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Research article

The influence of pollen storage area and *Varroa jacobsoni* Oudemans parasitism on temporal caste structure in honey bees (*Apis mellifera* L.)

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Summary. The influence of colony pollen storage and pupal infestation by the parasitic mite *Varroa jacobsoni* on worker longevity, foraging age, and behavior were investigated in the honey bee, *Apis mellifera* L. Workers reared in colonies with low pollen stores began foraging at younger ages and may have had shorter lifespans than workers reared in colonies with high pollen availability. Similarly, workers began foraging at younger ages and had shorter lifespans when they had been infested by *V. jacobsoni* as pupae. The decrease in foraging age and possibly lifespan caused by the pupal infestation was offset by the colony's pollen environment during brood rearing. Therefore, temporal task schedules are affected by both colony investment and parasitism by *V. jacobsoni* during brood rearing.

Key words: Varroa jacobsoni, pollen, honey bees, *Apis mellifera*, temporal polyethism.

Introduction

Workers in a honey bee colony (*Apis mellifera* L.) perform different tasks throughout their lives, and each task is intricately coordinated with the activities of other workers in the nest. As they age, workers move from inside-nest activities such as cell cleaning and brood rearing to outside-nest activities such as foraging and guarding (Seeley, 1982; Winston, 1987). Considerable research has been devoted to elucidating the mechanisms by which workers allocate tasks in this aged-based division of labour (Robinson, 1992; Seeley, 1982). Many factors have been identified that affect worker behavioral schedules, from factors external to the worker such as colony condition and changing environment, to internal factors including genes, morphology and hormones (Gordon, 1996, reviewed by Robinson, 1992) The age at which workers perform tasks is highly variable due to changing colony conditions and individual variation, making it difficult to discern the underlying mechanisms (Gordon, 1996).

Flexibility in worker behavioral schedules has been demonstrated in the honey bee through manipulations of factors important to colony survival. For example, a decrease in worker population (Kolmes and Winston, 1988) and extreme wax deprivation (Fergusson and Winston, 1988) caused workers to begin foraging earlier. This change demonstrated that workers can increase the rate at which they move between tasks in response to changing colony condition. Thus, any variation in the ability of workers to alter their behavioral schedules may have an impact on colony fitness.

Variation exists between individual workers in the same age group which further subdivides workers between tasks (Robinson, 1992) and may affect how workers move between tasks. This variation is thought to be due primarily to factors internal to the worker (Gordon, 1996). These factors may render some workers physiologically adapted to particular tasks, and these workers may perform some tasks more efficiently than their counterparts (Gordon, 1989). Previous research has focused on how worker size may contribute to the efficiency with which workers perform tasks (Kerr and Hebling, 1964), although a clear relationship has not been established (reviewed by Nowogrodzki, 1984). Elucidating the effects of parasitism on individual behavior and relating these effects to the functioning of the colony as a whole may provide a useful approach to the question of individual variation and colony organization.

Little is known about the effects of parasitic infestation on temporal division of labour and how these effects might affect overall colony functioning. The most serious parasitic infestation of honey bees is the mite *Varroa jacobsoni* Oudemans, which feeds and reproduces on honey bee pupae and is

reported to feed on adults (Tewarson, 1983). Honey bee colonies typically die within a few years after mite infestation (de Jong et al., 1982). Workers infested as pupae weigh less, have smaller hypopharyngeal glands and lower haemolymph protein concentrations than workers unparasitized as pupae (Schneider and Drescher, 1987a). Parasitized bees appear to fly sooner and exhibit decreased longevity (Schneider and Drescher, 1987b). Therefore, parasitism by *V. jacobsoni* can increase the variation between individuals in the colony, and lead to altered worker behavioral schedules. However, another study demonstrated no differences between longevity and foraging ontogeny of parasitized and healthy workers observed in the same colony (Kovac and Crailsheim, 1988). Thus, *V. jacobsoni* infestation appears to have a direct impact on temporal caste structure in some contexts and not in others. These discrepancies suggest that individual variation also may be governed by factors external to the worker.

Colony condition during brood rearing may play a pivotal role in the determination of temporal caste structure and individual variation. A common result of disease or parasitic infestation is protein deprivation. Insufficient pollen supply during larval periods leads to decreased lifespan (Kunert and Crailsheim, 1988) and during early adulthood speeds up the adult behavioral sequence (Free, 1961). Workers deprived of pollen may have insufficiently developed hypopharyngeal glands, suggesting that pollen-deprived workers may omit nursing duties and begin foraging at earlier ages (Winston and Fergusson, 1985). Therefore, some individual variation may be due to physiological differences caused by nutritional deficiencies during brood rearing, and adequate nutrition may alleviate variation caused by parasitism. Access to sufficient protein may play an important role in governing individual variability and the flexibility of temporal castes.

Many studies have demonstrated the negative effects of pupal infestation by *V. jacobsoni* on workers, but these effects have not been studied under different colony conditions nor have they been related to overall colony functioning. The objectives of the present study were to determine how pollen deficit and the presence of *V. jacobsoni* interact to affect worker temporal caste schedules.

Methods

This study was conducted from May to August 1996 at Simon Fraser University, Burnaby, British Columbia, Canada. Worker bees were reared in colonies with high or low access to pollen. Some of these bees were experimentally infected as larvae with *V. jacobsoni* mites. This resulted in four treatment groups: high pollen-control, low pollen-control, high pollen-parasitized, and low pollen-unparasitized workers. Workers in each treatment group were individually marked and introduced into an observation hive, and their fates were followed.

Prior to the experiment, two brood rearing colonies, with sister queens, were established and equalized in brood area, adult population and honey stores (16,000 bees, 1400 cm^2 open brood). One colony received additional pollen stores for a total of 2844 cm^2 of pollen and was designated the high pollen brood rearing colony. The low pollen brood rearing colony contained 625 cm^2, and was fitted with a pollen trap to collect incoming pollen.

To dilute genetic effects, frames of eggs were exchanged between the two colonies, and additional frames of eggs were placed into each colony from an outside colony. Only frames with little or no pollen were added. After 8 days, all capped and partially capped cells on the manipulated frames were mapped onto transparent plastic sheets. The map was made in the early evening. On the following morning (12 h later), female *V. jacobsoni* mites were introduced into 300 newly sealed cells that had been sealed since the previous evening in the brood rearing colony. The edge of the capping was cut with a scalpel, a *V. jacobsoni* mite was slipped through the cut, and the opening was then tamped down (de Ruijter, 1987). An additional 300 larvae from each colony received a sham treatment, in which the capping was opened and closed, but no mites were added.

To obtain female mites for introduction, frames of emerging bees were taken from colonies heavily infested with *V. jacobsoni* and were kept at 34 °C. After 3 days, female *V. jacobsoni* mites were removed from the infested bees using the method of Boecking and Ritter (1993). Two days prior to capping, fluvalinate impregnated strips (Apistan ™) were applied to the brood rearing colonies to reduce the likelihood of mite invasion into the larval cells required for the experiment.

These manipulations resulted in four treatment groups: 1) bees reared in a high pollen colony, 2) bees reared in a low pollen colony, 3) infested bees reared in a high pollen colony, and 4) infested bees reared in a low pollen colony. Only workers observed to emerge from a cell were included, so that the cells could be scored for the presence of a mite, and for evidence of mite reproduction. Bees emerging from cells with a dead mite were not included in the experiment. Upon emergence, bees were individually marked with number tags glued on the thorax and matching paint on the abdomen, and were introduced to an observation hive. Four weeks prior to the experiment, a four frame observation hive was set up with 2 frames of brood and some pollen, 1 frame of honey and one empty frame. Wet weights of 20 bees per treatment group were obtained following emergence.

Longevity and foraging observations

The observation hive was surveyed for surviving marked bees every day for the first 5 days and then every sixth day at dawn. Foraging observations were conducted beginning 5 days following the addition of the marked bees to the hive. Bees absent from the colony in the present and subsequent longevity observations were presumed dead. Hive entrances were observed every second day for 30 minutes in the morning and afternoon for marked bees returning to the hive. Foraging flights less than five minutes were discarded as orientation flights. Large increases in short flights, presumably orientation flights, were observed to occur in the afternoon and foraging observations were not conducted at this time. Workers were identified by number and color.

Statistical analyses

To analyze foraging ontogeny and lifespan of observed workers, the Lifereg procedure available on SAS Version 6.0 was used. The Lifereg procedure produces maximum likelihood estimates of parametric regression models of censored survival data. Foraging ontogeny and longevity observations were conducted at intervals and the obtained data were coded as intervals. Those marked workers that were not seen during foraging observation periods but were seen in the longevity observations, were presumed to have begun foraging after the last observation period. Since the observations were conducted at intervals, medians are calculated for both the upper and lower estimates of foraging ontogeny and longevity.

Coefficients were transformed using the equation e^{β}, to yield the estimated ratio of the expected (mean) survival times for the two groups being compared (Allison, 1995). Since the Lifereg analysis does not test for interactions between effects, the combined effect of the two factors were obtained from analysis on the treatments coded as four separate groups. Wald statistics were used to analyze these four groups, with a

Bonferroni adjusted alpha level of 0.008 to decrease the possibility of a Type I error due to multiple comparisons. For further discussion of the Lifereg procedure see Allison (1995).

Pollen status of the brood rearing colony, *V. jacobsoni* infestation and the egg source were included in the Lifereg model as covariates. Likelihood ratio statistics were used to compare models based on the different distributions. The statistical analyses for emergence weights were performed in SAS JMP IN 3.1.5. Means and standard deviations are reported unless otherwise stated.

Results

Workers eclosing from unparasitized pupae weighed 0.10 ± 0.01 g, and had a 12% higher emergent weight than workers parasitized by *V. jacobsoni,* which weighed 0.09 ± 0.01 g ($F = 32.9$, $df = 1,108$, $p = 0.0001$, two-way general linear model with mite reproduction nested in *V. jacobsoni* treatment group). Reproduction by mites in cells further decreased worker emergent weight by 9%, and these workers weighed 0.083 ± 0.012 g ($F = 7.02$, $df = 1,108$, $p = 0.0093$, for reproduction nested in *V. jacobsoni* treatment group). No difference was found in emergent weight between workers reared in a low pollen environment versus workers reared in a high pollen environment ($F = 0.98$, $df = 1,108$, $p = 0.33$).

Workers that had been parasitized by *V. jacobsoni* as pupae began foraging significantly earlier, at the upper and lower median values of 9 days, as compared to unparasitized workers that began foraging between the median values of 13 and 14 days. A 28% decrease in the expected foraging age was estimated from the survival analysis' coefficient using the equation e^{β} ($\chi^2 = 9.8$, $df = 1$, $p = 0.0017$, Lifereg procedure based on a Weibull distribution). Similarly, workers reared in a low pollen colony began foraging between median values of 9 and 10 days, as compared to workers reared in a high pollen colony that began foraging between 15.5 and 19 days. A 21% decrease in the expected foraging age was estimated from the Lifereg coefficient ($\chi^2 = 4.43$, $df = 1$, $p = 0.035$, Lifereg procedure based on a Weibull distribution). When analyzed as four treatment groups, workers reared in a high pollen colony unparasitized as pupae began foraging significantly later (upper and lower medians: 19.5 days) than workers reared in a low pollen colony infested as pupae (upper and lower medians: 9 days) ($\chi^2 = 14.4$, $df = 1$, $p = 0.0001$) (Fig. 1). Egg source was also found to significantly affect foraging age. Workers reared from eggs of sister queens began foraging later than workers reared from an external egg source ($\chi^2 = 8.2$, $df = 2$, $p = 0.016$).

For all workers added to the colony (including both those seen foraging or not), workers that had been parasitized by *V. jacobsoni* as pupae lived between median values of 11 and 13 days, as compared to unparasitized workers that lived between median values of 12 and 15 days. A 20% decrease in expected lifespan was estimated from the survival analysis coefficients for parasitized workers ($\chi^2 = 4.04$, $df = 1$, $p = 0.05$, Lifereg procedure based on a gamma distribution). However, the lifespan of workers reared in a low pollen colony did not differ from workers reared in a high pollen colony ($\chi^2 = 0.18$, $df = 1$, $p = 0.67$, Lifereg procedure based on a gamma distribution). No differences were found when the treatments were analyzed as four separate treatment groups (Fig. 2). Egg source was found to affect longevity, although the effect was marginally significant ($\chi^2 = 0.07$, $df = 2$, $p = 0.07$).

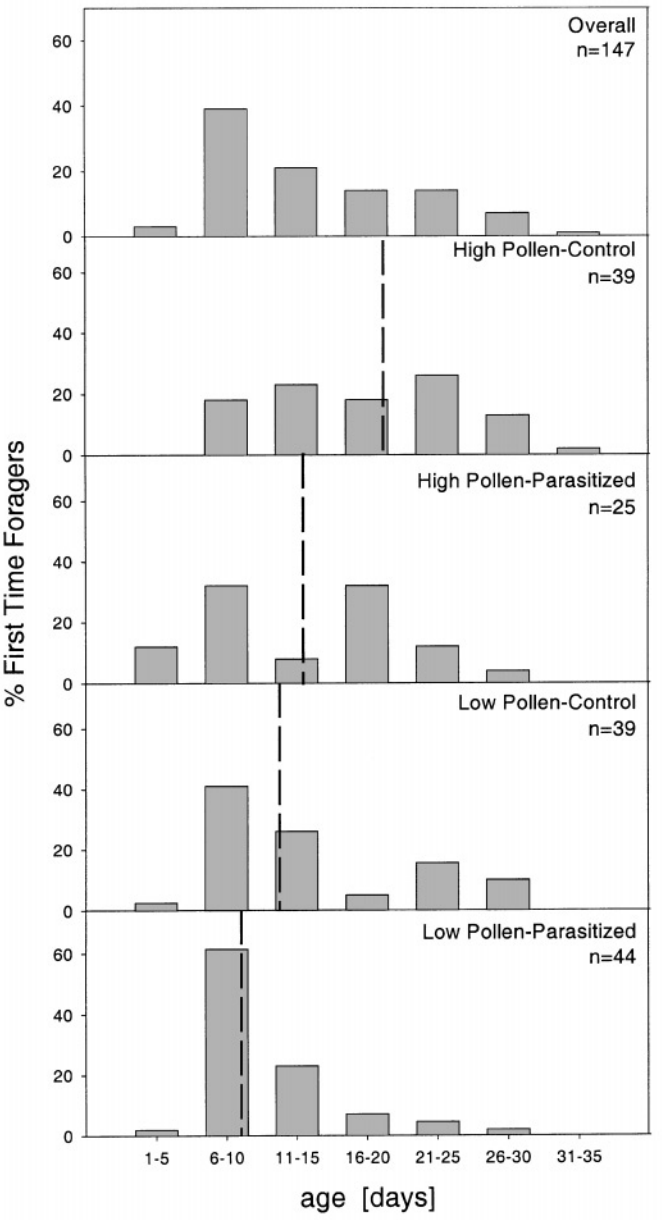

Figure 1. The percentage of foragers that begin foraging during each age interval is displayed for all of the marked foragers and for each treatment group separately. The dashed lines represent mid points between the upper and lower medians for each treatment group

To elucidate the connection between foraging ontogeny and longevity and to remove the effects of colony rejection of marked bees, the longevity of workers seen foraging was analyzed separately. Foragers that had been parasitized by *V. jacobsoni* as pupae lived between median values of 16 and 21 days, as compared to unparasitized workers that lived between 21 and 35 days. A 13.5% decrease in expected lifespan

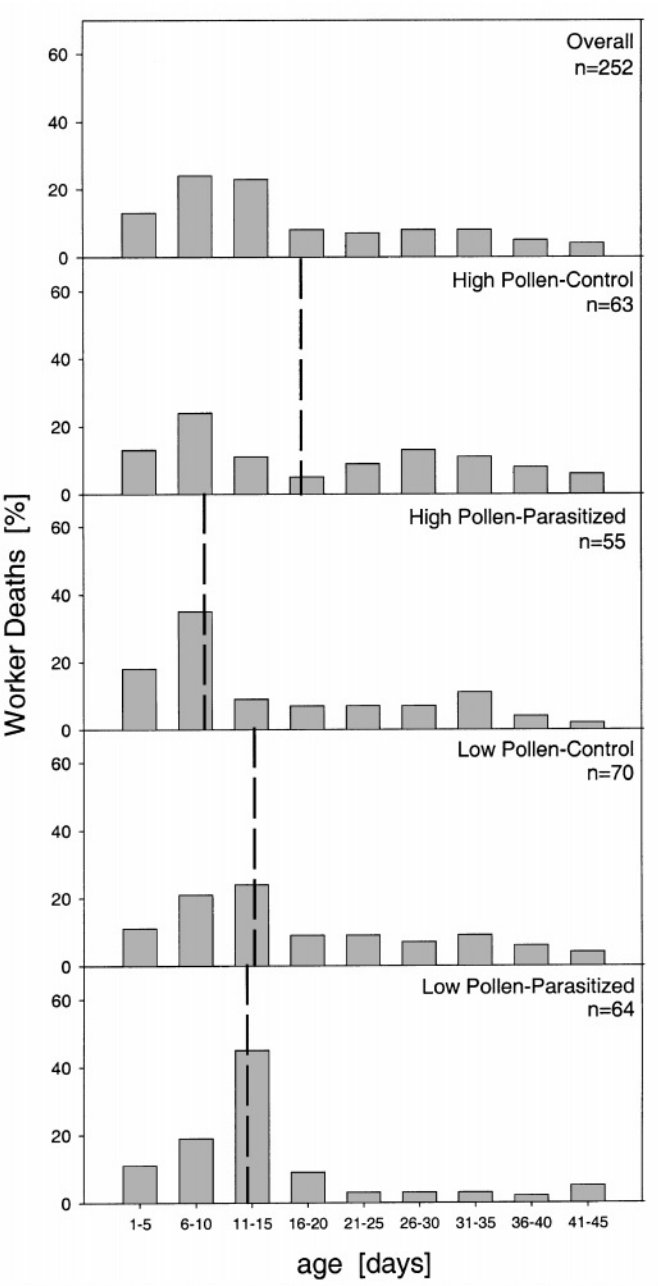

Figure 2. The percentage of workers that die during each age interval is displayed for all of the marked workers and for each treatment group separately. The dashed lines represent mid points between the upper and lower medians for each treatment group

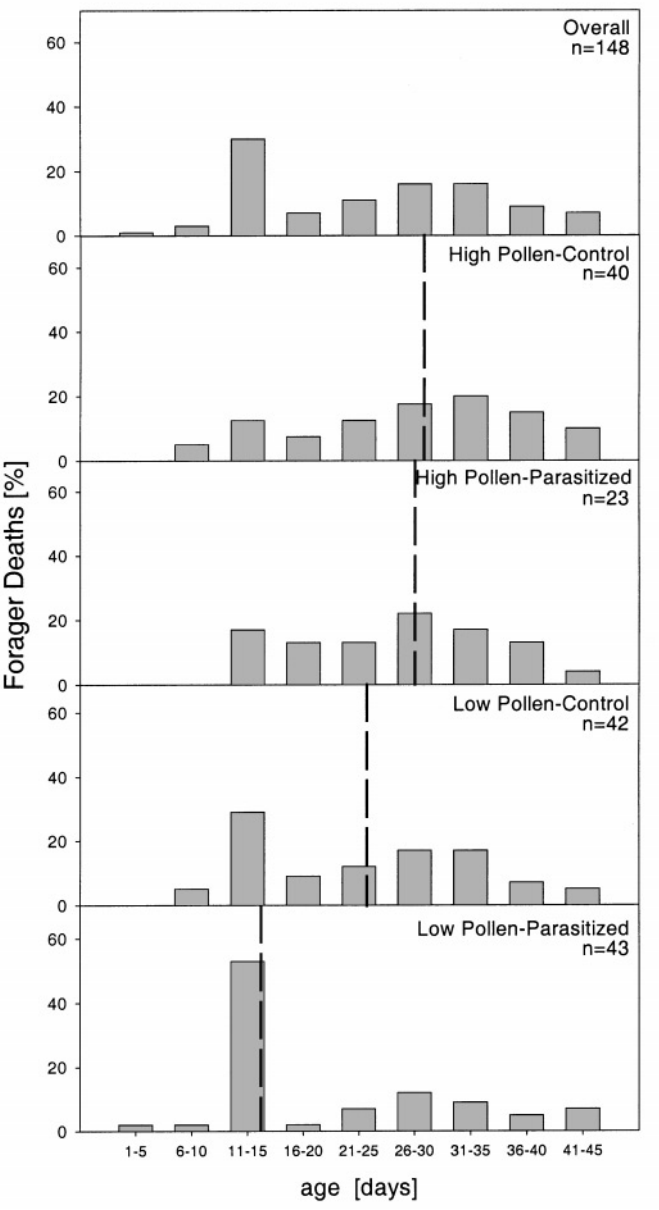

Figure 3. The percentage of foragers that die during each age interval is displayed for all of the marked foragers and for each treatment group separately. The dashed lines represent mid points between the upper and lower medians for each treatment group

was estimated from the survival analysis, although the difference was not significant ($\chi^2 = 2.74$, df = 1, p = 0.1, Lifereg procedure based on a lognormal distribution). Similarly, foragers reared in a low pollen colony had shorter lives (upper and lower medians: 15 and 21 days) as compared to foragers reared in a high pollen colony (upper and lower medians: 22 and 35.5 days). Again the difference was not significant although a 15% decrease in expected lifespan was estimated from the survival analysis ($\chi^2 = 2.79$, df = 1, p = 0.1, Lifereg procedure based on a lognormal distribution). When analyzed as four treatment groups, workers reared in a high pollen colony unparasitized as pupae lived between 22 and 36 days, as compared to an interval of 13 and 16 days for workers reared in a low pollen colony infested with *V. jacobsoni* as pupae. A 31% increase in expected lifespan was estimated from the Lifereg procedure, although the difference was not significant, since a Bonferroni adjusted alpha level of 0.008 was used ($\chi^2 = 6.22$, df = 1, p = 0.013, Lifereg procedure based on a lognormal distribution) (Fig. 3). Again egg source was found to affect forager longevity in a similar manner to its

effect on foraging ontogeny. Workers reared from an external egg source died earlier than workers reared from sister queens ($\chi^2 = 6.17$, df = 2, p = 0.05).

Discussion

The results of this study demonstrate that the age at which workers perform tasks is affected by brood rearing history. Workers begin foraging earlier when reared in a colony with low pollen stores, and they may die earlier. Similarly, an infestation by *V. jacobsoni* during the pupal period caused workers to begin foraging earlier and die younger. Thus, foraging ontogeny and possibly lifespan are determined through a combination of worker genotype, physiological development and colony condition (Gordon, 1996; Robinson, 1992).

Foraging ontogeny

As workers age they typically move from inhive tasks, such as brood rearing, to tasks outside the safety of the hive, such as foraging. The age at first foraging is highly variable, and can range from 3–65 days (Winston and Punnett, 1982), and it is used to indicate how quickly workers are progressing through this ontogenic task sequence. Genetic differences are known to contribute to the variation in foraging ontogeny (Calderone and Page, 1991; Nova and Gary, 1983), and these differences were also noted in the present study. Workers reared from sister queens began foraging later than workers reared from a genetically unrelated queen. The variability in foraging ontogeny is further exaggerated by a worker's ability to adjust the temporal task sequence to changes in colony condition (Winston and Fergusson, 1985).

Aside from genetic effects and variable temporal caste sequences, the effects of the colony environment on the physiology of the individual worker has received little attention. Previous studies have demonstrated that pollen deprivation during early adulthood (Free, 1961), pupal parasitism by *V. jacobsoni* (Downey et al., 2000; Schneider and Drescher, 1987b), and treatment of workers with juvenile hormone (reviewed by Robinson, 1992) leads to younger foraging ages. Similarly, our study has shown that both a poor pollen environment during brood rearing and pupal infestation decrease age at onset of foraging, thereby altering adult worker behavior. Therefore, the age at first foraging is affected by both colony condition, or the magnitude of the foraging task, and worker physiology.

Interestingly, the decrease in foraging age caused by the pupal infestation was offset by the colony's pollen environment during brood rearing. These factors appear to affect workers in a similar fashion, presumably through a decrease in worker protein concentration, and compound in an additive manner. Thus, the overall impact of a *V. jacobsoni* infestation on the adult behavior of a honey bee pupa is affected by the nutritional state of the colony during the worker's larval period. Therefore, with the presence of *V. jacobosoni*, beekeepers need to pay closer attention to protein availability, and possibly feed colonies more pollen supplement when infested with *V. jacobsoni*.

Worker longevity

Worker longevity is one of the most important factors determining growth rates of honey bee colonies (Schmid-Hempel et al., 1993). Previous studies have demonstrated that pollen deprivation during larval periods induces shorter lifespans (Kunert and Crailsheim, 1988) and during early adulthood leads to younger foraging ages (Free, 1961) of deprived workers. Young bees reared in a colony fed a pollen mix lived longer than bees reared in a colony fed a sugar diet (Wahl and Ulm, 1983). In this study, no differences in longevity or emergence weight were found between bees reared in low pollen compared to high pollen colonies. However, there was a strong *V. jacobsoni* effect; workers infested as pupae died significantly earlier and weighed less than uninfested workers. A large proportion of the introduced workers were found to die within the first week after introduction, and it is possible that the marking and introduction procedure contributed to these early losses. A high proportion of workers infested as pupae were rejected from the colony, presumably due to their physical condition and the presence of deformed wings (personal observation). Similarly, other studies have found that bees infested as pupae live significantly shorter lives than uninfested bees (Downey et al., 2000; de Jong et al., 1982; Kovac and Crailsheim, 1988; Schneider and Drescher, 1987).

Worker longevity also is positively correlated with the age at which foraging begins (Winston and Katz, 1981). Worker mortality may occur due to environmental hazards, such as predation and climate, and physical aging (Fukuda and Sekiguchi, 1966), both of which are increased as foraging ages decrease. Therefore, differences detected in longevity were most likely due to foraging ontogeny differences and further treatment effects on longevity cannot be seperated from these effects. Foragers uninfested as pupae, and reared in a high pollen colony may live longer than workers infested as pupae and reared in a low pollen colony (Fig. 3). Although these results were not significant, when using a Bonferroni adjusted p-value, they are analogous to those obtained for foraging ontogeny, and provide further evidence that worker longevity is tied to the age at onset of foraging. Further, they reveal that low pollen availability during brood rearing may increase the impact of pupal infestation on worker lifespan.

The effect of low pollen availability on worker longevity may be further magnified if nurses tending brood had been reared during periods of low pollen availability. Nurse bees require an adequate supply of pollen both during larval and early adult stages to develop adequate hypopharyngeal glands, as well as during their nurse activity to produce protein-rich brood food (Dustmann and von der Ohe, 1988). Preliminary observations suggest that nurse bees reared in low pollen colonies spend less time with brood when placed

together with nurses reared in high pollen colonies (personal observation), indicating that the nursing ability of bees reared in low pollen colonies may be compromised. Together, these observations suggest that low pollen availability may compromise a worker's future ability to nurse brood and the impact of pollen deprivation will extend beyond the immediate brood rearing cycle.

Conclusions

This study has shown that temporal task schedules are affected by past colony investment and worker parasitism by *V. jacobsoni*. Worker response to foraging stimuli was affected by the presence of pollen and/or a parasite during brood rearing, indicating that variation in temporal caste schedules is affected by the condition of the honey bee colony. Further, the effects of pupal parasitism by *V. jacobsoni* are mediated if pollen availability is high during brood rearing. Therefore, factors such as *V. jacobsoni* parasitism and pollen availability provide a new approach to the question of individual variation and colony organization, and they further illuminate the dynamic nature of worker temporal caste schedules. Further studies will lead to a deeper understanding of social insect organization, and provide some management options for beekeepers struggling to manage honey bee colonies infested with parasitic mites or other pests and diseases.

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