated) and Julian day on nectar volume ( $\mu$ l), sugar quantity (mg), and sugar concentration (%) were analyzed before and after one bee visit with a completely randomized design analysis of variance (ANOVA), recognizing the interaction of day $\times$ flower type as test term. An interaction was detected for these variables ( $F \geq 5.1$ ;  $df=2$ ,  $\geq 175$ ;  $P \leq 0.002$ ), so each was analyzed by day using residual error as test term (Table 1). The effects of flower type (intact, perforated) on percentage of available nectar ( $\mu$ l), percentage of available sugar (mg), and absolute amount of sugar (mg) removed by one bee visit were analyzed with analysis of variance recognizing residual error as test term (Table 2).

#### Honey bee observations and foraging energetics

Foraging in insects involves four components that have unique thermoregulatory requirements and constraints (Heinrich 1993): warm-up prior to take off, intermittent flight between flowers, perching or walking on flowers, and continuous flight to and from the nest. As the first and fourth responses in our study were assumed the same for both legitimate and robbing foragers (experi-

mental orchard and apiary are next to each other), we focused only on the intermittent flight between flowers and perching or walking on flowers.

The intermittent flight time between flowers (Heinrich 1993) or inter-flower movement (Seeley 1985) spent by honey bees approaching (either hovering or not) and landing at flowers was defined as the discrimination time (*D*), as honey bees spend this time discriminating between inflorescences (Gilbert et al. 1991), while the time spent probing floral apertures or, in our case lateral robbery holes, was defined as handling time (*H*) (Seeley 1985; Dafni 1992). We assume (after Gilbert et al. 1991) that handling time corresponds to ingestion time. While the term handling time is well defined and used in the literature (Seeley 1985; Gilbert et al. 1991; Dafni 1992; Kearns and Inouye 1993), for our purposes we define total observation time as (Discrimination+Handling time), noted as (*O*).

Over the 6 days of sampling for nectar standing crop (see above), we monitored and timed (with a hand-held stopwatch) the foraging activity of 102 honey bees on *V. ashei* flowers. These observations were made as soon as possible after measuring standing crop. On each day, 10–20 bees performing different types of visitation (legitimate or robbing) were each opportunistically noticed (seconds=0) and followed until they were lost to sight (Stout et al. 2000). For each bee, total time of observation (*O*), time spent discriminating (*D*), time spent probing and ingesting (*H*), as well as number of flowers visited and type of visit performed, were recorded. Individual honey bees displaying mixed behaviors (legitimate+robbing, legitimate+rejection, or robbing+rejection) were excluded from analysis as their number was low ( $n=3$ ). Rejection is indicated when a forager inspects the proximal base of corollas and rejects those without perforations.

Two stopwatches were used to monitor honey-bee foraging behavior. With one stopwatch, the total time of observation (*O*) for an individual bee was recorded, while with the other, the handling time (*H*) of the same bee was recorded for every flower visited as long as the bee was observed. The second stopwatch was stopped every time the bee stopped probing one flower and was restarted when it began probing another. (*D*) was derived as the difference between (*O*) and (*H*).

The net energy gain (*J*) was calculated for both legitimate and robbing honey bee foragers using the following equation modified from Harder and Cruzan (1990):

$$N_E = I_E - O_E$$

where  $N_E$ =Net energy gain,  $I_E$ =Intake energy and  $O_E$ =Output energy (energy spent for flight activity during discrimination and handling).

Intake energy (*J*) was calculated as:

$$I_E = nSe$$

where  $n$ =number of flowers visited during total observation time (*O*),  $S$ =average quantity of sugar ingested from one flower visited (mg) (see above), and  $e$ =energy content (J) of 1 mg sugar [1 mg sugar is equivalent to 4.2 calories or 17.6 J (4.2 $\times$ 4.186=17.6 J)] (Schmidt-Nielsen 1997).

The output energy (*J*) was calculated as:

$$O_E = D_E + H_E$$

where  $D_E$ =quantity of energy spent by honey bee during discrimination time and  $H_E$ =energy spent during handling time. These were derived from:

$$D_E = wt_d k_d$$

and

$$H_E = wt_h k_h$$

where  $w$ =bee mass (125 mg),  $t_d$ = total time spent during intermittent flights to inflorescences (seconds) (discrimination time),  $t_h$ =total time (seconds) spent handling flowers during observations, and  $k_d$  and  $k_h$ =honey bee's mass-specific rates of energy expenditure during inter-floral flight and handling, respectively (J/g/sec);  $k_d$  and  $k_h$  were derived from published values of honey bee oxygen

consumption. Mass-adjusted oxygen consumption rates during discrimination time were calculated as an average of values of Wolf et al. (1989) for hovering bees and bees during free directional flight (on a 125-mg bee basis), Suarez et al. (1996) for unloaded bees exiting their nest, and Stabentheiner et al. (2003) for “active” foraging-aged bees (at 25°C), arriving at a mean value of 75.5 ml O<sub>2</sub>/g per hour. To calculate energy expended in joules, the volume of oxygen consumed was multiplied by 21.3 (1 ml oxygen consumption for honey bees is equivalent to 21.3 J; Harrison et al. 2001), giving us a value of 1,608.2 J/g per hour or 0.447 J/g per second. For handling, we used the values of Wolf et al. (1989) for walking and motionless bees, and those of Stabentheiner et al. (2003) for non-flying “medium activity” foraging-aged bees (at 25°C), arriving at a mean value of 59.1 ml O<sub>2</sub>/g per hour, which when multiplied by 21.3 J gives us a value of 1,258.8 J/g per hour or 0.350 J/g per second. Using these values and average bee mass of 125 mg, we determined the rate of energy expenditure per bee to be 0.056 J/s for discrimination (*k<sub>d</sub>*) and 0.044 J/s for handling (*k<sub>h</sub>*).

Effects of type of flower visit performed by honey bees (legitimate or robbing) on time spent probing and ingesting per flower, energy spent per bee handling one flower (Table 3), number flowers visited per minute, total foraging time per flower, net energy gain per flower, net energy gain per second handling, and nectar ingestion rate (Table 4) were tested with a completely randomized ANOVA blocked on Julian days and recognizing the interaction of day×type of visit as test term. When type of visit and day interacted, we analyzed independent variables by day and used residual error as test term (Table 4). Means were separated by Duncan’s test, and differences accepted at the  $\alpha \leq 0.05$  level (SAS Institute 1992).

**Results**

Nectar standing crop in intact and *X. virginica*-perforated flowers and quantity of nectar removed by honey bees per *V. ashei* flower visit

Nectar volume was higher in intact than perforated flowers on every sampling day, and this pattern was the same in flowers before or after one bee visit ( $F \geq 6.7$ ;  $df=1, \geq 29$ ;  $P=0.0001$ ) (Table 1). This pattern was the same for sugar quantity ( $F \geq 10.2$ ;  $df=1, \geq 29$ ;  $P \leq 0.0025$ ) (Table 1), but for sugar concentration there was no interpretable trend, with highest values switching repeatedly between intact or perforated flowers by day (Table 1). Flower type (intact, perforated) affected the percentage of available nectar and sugar removed by one bee visit ( $F \geq 11.5$ ;  $df=1,10$ ;  $P \leq 0.0069$ ), but not absolute amount of sugar removed (Table 2).

**Honey bee observations and foraging energetics**

In this section we present first those results concerning honey-bee foraging observations, and then report results on foraging energetics. Mean values for variables are distributed between Tables 3 and 4 depending on the presence or absence of ANOVA interactions in their respective analyses.

The number of *V. ashei* flowers visited per minute was either unaffected by type of bee visit or (on 4 of 6 sampling days) higher for robbing than legitimate *A. mellifera* flower visitors ( $F \geq 5.5$ ;  $df=1, \geq 10$ ;  $P \leq 0.0309$ ) (Ta-

are indicated with different letters ( $\alpha=0.05$  level). We do not report mean values for cells indicated “NA” because flowers in those groups did not yield enough nectar to measure concentration. For subsequent energetic calculations requiring these values, however, we derived estimates based on average concentration values of the same flower type for that day.

**Table 1** Volume, sugar quantity, and sugar concentration of nectar standing crop in intact or perforated *V. ashei* flowers before or after being visited by one honey bee. The rare occasions when a bee visited a perforated flower legitimately (at the aperture) were excluded from the data set, so that “intact”=legitimate visits and “perforated”=robbing. Data were collected over 6 sampling days (Julian). Values are mean±standard error, with *n* in parentheses. Differences between intact or perforated flowers within variable within day

| Julian day | Before one bee visit        |                |                        |                |                         |                | After one bee visit         |                 |                        |                 |                         |                |
|------------|-----------------------------|----------------|------------------------|----------------|-------------------------|----------------|-----------------------------|-----------------|------------------------|-----------------|-------------------------|----------------|
|            | Volume of nectar ( $\mu$ l) |                | Quantity of sugar (mg) |                | Sugar concentration (%) |                | Volume of nectar ( $\mu$ l) |                 | Quantity of sugar (mg) |                 | Sugar concentration (%) |                |
|            | Intact                      | Perforated     | Intact                 | Perforated     | Intact                  | Perforated     | Intact                      | Perforated      | Intact                 | Perforated      | Intact                  | Perforated     |
| 87         | 3.4±0.5a (25)               | 1.9±0.2b (25)  | 1.1±0.2a (25)          | 0.5±0.1b (25)  | 28.9±1.3a (25)          | 25.5±1.1b (25) | 1.9±0.3a (22)               | 0.3±0.1b (20)   | 0.6±0.1a (22)          | 0.07±0.03b (20) | NA                      | NA             |
| 88         | 4.7±0.3a (20)               | 0.9±0.4b (20)  | 1.5±0.1a (19)          | 0.3±0.1b (20)  | 26.2±1.1a (19)          | 26.9±0.9a (20) | 2.7±0.4a (20)               | 0.05±0.02b (20) | 0.9±0.1a (20)          | 0.01±0.01b (20) | NA                      | NA             |
| 91         | 2.8±0.2a (23)               | 0.6±0.1b (20)  | 1.4±0.2a (22)          | 0.4±0.1b (20)  | 50.1±2.3b (22)          | 58.7±0.2a (20) | 1.3±0.2a (10)               | 0.1±0.03b (21)  | 0.8±0.1a (10)          | 0.07±0.02b (21) | NA                      | NA             |
| 92         | 2.6±0.2a (25)               | 1.2±0.1b (25)  | 1.0±0.1a (23)          | 0.5±0.05b (25) | 32.8±1.8b (23)          | 41.3±1.3a (25) | 1.7±0.2a (25)               | 0.3±0.06b (25)  | 0.7±0.1a (25)          | 0.2±0.03b (25)  | 33.9±1.4b (25)          | 42.3±0.2a (25) |
| 94         | 4.9±0.4a (25)               | 2.4±0.2b (25)  | 2.5±0.2a (25)          | 0.9±0.1b (25)  | 40.3±1.6a (25)          | 31.0±1.5b (25) | 2.6±0.2a (25)               | 0.3±0.07b (30)  | 1.4±0.1a (25)          | 0.1±0.03b (30)  | 43.4±1.3a (25)          | 33.8±1.0b (30) |
| 104        | 1.8±0.2a (41)               | 0.3±0.09b (25) | 0.7±0.1a (41)          | 0.2±0.03b (25) | 33.6±1.2b (41)          | 42.2±0.9a (25) | 1.7±0.3a (22)               | 0.2±0.04b (35)  | 0.6±0.1a (22)          | 0.1±0.01b (35)  | 30.6±1.3a (22)          | 30.0±0.4a (35) |

**Table 2** Percentage of available nectar, percentage of available sugar, and absolute amount of sugar removed by one honey bee visit to *V. ashei*. The rare occasions when a bee visited a perforated flower legitimately (at the aperture) were excluded from the data

|   | Type of flower      |                     |
|---|---------------------|---------------------|
|   | Intact              | Perforated          |
| Percentage of available nectar ( $\mu\text{l}$ ) removed by one bee visit | 37.9 $\pm$ 6.9b (6) | 76.3 $\pm$ 9.0a (6) |
| Percentage of available sugar (mg) removed by one bee visit               | 36.1 $\pm$ 4.9b (6) | 77.4 $\pm$ 7.4a (6) |
| Absolute amount of sugar (mg) removed by one bee visit                    | 0.5 $\pm$ 0.1a (6)  | 0.4 $\pm$ 0.1a (6)  |

**Table 3** Average time and energy spent by one honey bee handling one flower during legitimate or robbing flower visits to *V. ashei*. Data were collected only for individual bees successively expressing one behavior type. Values are mean $\pm$ standard error, with *n*

|   | Type of bee visit on flowers |                      |
|---|------------------------------|----------------------|
|   | Legitimate                   | Robbing              |
| Time (seconds) spent probing and ingesting per flower ( <i>H</i> )      | 11.4 $\pm$ 0.6a (50)         | 5.8 $\pm$ 0.3b (52)  |
| Energy (J) spent handling one flower ( $k_{\text{h}}$ seconds handling) | 0.5 $\pm$ 0.03a (50)         | 0.3 $\pm$ 0.01b (52) |

set, so that “intact”=legitimate visits and “perforated”=robbing. Values are mean $\pm$ standard error, with *n* in parentheses. Means within a row followed by the same letter are not significantly different at the  $\alpha=0.05$  level.

in parentheses. Means within a row followed by the same letter are not significantly different at the  $\alpha=0.05$  level. As no interactions were noted between type of bee visit and sampling day, data are pooled by type of visit.

ble 4). Total foraging time per flower (*O*) (Discrimination+Handling time) was either unaffected by type of visit or (on 3 of 6 sampling days) longer for legitimate flower visitors ( $F \geq 4.6$ ;  $df=1,18$ ;  $P \leq 0.0473$ ) (Table 4). Nectar ingestion rate was either unaffected by type of visit or (on 3 of 6 sampling days) significantly higher for robbers ( $F \geq 15.7$ ;  $df=1, \geq 10$ ;  $P \leq 0.001$ ) (Table 4). Average time spent probing and ingesting per flower (*H*) was affected by type of bee visit ( $F=48.1$ ;  $df=1,5$ ;  $P=0.001$ ) but not day. On average, honey bees spent more time handling a flower during legitimate visits than during robbing (Table 3).

There were significant effects of type of bee visit for net energy gain per flower on 5 of 6 sampling days ( $F \geq 7.3$ ;  $df=1, \geq 9$ ;  $P \leq 0.0144$ ); however, the trend was inconsistent, with higher net energy gain for legitimate visitors on 3 of 5 days and the reverse pattern the other 2 (Table 4). Energy spent per bee handling one flower was significantly affected by type of bee visit ( $F=48.1$ ;  $df=1,5$ ;  $P=0.001$ ) but not day; on average, honey bees spent more energy handling one flower during legitimate than robbing visits (Table 3). Net energy gain per second handling time was either unaffected by type of bee visit or (on 4 of 6 sampling days) significantly higher for robbers ( $F \geq 7.3$ ;  $df=1, \geq 10$ ;  $P \leq 0.0151$ ) (Table 4).

## Discussion

Nectar standing crop in intact and *X. virginica*-perforated flowers and quantity of nectar removed by honey bees per *V. ashei* flower visit

Nectar standing crop per flower, whether measured by volume ( $\mu\text{l}$ ) of nectar or quantity (mg) of sugar, was higher in intact than perforated flowers, whether before or after one honey bee visit (Table 1). The most straight-

forward explanation is a higher frequency of bee visitation and nectar depletion in robbed (perforated) versus unrobbed (intact) flowers. However, it is important to note that these measures were taken before bee visitation in early morning (or in tents), so that any effect of depletion had carried over from the previous day. Under natural conditions, honey bees strongly prefer perforated flowers of *V. ashei* over intact ones (Dedej and Delaplaine 2004). Our findings with *V. ashei* are incongruent with the conclusion of Navarro (2001) that robbed versus unrobbed flowers in *Macleania bullata* Yeo do not differ with respect to nectar standing crop, but are congruent with the results of Maloof (2001) who found less nectar in robbed than unrobbed flowers of *Corydalis caseana* Gray, and with those of Stout et al. (2000) who found half the nectar in robbed versus unrobbed flowers of *Linaria vulgaris* P. Mill.

After one visit, robbing visitors removed a higher fraction of available nectar from perforated flowers (% of volume,  $\mu\text{l}$ ) than did legitimate visitors from intact flowers; the same held true for percentage of available sugar (mg) (Table 2). In spite of these relative results, the absolute amount (mg) of sugar removed by one bee visit was not different between legitimate visitors or robbers, the significance of which is discussed below.

## Honey-bee observations and foraging energetics

From the results presented in Tables 3 and 4, we summarize the following: honey bees expressed a higher rate of *V. ashei* flower visitation if they engaged in nectar larceny (Table 4). These robbing visits were associated with comparatively reduced foraging time per flower, higher bee nectar ingestion rates (Table 4), and lower flower handling times (Table 3). When legitimate versus robbing foragers are compared in terms of energetic pa-

**Table 4** Foraging rates, net energy gain, and nectar ingestion rates per honey bee during legitimate (*Leg*) or robbing (*Rob*) *V. ashei* flower visits. Data were collected only for individual bees successively expressing one behavior type. As interactions between type of bee visit and sampling day were noted for these dependent variables, data are presented by day. Values are mean±standard error, with *n* in parentheses. Means within a row for each variable followed by the same letter are not significantly different at the  $\alpha=0.05$  level.

| Julian day | Number flowers visited per min |               | Total foraging time (s) per flower |                | Net energy gain (J) ( $N_E=I_E-O_E$ ) per flower |                | Net energy gain (J) ( $N_E=I_E-O_E$ ) per second handling time |                | Nectar ingestion rate ( $\mu\text{l/s}$ ) |                  |
|------------|--------------------------------|---------------|------------------------------------|----------------|--|----------------|--|----------------|---|------------------|
|            | Leg                            | Rob           | Leg                                | Rob            | Leg  | Rob            | Leg  | Rob            | Leg                                       | Rob              |
| 87         | 2.6±0.3b (5)                   | 6.3±0.9a (7)  | 25.6±4.4a (5)                      | 12.7±3.9a (7)  | 6.5±0.2a (5)                                     | 7.1±0.2a (7)   | 0.6±0.03b (5)  | 1.2±0.1a (7)   | 0.1±0.01b (5)                             | 0.3±0.02a (7)    |
| 88         | 2.5±0.2b (10)                  | 6.8±0.6a (10) | 26.2±2.5a (10)                     | 10.0±1.5b (10) | 8.2±0.1a (10)                                    | 3.8±0.1b (10)  | 0.9±0.2a (10)  | 0.8±0.1a (10)  | 0.2±0.04a (10)                            | 0.2±0.02a (10)   |
| 91         | 3.3±0.5a (5)                   | 4.2±0.4a (6)  | 20.6±3.8a (5)                      | 15.1±1.8a (6)  | 9.2±0.2a (5)                                     | 5.6±0.1b (6)   | 1.2±0.3a (5)   | 1.0±0.2a (6)   | 0.1±0.03a (5)                             | 0.1±0.02a (6)    |
| 92         | 4.0±0.3a (10)                  | 4.2±0.5a (10) | 16.0±1.3a (10)                     | 16.0±1.7a (10) | 4.8±0.1b (10)                                    | 5.6±0.1a (10)  | 0.5±0.08b (10)   | 0.9±0.1a (10)  | 0.1±0.01a (10)                            | 0.1±0.02a (10)   |
| 94         | 2.6±0.3b (10)                  | 4.4±0.7a (9)  | 26.3±3.6a (10)                     | 16.7±2.6b (9)  | 17.7±0.2a (10)                                   | 12.6±0.1b (9)  | 1.4±0.1b (10)  | 2.4±0.4a (9)   | 0.2±0.02b (10)                            | 0.4±0.05a (9)    |
| 104        | 4.3±0.3b (10)                  | 8.7±0.5a (10) | 14.6±1.1a (10)                     | 7.1±0.4b (10)  | 1.0±0.05b (10)                                   | 1.2±0.02a (10) | 0.1±0.02b (10)   | 0.3±0.02a (10) | 0.01±0.001b (10)                          | 0.03±0.002a (10) |

rameters, there is either parity between the two or advantage for robbers; the only parameter in which an apparent advantage was detected for legitimate foragers was net energy gain per flower, which was higher for legitimate foragers on 3 of 5 sampling days (higher for robbing the other 2) (Table 4). For handling energy spent per flower (Table 3), there was unambiguous advantage for robbers, and for net energy gain per second handling time there was either parity or, on 4 of 6 days, advantage for robbers (Table 4). Thus, we conclude that the majority evidence indicates an energetic advantage for honey bees that engage in nectar thievery in *V. ashei*.

The proximal causes of this advantage appear to be foraging and flower handling habits that result in comparatively higher rates of flower visitation and energy intake; so, honey bees gain temporal energetic advantage by accessing the nectar in *V. ashei* corollas via the lateral perforations made by *X. virginica*.

The distal cause may be flower morphology that impairs rapid access to the basal nectaries via legitimate (aperture) visits. Lyrene (1994) suggested that *Vaccinium* spp. flowers with comparatively short and wide corollas and large apertures are more amenable to honey bee visitation. Flowers of *Vaccinium* spp. generally express the unfavorable end of these spectra, especially depth of corollas at ca. 9–11 mm (Free 1993). European subspecies of *A. mellifera*, with tongue length of 5.7–6.6 mm (Winston 1987), are handicapped and sometimes compensate in behaviors other than robbing. Honey bees have been reported to visit other Ericaceae (*Echium* spp.) with deep corollas by pushing their heads through the aperture to reach nectaries (Corbet et al. 1995). In our case, the lateral robbery holes made by *X. virginica* afford faster access by *A. mellifera* to the basal nectaries of *V. ashei*, improving energetic profitability of a resource otherwise compromised by inconvenient morphology. It is also noteworthy that the absolute amount (mg) of sugar removed by one bee visit was not different between legitimate or robbing foragers even though the percentage of available nectar ( $\mu\text{l}$ ) and sugar (mg) removed was higher for robbers (Table 2). This suggests that the flower perforations enable short-tongued honey bees to extract available resources more efficiently, to the point that the energetic profitability of a perforated flower (otherwise inferior, Table 1) is rendered similar to an intact flower (Table 2). Add to this the fact that perforated flowers enable more rapid foraging (Tables 3 and 4), and the temporal energetic superiority of perforated flowers becomes apparent.

Nectar-collecting honey bees and bumble bees (*Bombus* spp.) are expected to forage in a manner that maximizes rate of net energy intake (Hodges and Wolf 1981; Harder and Real 1987). In our case, this optimality was realized by the expression of secondary nectar larceny which, in turn, was associated with the dual benefits of increased flower visitation rates and (more variably) nectar ingestion rates. Flower visitation rate (Table 4) is a product of flower handling time (Table 3); by probing lateral robbery holes, *A. mellifera* was able to reduce

flower handling time by half. Concerning nectar ingestion rates (Table 4), on the 6 sampling days, there was either parity between legitimate and robbing foragers or higher ingestion rates for robbers. Honey bees realizing higher nectar ingestion rates are able to maximize their nectar loads; conversely, bees with lower ingestion rates have extended foraging times and smaller crop loads (Núñez and Giurfa 1996). Our results are consistent with these published observations. Our results are also consistent with the idea that higher ingestion rates and reduced foraging times are associated with more profitable sites, as one would expect from the study of Farina and Wainelboim (2001) who associated increased crop loads and decreased feeding times at artificial feeders with higher sucrose flow rates. But in our case, it was the discriminatory behavior of the bees themselves that rendered a site more profitable (see discussion above) and actualized the benefits of higher ingestion rates and reduced foraging times.

The distinction between behavior-modified temporal site profitability versus inherent site profitability is further suggested by noting our results for net energy gain per flower (Table 4) for which energetic advantage fell to legitimate foragers 3 of 5 days. By examining energetic profit on a flower (not time) basis, the advantage goes to legitimate foragers who invest in longer visits (Table 3) at non-perforated flowers which are inherently richer (Table 1). But when foraging costs are added to the model [and indeed handling energy spent per flower is higher for legitimate foragers (Table 3)] to derive net energy gain per second handling time (Table 4), the advantage goes to robbers who extract available resources more efficiently (Table 2) from perforated flowers that are inherently poorer (Table 1). Thus, the benefit realized by nectar robbers in our study was achieved by behavioral differences in the bees themselves rather than inherent energetic superiority in the perforated flowers they prefer.

**Acknowledgements** We thank John Ruberson for supplying cages, Glenn O. Ware for assistance in experimental design and analysis, and Jennifer Berry for help in the field. The research described herein was conducted in compliance with all applicable laws of the United States of America and State of Georgia.

## References

- Corbet SA (2003) Nectar sugar content: estimating standing crop and secretion rate in the field. *Apidologie* 34:1–10
- Corbet SA, Saville NM, Fussell M, Prys-Jones OE, Unwin DM (1995) The competition box: a graphical aid to forecasting pollinator performance. *J Appl Ecol* 32:707–719
- Dafni A (1992) *Pollination ecology: a practical approach*. Oxford University Press, New York
- Dedej S (2004) Bee foraging behavior and pollinating activity on rabbiteye blueberry *Vaccinium ashei* Reade. PhD Thesis, University of Georgia, Athens
- Dedej S, Delaplane KS (2004) Nectar-robbing carpenter bees reduce seed-setting capability of honey bees (Hymenoptera: Apidae) in rabbiteye blueberry *Vaccinium ashei* Reade ‘Climax’. *Environ Entomol* 33:100–106
- Delaplane KS, Mayer DF (2000) *Crop pollination by bees*. CABI, Oxon
- Faegri K, Van der Pijl LW (1979) *The principles of pollination ecology* (3rd edn). Pergamon, Oxford
- Farina WM, Wainelboim AJ (2001) Changes in thoracic temperature of honey bees while receiving nectar from foragers collecting at different reward rates. *J Exp Biol* 204:1653–1658
- Free JB (1993) *Insect pollination of crops*. Academic, London
- Gilbert FS, Haines N, Dickson K (1991) Empty flowers. *Funct Ecol* 5:29–39
- Harder LD, Cruzan MB (1990) An evaluation of the physiological and evolutionary influences of inflorescence size and flower depth on nectar production. *Funct Ecol* 4: 559–572
- Harder LD, Real RA (1987) Why are bumblebees risk-averse? *Ecology* 68:1104–1108
- Harrison JF, Camazine S, Marden JH, Kirkton SD, Rozo A, Yang X (2001) Mite not make it home: tracheal mites reduce the safety margin for oxygen delivery of flying honeybees. *J Exp Biol* 204:805–814
- Heinrich B (1993) *The hot-blooded insects: strategies and mechanisms of thermoregulation*. Harvard University Press, Cambridge, Mass
- Hodges CM, Wolf LL (1981) Optimal foraging in bumblebees—why is nectar left behind in flowers? *Behav Ecol Sociobiol* 9:41–44
- Inouye DW (1983) The ecology of nectar robbing. In: Bentley B, Elias T (eds) *The biology of nectaries*. Columbia University Press, New York
- Irwin RE, Brody AK, Waser NM (2001) The impact of floral larceny on individuals, populations, and communities. *Oecologia* 129 (2):161–168
- Kearns CA, Inouye DW (1993) *Techniques for the pollination biologist*. University Press of Colorado, Boulder
- Lyrene PM (1994) Variation within and among blueberry taxa in flower size and shape. *J Am Soc Hortic Sci* 119:1039–1042
- Maloof JE (2001) The effect of bumble bee nectar robbery on plant reproductive success and pollinator behavior. *Am J Bot* 88:1960–1965
- Maloof JE, Inouye DW (2000) Are nectar robbers cheaters or mutualists? *Ecology* 81:2651–2661
- Navarro L (2001) Reproductive biology and effect of nectar robbing on fruit production in *Macleania bullata* (Ericaceae). *Plant Ecol* 152:59–65
- Núñez JA, Giurfa M (1996) Motivation and regulation of honey bee foraging. *Bee World* 77:182–196
- Pleasant JM (1983) Nectar production in *Ipomopsis aggregata* (Polemoniaceae). *Am J Bot* 70:1468–1475
- SAS Institute (1992) *SAS/STAT user’s guide*, version 6, 4th edn. SAS Institute, Cary
- Schmidt-Nielsen K (1997) Energy metabolism. In: Schmidt-Nielsen K (ed) *Animal physiology, adaptation and environment*, 5th edn. Cambridge University Press, Cambridge, pp 169–214
- Seeley TD (1985) *Honeybee ecology: a study of adaptation in social life*. Princeton University Press, Princeton
- Stabentheiner A, Vollmann J, Kovac H, Crailsheim K (2003) Oxygen consumption and body temperature of active and resting honeybees. *J Insect Physiol* 49:881–889
- Stout JC, Allen JA, Goulson D (2000) Nectar robbing, forager efficiency and seed set: bumblebees foraging on the self-incompatible plant *Linaria vulgaris* (Scrophulariaceae). *Acta Oecol* 21:277–283
- Suarez RK, Lighton JRB, Joos B, Roberts SP, Harrison JF (1996) Energy metabolism, enzymatic flux capacities, and metabolic flux rates in flying honeybees. *Proc Natl Acad Sci USA* 93:12616–12620
- Winston ML (1987) *The biology of the honey bee*. Harvard University Press, Cambridge
- Wolf THJ, Schmid-Hempel P, Ellington CP, Stevenson RD (1989) Physiological correlates of foraging efforts in honey-bees: oxygen consumption and nectar load. *Funct Ecol* 3:417–424