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RESEARCH ARTICLE

Individual forager profits in *Apis mellifera* unaffected by a range of colony *Varroa destructor* densities

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Abstract The parasitic mite *Varroa destructor* Anderson and Trueman negatively affects honey bee health, flight activity, and foraging behavior, all of which can be expected to affect foraging energetics. We tested this hypothesis in a 3-year field study. In each year, four-frame nucleus colonies with varying loads of varroa were placed under cages with mature rabbiteye blueberry plants, *Vaccinium ashei*. Individual bee weights consistently decreased as colony varroa populations increased, affirming that the design produced a range of colony mite effects. However, average forager flower handling times and nectar ingestion rates were unaffected by changes in colony varroa levels. Moreover, there were no significant effects of colony varroa levels on individual net foraging energy gain determined per flower, per second handling time, or per second total foraging time. We conclude that individual forager profits in *Apis mellifera* are unaffected by the range of colony *V. destructor* densities used in this study. These results are relevant to the question of the extent to which foraging of individuals relates to colony state in social Hymenoptera.

Keywords Energetics · Honey bee · Foraging

Introduction

Of the numerous pathogens and nest invaders that challenge *Apis mellifera*, the ectoparasitic mite *Varroa destructor* Anderson and Trueman is distinctively virulent. Varroa has been found to reduce colony honey stores (De Jong et al., 1982) and number of pollen foragers (Janmaat et al., 2000). Concerning individual bees, varroa causes smaller sperm loads in drones, weight loss, shortened life span, reduced size of mandibular glands, and reduced flight activity (Schmid-Hempel, 1998). Varroa has been shown to affect flight orientation, trip duration, and homing success of foragers (Kralj and Fuchs, 2006; Kralj et al., 2007).

It is possible that the negative effects of varroa on flight activity of bees translate to reduced foraging profits of individuals. Foraging is regulated by the dynamics of energetic benefits and costs (Wolf et al., 1989), the benefits being caloric returns (sugar procured per flower or unit effort) (Corbet et al., 1995) and costs the work of flight and flower handling (Seeley, 1985). Moreover, the equations used in calculating net energy gain require bee mass, one of the bee health variables most responsive to varroa. Therefore, it is reasonable to make a null hypothesis that varying loads of *V. destructor* at the colony level do not affect net foraging profits at the individual level. Characterizing this dynamic would expand our understanding of varroa parasitism on bee nutrient economy.

Materials and methods

General

The study was conducted at a 16-year-old plantation of bush-type blueberries, *Vaccinium ashei* Reade, during springs 2005, 2006, and 2007 at the Horticulture Farm of the University of Georgia, Oconee County, GA, USA (33°50′N, 83°26′W). Anthesis at this location occurs from mid-March to mid-April (Dedej, 2004).

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Three experimental colony varroa treatments (four replications each year) were as follows: low varroa (LV), high varroa (HV), or mite-treated control (C). In February of each year, full-sized Langstroth bee colonies were sampled for varroa using standard sticky screens. Using this information, we identified HV and LV colonies. A subset of colonies was made nearly varroa-free by mite-treating colonies with coumaphos, botanical oils, or powdered sugar; dusting bees with powdered sugar has been shown to dislodge a large fraction of the mite population (Fakhimzadeh, 2001). The resulting groups had the following initial daily mite drop counts (mean ± SE): 2005; HV (62.5 ± 4.9), LV (20.0 ± 1.3), C (3.1 ± 0.6); 2006; HV (56.7 ± 14.9), LV (12.4 ± 1.0), C (2.7 ± 0.4); 2007; HV (49.5 ± 2.3), LV (17.1 ± 1.4), C (0.7 ± 0.2). Delaplane and Hood (1999) considered February average mite drops of 10.2 a treatable threshold for the southeastern USA; therefore, the mite ranges derived here can be expected to generate a range of bee morbidities. In mid-March of each year, four-frame nucleus colonies, each with a population of ca. 6,600 honey bees (0.55 kg) were established from the colonies in which the varroa levels had been determined. Bees from colonies of each group were pooled into a large cage and subsequently distributed into individual nuclei, each with two empty frames, one frame of honey, one frame of capped brood, and a 1-in. queen pheromone (QMP) strip.

In early April of each year, twelve 1.8-m^3 plots were established, each with two *V. ashei* plants and one-four-frame nucleus bee colony. Each plot was enclosed by a 1.8-m^3 cage frame covered with Lumite screen. In an earlier study with this system, Dedej and Delaplane (2003) showed numeric increases in bee flower visitation rates and subsequent fruit-set in tents with bee densities ranging from 400 to 6,400; at 12,800 bees, however, response variables began decreasing. Therefore, with a density of 6,600 bees we believe resource scarcity was not a limiting factor in the present study. Measurements (see below) were made on each of five consecutive days each year.

Nectar standing crop in flowers

Before sunrise on each day of sampling, colony entrances were closed to prevent honey bee foraging within each cage. In order to establish the average nectar standing crop (µl) in unvisited flowers within each plot, 15 intact flowers were excised indiscriminately from plants in each plot and placed individually in a sealed container. Nectar was extracted using calibrated 1–5 µl disposable pipettes (Fischer Scientific, Pittsburgh, PA) and volume measured to the nearest 0.1 µl (Corbet, 2003). A bench-top refractometer (Fischer Scientific, Pittsburgh, PA) was used to measure sugar concentration as % Brix (g sucrose per 100 g solution) (Corbet, 2003). The quantity of sucrose per sample (mg) was derived by multiplying volume of nectar × the sucrose density values after Dafni (1992, p. 148). To derive volume of nectar removed by one bee visit (µl), we multiplied each volume by 0.379, the multiplier determined by Dedej and Delaplane (2005) as representing the percentage of available nectar removed by one honey bee visit in blueberry.

Honey bee observations and foraging energetics

At the completion of flower sampling, colony entrances were opened to allow honey bees to forage within the caged plot. Observations were limited to the hours of 10:00–12:00. Observations followed methods and guidelines described by Dedej and Delaplane (2005), and all time values are given in seconds. Heinrich (1993) describes four components of foraging in insects: pre-flight warm-up, intermittent flight between flowers, perching or walking on flowers, and continuous flight to and from the nest. Our observations focused on the time spent probing floral apertures, defined as handling time (*H*) (Seeley, 1985; Dafni, 1992) and the intermittent flight between flowers, defined as discrimination time (*D*) (Gilbert et al., 1991). Each observer used two stopwatches to monitor honey bee foraging behavior. One stopwatch was used to record total time of observation (*O*) for an individual bee. The other stopwatch recorded handling time of the same bee for every flower visited as long as the bee was observed, was paused every time the bee stopped probing a flower, and was restarted when it began probing another (Dedej and Delaplane, 2005). The total number of flowers visited during an observation was recorded. The average mass (mg) of ten forager bees per plot was determined by capturing probing bees and weighing them in pre-weighed containers.

The net energy gain (J) was calculated using the following equations and values described by Dedej and Delaplane (2005):

$$N_E = I_E - O_E$$

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 an observation, S = average quantity of sugar ingested from one flower visited (mg), and e = energy content (J) of 1 mg sugar, which is 17.6 J (Schmidt-Nielsen, 1997).

Output energy (J) was calculated as:

$$O_E = D_E - H_E$$

where D_E = quantity of energy spent by honey bees during discrimination and H_E = energy spent during handling time. These were calculated as:

$$D_E = wt_d k_d$$

and

$$H_E = wt_h k_h$$

where w = bee mass (mg), t_d = total time spent during intermittent flights to flowers and t_h = total time spent handling and k_d and k_h = honey bee's mass-specific rates of energy expenditure during discrimination and handling, respectively. For w we used the specific forager masses calculated for each plot each sampling day. Published values of honey bee oxygen consumption by Wolf et al. (1989) were used to derive k_d and k_h. Mass-adjusted oxygen consumption values during discrimination time were calculated as average oxygen consumption (O_2/g per hour) during forward flight and hovering. Handling time rates were based on consumption rates of walking and motionless bees. The oxygen consumption rates for each activity were calculated based on the following values published by Wolf et al. (1989):

forward flight $= 0.514m^{0.629}$
hovering $= 0.417m^{0.648}$
walking and motionless bees $= 0.444m^{0.492}$
where m = bee mass (mg)

To calculate energy expended in joules, each volume of oxygen consumed was multiplied by 21.3 J (Harrison et al., 2001) which yielded a value of J/g per hour that could be reduced to J/g per second. Using our mass-adjusted values, we determined plot and sampling day specific rates of energy expenditure per bee for discrimination (k_d) and handling (k_h).

Statistical analysis

The effects of treatment on bee weight, handling time per flower, total foraging time per flower, nectar ingestion rate, number of flowers visited per minute, net energy gain per flower, net energy gain per second handling time, and net energy gain per second total foraging time were tested by year with a repeated measure analysis of variance blocked on day and recognizing rep × treatment interaction as test term. One replication was the average values per cage per day per year; thus, our design compares the mean effects of colony-level parasitism, not individual parasitism. Least square means were separated by paired t tests and differences accepted at the $\alpha \leq 0.05$ level (GLM Procedure, SAS Institute, 2002–2003).

Results

Overall, nectar measurements were made from 2,700 flowers. We captured and weighed 1,800 foragers and completed 1,266 forager observations. Bee weight was affected by treatment in 2005 ($F = 23.61$; $df = 2, 6$; $P = 0.0014$) and 2007 ($F = 10.86$; $df = 2, 6$; $P = 0.0101$), but not in 2006 ($F = 3.53$; $df = 2, 6$; $P = 0.0969$). In 2005, bee weight was significantly reduced in LV and HV colonies, while in 2007 bee weight was significantly lower in HV colonies (Table 1). Handling time per flower was unaffected by treatment (2005: $F = 1.06$; $df = 2, 6$; $P = 0.4028$, 2006: $F = 0.23$; $df = 2, 6$; $P = 0.8033$, and 2007: $F = 0.34$; $df = 2, 6$; $P = 0.7268$). The total foraging time per flower was affected by treatment in 2005 ($F = 5.55$; $df = 2, 6$; $P = 0.0432$) but unaffected in 2006 ($F = 0.38$; $df = 2, 6$; $P = 0.6997$) and 2007 ($F = 0.90$; $df = 2, 6$; $P = 0.4561$). In 2005, the total foraging time per flower was significantly greater for C foragers than HV foragers (Table 1). Nectar ingestion rate was unaffected by treatment in all years (2005: $F = 0.07$; $df = 2, 6$; $P = 0.9296$, 2006: $F = 0.31$; $df = 2, 6$; $P = 0.7452$, and 2007: $F = 0.14$; $df = 2, 6$; $P = 0.3175$). The number of flowers visited per minute was affected by treatment in 2005 ($F = 8.6$; $df = 2, 6$; $P = 0.0173$), but not in 2006 ($F = 0.49$; $df = 2, 6$; $P = 0.6373$) and 2007 ($F = 1.62$; $df = 2, 6$; $P = 0.2735$). In 2005, the number of flowers visited per minute was significantly lower for C foragers than HV or LV foragers (Table 1).

Overall net energy gain values were unaffected by treatment (Table 2). Net energy gain per flower was unaffected by treatment (2005: $F = 1.37$; $df = 2, 6$; $P = 0.3233$, 2006: $F = 0.15$; $df = 2, 6$; $P = 0.8598$, and 2007: $F = 0.37$; $df = 2, 6$; $P = 0.7058$). Net energy gain per second handling time was unaffected by treatment (2005: $F = 0.6$; $df = 2, 6$; $P = 0.5765$, 2006: $F = 0.13$; $df = 2, 6$; $P = 0.8792$, and 2007: $F = 0.57$; $df = 2, 6$; $P = 0.5920$). Net energy gain per second total foraging time was unaffected by treatment (2005: $F = 0.63$; $df = 2, 6$; $P = 0.5665$, 2006: $F = 0.23$; $df = 2, 6$; $P = 0.8035$, and 2007: $F = 0.65$; $df = 2, 6$; $P = 0.5536$).

Discussion

Our study supports previous studies which show that bee weight is negatively associated with increasing numbers of mites (Bowen-Walker and Gunn, 2001; Schmid-Hempel, 1998). In each year, bee weights decreased as colony varroa densities increased (Table 1). However, individual forager flower handling times and nectar ingestion rates are apparently unaffected by colony varroa levels within the ranges used in this study (Table 1). Total foraging time per

Table 1 Results for honey bee forager weights and foraging observations

Treatment	Bee wt. (mg)	Handling time per flower (s)	Total foraging time per flower (s)	Nectar ingestion rate (µl)	No. flowers visited/min
2005					
Control	86.3 ± 1.6 (20) a	6.5 ± 0.6 (20)	11.8 ± 0.6 (20) a	0.04 ± 0.004 (20)	5.9 ± 0.2 (20) a
Low varroa	81.3 ± 1.6 (20) b	5.8 ± 0.4 (20)	10.5 ± 0.6 (20) ab	0.04 ± 0.005 (20)	6.7 ± 0.3 (20) b
High varroa	80.3 ± 1.1 (20) b	5.4 ± 0.4 (20)	9.3 ± 0.5 (20) b	0.04 ± 0.004 (20)	7.3 ± 0.3 (20) b
2006					
Control	84.7 ± 1.3 (20)	9.1 ± 0.6 (20)	14.9 ± 0.7 (20)	0.03 ± 0.007 (20)	4.7 ± 0.2 (20)
Low varroa	82.5 ± 1.1 (19)	9.0 ± 0.6 (19)	15.7 ± 0.9 (19)	0.02 ± 0.006 (19)	4.4 ± 0.2 (19)
High varroa	82.1 ± 0.9 (20)	8.8 ± 0.5 (20)	15.4 ± 0.7 (20)	0.02 ± 0.005 (20)	4.4 ± 0.2 (20)
2007					
Control	98.8 ± 2.2 (20) a	7.4 ± 0.4 (20)	15.2 ± 1.0 (20)	0.1 ± 0.02 (20)	4.7 ± 0.2 (20)
Low varroa	97.9 ± 3.2 (20) a	7.9 ± 0.5 (20)	16.6 ± 0.9 (20)	0.07 ± 0.01 (20)	4.4 ± 0.2 (20)
High varroa	91.1 ± 3.2 (20) b	7.9 ± 0.4 (20)	16.3 ± 0.8 (20)	0.09 ± 0.02 (20)	4.2 ± 0.2 (20)

Foragers came from colonies sustaining one of three levels of varroa mite: low, high, or a treated control with minimized mite loads. Values are mean ± SEM (n). One replication was the average values per cage per day per year. Column means within year with different letters are significantly different ($\alpha \leq 0.05$)

Table 2 Net foraging energy gain for honey bee foragers from colonies sustaining one of three levels of varroa mite: low, high, or a treated control with minimized mite loads

Treatment	Net energy gain per flower (J)	Net energy gain per second handling time (J)	Net energy gain per second total foraging time (J)
2005			
Control	1.4 ± 0.2 (20)	0.3 ± 0.04 (20)	0.13 ± 0.02 (20)
Low varroa	1.1 ± 0.2 (20)	0.2 ± 0.04 (20)	0.12 ± 0.02 (20)
High varroa	0.6 ± 0.1 (20)	0.2 ± 0.03 (20)	0.08 ± 0.01 (20)
2006			
Control	1.1 ± 0.3 (20)	0.1 ± 0.04 (20)	0.08 ± 0.02 (20)
Low varroa	0.9 ± 0.2 (19)	0.1 ± 0.03 (19)	0.07 ± 0.02 (19)
High varroa	0.9 ± 0.2 (20)	0.1 ± 0.03 (20)	0.06 ± 0.01 (20)
2007			
Control	3.1 ± 0.7 (17)	0.5 ± 0.1 (17)	0.22 ± 0.05 (17)
Low varroa	2.5 ± 0.6 (17)	0.4 ± 0.1 (17)	0.18 ± 0.05 (17)
High varroa	3.3 ± 0.8 (17)	0.5 ± 0.1 (17)	0.24 ± 0.06 (17)

Values are mean ± SEM (n). One replication was the average values per cage per day per year

J joules

flower was significantly greater in control colonies in 2005, but other years did not show the same trend (Table 1). Similar inconsistencies were observed with the number of flowers visited per minute, being significantly higher for colonies with varroa in 2005 but not different among groups in 2006 and 2007 (Table 1).

There were no significant effects of colony varroa levels on net energy gain determined per flower, per second handling time, or per second total foraging time (Table 2). Other studies (Kralj and Fuchs, 2006; Kralj et al., 2007) have shown that varroa influences foraging behavior of individual bees in terms of flight duration (nest exit and return times), whereas our study focused on inter-flower movement, flower handling, and nectar ingestion rates. Overall, our data indicate that average honey bee forager energetics were unaffected by colony varroa levels within the ranges used in this study.

In most cases, the design failed to reject a null hypothesis. We have confidence in our design and its null conclusions, however, because (1) average bee weight (mg) predictably and consistently decreased with increasing varroa loads (Table 1), confirming that our methods reliably produced different colony varroa levels, and (2) the experiment was replicated three seasons. Therefore, we

believe that our design is sufficient to accept the null hypothesis that average individual forager profits in *A. mellifera* are unaffected by the range of colony *V. destructor* densities used in this study.

Our results are relevant to the question of the extent to which foraging of individuals relates to colony state in social Hymenoptera. The foraging behaviors of individuals can be expected to integrate with colony state (reviewed by Schmid-Hempel et al., 1993). But it is unclear if this principle applies in the case of varroa. The amount of honey stored per bee per day did not differ among colonies with different varroa levels (Murilhas, 2002); this is consistent with the present results showing that foraging profits per bee did not differ among colonies with different varroa levels.

It may be informative to revisit the hypothesis using the individual as the unit of inquiry, i.e., compare foraging energetics of individuals with different parasite loads. However, the effects of varroa are ambiguous on individual forager rate, a key component in calculating energy consumption. Specifically, the duration of foraging bouts is longer if the bee is presently carrying a phoretic mite (Kralj and Fuchs, 2006) but unaffected if the bee's parasitism is known only as a legacy effect from the pupal stage (Kovac and Crailsheim, 1988). Moreover, it is possible that individual state in a social colony does not predict colony fitness, at least for the short term. One reason for this is that a colony can house individuals with a range of disease or parasite loads. A second reason is the principle that disease- or parasite-handicapped individuals can display precocious foraging or caste ontogeny, phenomena which may temporarily increase, not decrease, colony resource collection (Wang and Moeller, 1970; Schneider, 1986; Schmid-Hempel et al., 1993; Downey et al., 2000).

These kinds of ambiguities are resolved by emphasizing parasites at the level of colony, and we affirm with other authors the pre-eminence of colony as the most appropriate level for studying fitness components in social insects. It is the level of colony at which natural selection acts in social insects generally (Seeley, 1995; Hamilton et al., 2009), in the case of parasites specifically (Schmid-Hempel, 1994; Neumann and Moritz, 2000; Tarpy, 2003), and which most appropriately frames models of host–parasite epidemiology (Schmid-Hempel, 1995).

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