THE RELATIONSHIP BETWEEN COLONY STATE AND

INDIVIDUAL FORAGING BEHAVIOUR IN THE HONEY BEE,

Apis mellifera L.

by

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ABSTRACT

This study investigated the relationship between colony state and foraging behaviour in honey bees, *Apis mellifera* L., with an emphasis on the potential for individual foragers to adjust their foraging strategies according to colony needs. In the first study I manipulated colony population sizes and assigned eight honey bee colonies to either SMALL, adult population of 10,000, or LARGE, adult population of 35,000, treatments and observed the responses of individual foragers. Predictions based on a model by Houston and co-workers (1988) suggested that an increase in population size would decrease the relative value of nectar resources. Individual nectar foragers from SMALL colonies should therefore expend a greater work effort than nectar foragers from LARGE colonies. While results were contrary to the specific predictions, and indicated that individual nectar foragers from LARGE colonies exhibited a greater work effort, they did not refute the general model by Houston et. al. (1988). Rather, they indicate that an increase in population size is associated with increases in the relative value of nectar resources. Observations of individual pollen foragers indicated that the relative value of pollen resources increased in SMALL colonies.

In a second experiment I investigated the relationship between colonial brood levels and the behaviour of individual pollen foragers. I manipulated brood levels in eight colonies to either LOW, 1600 cm^2 of brood, or HIGH, 9600 cm^2 of brood, and observed the responses of individual pollen foragers. Pollen provides the only protein source for honey bee colonies, and a positive relationship between colonial brood levels and the relative value of pollen resources to the colony was predicted. Results supported this prediction and indicated an increased pollen demand in

HIGH brood colonies. Observations of individual pollen foragers were consistent with colonial pollen demand, as individuals from HIGH brood colonies carried significantly larger pollen loads than those from LOW brood colonies.

These experiments provide evidence that individual workers can assess their colony's nutritional status and can vary their specific foraging strategies according to the relative value of resources.

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INTRODUCTION

One of the striking characteristics of highly social insects is their ability to integrate efficiently the activities of many individuals into a complex functioning colony. Colony-level selection favours behaviours by individual insects that benefit the colony's reproductive success rather than their own (Darwin 1859; Emerson 1960; Wilson 1971; Oster and Wilson 1978; Seeley 1985). This concept is not incompatible with individual selection since behaviours that benefit the colony's reproduction are likely to favour an individual's own inclusive fitness (Seeley 1985). The result, however, is the emergence of colony-level behavioural strategies which may require individuals to forego optimality in their own behaviours in order to increase the overall success of the colony.

The responses of social insects to changes in colony state can be observed at both the colony level and in individual behaviours. While past research has examined the relationship between colony state and colony level behaviour, relatively little is known about how individuals vary their behaviour in response to changes in colony state. For example, how does an individual pollen forager alter her specific foraging strategy as colonial pollen needs change? How do changes in colony size affect the activity level of an individual nectar forager?

In honey bees, *Apis mellifera*, research has focused on numerous colony-level behaviours that vary in response to changes in colony state. The presence of empty comb is associated with increased nectar collection (Jaycox 1970a,b; Rinderer 1981) and worker temporal polyethism shifts to advance the age of first foraging in response to population loss or wax

deprivation (Winston and Fergusson 1985; Fergusson and Winston 1988). There is a strong positive correlation between foraging age and colony population size (Winston and Punnett 1982) and worker loss results in a downward shift in the age of first foraging (Winston and Fergusson 1985). Winston and Fergusson (1985) also noted an inverse correlation between foraging age and the amount of eggs and larvae in a colony, although a subsequent experiment failed to confirm this effect (Winston and Fergusson 1986). There is also a strong positive correlation between the proportion and number of pollen foragers and the amount of eggs and larvae (Filmer 1932; Fukuda 1960; Free 1967; Todd and Reed 1970; Al-Tikrity et.al. 1972).

Foraging strategies are likely to have a significant effect on colony growth and survival, and present an excellent opportunity for assessing the relationship between individual behavioural strategies and colony state. While honey bee foragers collect a variety of resources including nectar, pollen, propolis and water, it is nectar and pollen which satisfy the energetic and protein requirements of the colony (Winston 1987). In order to rear brood, reproduce, and survive the winter, colonies require annual inputs of between 15 and 30 kg of pollen (Hirschfelder 1951; Louveaux 1958; Seeley 1985) and 60 to 80 kg of honey (Weipple 1928; Rosov 1944; Seeley 1985). Associated with these requirements are mechanisms which increase colony-level foraging efficiency and direct shifts in colony-level foraging behaviours in response to changes in colony needs.

The allocation of workers to either nectar or pollen foraging may be affected by numerous factors. While the actual mechanisms are not well understood, queen odors, the presence of worker larvae, and empty comb

have been found to stimulate nectar collection (Jaycox 1970a,b; Rinderer 1981). Brood odors (Free 1967; Scott 1986), and increased egg laying rates by the queen stimulate pollen collection (Cale 1968), and increased pollen stores reduces pollen collection (Free 1967b; Barker 1971; Moeller 1972; reviewed in Winston 1987). Nectar foragers are also part of a highly organized resource collection system that processes information about the resource distribution in the environment and directs foragers accordingly (von Frisch 1967; Lindauer 1967; Gould 1976; Dyer and Gould 1983; Seeley and Visscher 1988; Seeley 1989).

While workers may be affected by a variety of hierarchical influences that act to integrate their behaviours into an efficient, colony-level strategy, these influences may not necessarily allow the individual forager to assess her colony's nutritional requirements. However, if an individual forager is capable of directly assessing her colony's nutritional status, then variation in her specific foraging strategy is expected. The potential for individual foragers to modify their behaviour according to colony state has generally been overlooked.

This study consists of two separate but related experiments focusing on the relationship between colony state and individual foraging behaviour. The first experiment examined the behavioural response of individual nectar foragers to different colony population sizes. The second examined the relationship between colonial brood levels and pollen collection. These studies provide evidence that colony state affects the relative value of resources, either pollen or nectar, and that individual workers have some

basis for assessing the relative value of resources, based on their colony's nutritional state, and are able to adjust their foraging behaviour accordingly.

POPULATION SIZE AND INDIVIDUAL FORAGING BEHAVIOUR

Introduction

Population size is of critical importance to social insects; a larger population increases colony survival and reproduction (Richards and Richards 1951; Michener 1964; Pomeroy 1979; Little 1979; Cole 1984). A large population size increases survival over winter (Seeley and Visscher 1985; Seeley 1985; Lee and Winston 1987; Winston 1987). Also honey bees reproduce through swarming, and larger swarms that issue relatively early in the spring show considerably better growth and survival than small, late swarms (Lee and Winston 1985a,b; Lee 1985; Seeley and Visscher 1985). Therefore, colonies should strive for maximum growth during the ergonomic stage when the emphasis is on worker production (Oster and Wilson 1978). In this chapter I investigate the effect of population size on individual foraging behaviour in the honey bee, *Apis mellifera*.

The relationship between colony state and individual behaviour has generally been overlooked. For example, optimal foraging theory usually assumes that foragers maximize long-term rate of net energy gain in order to maximize reproductive success (Eg. Schoener 1971; Pyke et.al. 1977; Stephens and Krebs 1986). Some authors, however, have pointed out that this is an over-simplification, and that life history tactics need to be considered (McNamara and Houston 1986; Houston et.al. 1988). This is particularly true for social insects where factors such as colony population size and growth are likely to have strong effects on foraging behaviour.

Colony growth is a function of the production of new workers and the mortality of existing workers, such that maximum growth is achieved when there is greatest difference between production and mortality. However, a foraging strategy that maximizes production may not maximize colony growth rate if the strategy is also associated with a rise in mortality (Houston et.al. 1988). This is supported by Neukirch (1982) who found that worker honey bees that performed tasks requiring high energetic expenditures died sooner. Experimental manipulations of load sizes in honey bees by Schmid-Hempel (1986) indicated that foraging bees take their cumulative metabolic expenditures into account. Workers may be constrained by an effort-related mortality, and should maximize rate of resource retrieval while minimizing energy expenditure. Honey bee behaviour has been found to more closely fit an efficiency maximizing strategy, (benefit−cost)/cost, than a rate maximizing one, (benefit−cost)/time (Schmid-Hempel et.al. 1985; Kacelnik et.al. 1986; Schmid-Hempel 1987)

The value of nectar resources to a colony may vary depending on colony size. Resources delivered to the colony by foragers are either converted into new workers or stored. The effectiveness of the conversion may be affected by colony-state variables such as the number of workers relative to the number of empty cells. Colony size may thus affect conversion efficiency, a hypothesis supported by the observation that colony growth rate is often logistic (Wilson 1971; Brian 1983), such that the per capita growth rate declines in larger colonies (Brian 1953; Allen and Jeffree 1956; Brian 1966; Wilson 1971; Seeley and Visscher 1985). Colony state-dependent conversion efficiencies have significant consequences for individual foraging behaviour (Houston et.al. 1988). Workers in colonies

characterized by a large adult population, thus a low conversion efficiency, should adopt a foraging strategy associated with low energy expenditure in order to maximize colony growth rate. Workers in colonies characterized by a small adult population, thus a high conversion efficiency, can adopt a foraging strategy associated with higher energy expenditure and still maximize colony growth rate (Houston et.al. 1988).

In this chapter I describe a field experiment conducted to observe the behavioural response of individual foragers subjected to large and small population treatments. Using Houston and co-workers (model) I predicted that individual nectar foragers from SMALL colonies should work harder than individuals from LARGE colonies. While my results indicate that individual foragers can vary aspects of their foraging strategy depending on colony population size, they do not support the specific predictions of the model. I therefore discuss a post-hoc modification to the original model.

Materials and Methods

Colony Manipulations

This study was conducted during July and August of 1988, near Fort Langley, British Columbia, Canada. I used eight honey bee colonies, *Apis mellifera* L., housed in standard deep Langstroth equipment. Colonies were randomly assigned to one of two treatments; LARGE and SMALL population size. LARGE colonies were manipulated to contain an adult population of 35,000 ± 1700 workers. SMALL colonies were manipulated to contain an adult population of 10,000 ± 500 workers.

Measurements of brood, honey and pollen areas were made using a frame-sized, plexiglass grid consisting of 32 squares, each with an area of 25 cm^2. The relative brood areas, capped and uncapped larvae and eggs, were balanced between treatment groups to retain the same worker to brood ratio of 10:1. LARGE colonies were stocked with 3500 ± 175 cm^2 brood, while SMALL colonies were stocked with 1000 ± 50 cm^2 of brood. All colonies contained 6400 ± 320 cm^2 of honey, 1600 ± 80 cm^2 pollen and ten frames of drawn-out comb to allow for colony growth.

The day of the manipulation, July 15, was considered to be 'day 0' and all colonies were checked on day 11 for the presence of a healthy queen. All colonies were censused on days 17, 30, and 44 to measure colony growth and reconfirm the presence of a healthy queen. Hive inspections on day 11 and censuses on day 17 revealed that two hives, one from each treatment, had lost their queens, and these hives were deleted from the experiment.

Colony-level Foraging Behaviour

The proportion of pollen foragers in the foraging force was used as an indicator of colony-level response. Throughout the experiment I conducted 10 minute entrance observations on each colony during which the number of pollen carrying and non-pollen carrying foragers returning to the hive was recorded.

Individual Foraging Behaviour

I introduced two cohorts of 100 newly-emerged, individually-marked workers into each colony; the first, 14 days before the manipulation and the second, five days after the manipulation. All marked workers were taken from the same source colony. These workers began to forage at 15 to 20 days after their introduction. Observations of marked foragers were made during 90 minute entrance observations, during which trip times, trip frequencies and load types, either pollen or non-pollen, were recorded. The turn-around time, recorded as hive time, was calculated for bees that were observed both arriving and departing during the observation period.

I compared nectar loads as an additional measure of individual foraging behaviour. On days 13, 15, 20, 27 and 37, I randomly collected 10 returning nectar foragers from each colony at about 10:30 A.M.. Measurements of nectar load volumes were taken directly from the crop of dissected bees using 100 μl pipettes. Sugar concentrations were measured by weight using a Leitz refractometer and converted to concentrations in mg

sugar per μl nectar using the correction factor;

mg sugar/μl nectar $= 1.9149 \times 10^{-7}(\% \text{ sugar})^3 + 3.572 \times 10^{-5}(\% \text{ sugar})^2 + 1.00252 \times 10^{-2}(\% \text{ sugar}) - 0.00018$ (Bolten et.al. 1979; Inouyé et.al. 1980; Otis et.al. 1981).

The actual sugar mass (mg) of each load was then calculated using the converted value for concentration; sugar mass (mg) = concentration (mg/μl) x volume (μl).

Statistics

Data were analyzed in a nested ANOVA design (Sokal and Rohlf 1981, pp.271-320), and intrinsic differences among experimental hives were accounted for using factor "HIVE" nested within "TREATMENT" to identify significant sources of variance. In all cases "TREATMENT*HIVE" was used as an error term. Proportional data were transformed using an arcsine transformation. All data were tested for the assumptions required by an ANOVA and, where the data did not meet these assumptions, the appropriate transformations were made. For all data tables, mean values are listed plus or minus one standard error. Sample sizes are listed as "N" and represent the number of data points entered into the analysis, and in all cases, significance was accepted noted at the 0.05 level.

Results

Hive Census

Brood: Brood area increased significantly in SMALL colonies ($F_{2,4} = 50.23$, $P = 0.001$, Fig. 1) but remained constant in LARGE colonies ($F_{2,4} = 2.20$, $P = 0.23$, Fig. 1) until day 17, after which point brood levels in SMALL colonies could not be distinguished statistically from the levels in LARGE colonies ($F_{1,2} = 0.67$, $P = 0.50$, Fig. 1).

Population: Over the course of the experiment colony population size increased significantly in SMALL colonies from 10,000 to a final average of 18,386, while population levels in LARGE colonies remained constant at approximately 35,000 (Table 1).

Colony-level Response

The proportion of pollen foragers recorded at a set time of day, (10:30 A.M.), for SMALL colonies was significantly greater (36 per cent of the foraging force) than LARGE colonies (19 per cent of the foraging force) (Table 2).

Individual Response

Nectar foragers: Individual foragers from LARGE colonies made longer and more frequent trips than foragers from SMALL colonies. Hive times were not different between treatments (Table 3).

Nectar foragers from LARGE colonies carried larger loads, by volume, than foragers from SMALL colonies (Table 4). Since foragers from SMALL colonies collected nectar with a slightly higher sugar content, the overall mass of sugar per load delivered to the hive was not different between treatments (Table 4).

Pollen foragers: Trip times, trip frequencies and hive times were not different between treatments for pollen foragers (Table 3).

Discussion

Resources delivered to the colony by foragers are either converted into new workers or stored. The simple model by Houston and co-workers (1988) assumes that small colonies convert resources more effectively than large colonies, thus increasing the value of nectar resources for small colonies. Their model predicts that small colonies will accept a greater work effort than large colonies per unit of resource.

Conversion efficiency was higher in SMALL colonies, which increased brood area significantly faster than LARGE colonies (Fig.1) resulting in a significant increase in SMALL colony population sizes (Table 1). Population sizes in LARGE colonies did not change significantly (Table 1). However, observations of individually-marked, nectar-foraging bees foraging from LARGE and SMALL colonies were contrary to the specific predictions of the model; nectar foragers from LARGE colonies exhibited a greater individual work effort than nectar foragers from SMALL colonies. Nectar foragers from LARGE colonies made longer, more frequent trips (Table 3) and carried larger nectar loads (Table 4) than nectar foragers from SMALL colonies.

These results are consistent with observations on the same experimental colonies made by Wolf and Schmid-Hempel (1990). They observed the behaviour of individuals foraging in an artificial patch of flowers and found that nectar foragers from LARGE colonies visited more flowers per trip, with a reduced handling time per flower, than nectar foragers from SMALL colonies.

While my results do not support these specific predictions, they do not necessarily refute the general model. In a general framework, Houston and co-workers' (1988) model merely dictates that colonies which place a higher value on nectar resources should exhibit a greater individual work effort focused on nectar collection. The significance of my results can be considered with respect to colony size, time of year and the value of both nectar and pollen. Rather than emphasize a direct comparison between large and small colonies, a more relevant question might be: What is the best strategy for a colony of a specific size at a particular point in time? Factors of time of year and colony size may interact to affect the value of incoming resources, either pollen or nectar.

Here I consider a post-hoc modification of the original hypothesis. If a colony has attained a large size by mid-summer, then colony-level and individual foraging behaviour should be designed to build the nectar stores needed to ensure over-wintering survival. Nectar resources are therefore assigned a high value. Also, a large colony may be able to bear the costs, in terms of worker mortality, of a greater work effort in order to secure adequate nectar stores. For a small colony in mid-summer seeking to over-winter successfully, the primary goal should be to increase its population rather than nectar stores. In this case the value of pollen, which is required for brood rearing, increases, and nectar may be devalued. Also, a small colony may be unable to bear the short-term costs, in terms of worker mortality, of an increased work effort.

If the effect of season decreases the value of nectar resources for small colonies in mid-summer then individual nectar foragers from larger colonies should exhibit a greater work effort than those from smaller colonies. Also,

small colonies should exhibit an increased colony-level focus on pollen collection.

My results for both nectar and pollen foragers are consistent with these modifications. I observed that, at the colony-level, an emphasis on pollen collection was greater in SMALL colonies which had a greater proportion of pollen foragers than LARGE colonies (Table 2). Unlike the observations for nectar foragers, trip times and frequencies recorded for individual pollen foragers from SMALL and LARGE colonies were not significantly different (Table 3). These data indicate that pollen foragers from SMALL colonies, whose foraging effort was not significantly less than pollen foragers from LARGE colonies, were therefore expending a greater work effort than non-pollen foragers from SMALL colonies, whose foraging effort was significantly less than non-pollen foragers from LARGE colonies. This indicates an increased value of pollen resources in SMALL colonies.

While most studies of foraging behaviour on honey bees have emphasized nectar collection, my results indicate that pollen demand plays a major role in colonial foraging dynamics. The value of both pollen and nectar resources may vary according to colony state, and colony-level foraging behaviour must balance the make up and size of the foraging force according to resource demands. An individual's foraging strategy should balance its work effort with the value of that resource to the colony. However, an increase in the value of pollen resources to a hive does not necessarily require a corresponding decrease in the value of nectar resources to that hive, as there may be colony state conditions which increase the value of both pollen and nectar resources. The value of resources to a hive

may be affected by the interaction of numerous factors including colony size and time of year.

The LARGE and SMALL treatments likely emulate two different stages in colony development, with SMALL colonies behaving like newly-established colonies and LARGE colonies behaving like well-established colonies. The value of pollen is high to a newly-established colony which needs to build up its population to ensure over-wintering success, and colony-level and individual foraging behaviour reflect this increased value. In SMALL colonies, colony population sizes changed over time in accordance with the increased work effort for pollen resources; SMALL colonies grew over the course of the experiment, while the population levels in LARGE colonies remained constant (Table 1). As a colony attains a size adequate to ensure over-winter survival, shifts in the values of pollen and nectar resources are expected. The colony should place a higher value on the nectar resources needed to sustain that population over the winter, while the importance of pollen resources to the colony likely decreases as brood rearing diminishes. This study indicates that individual foragers are able to assess the value of pollen and nectar resources based on their colony state, and can vary their specific behaviours accordingly.

Table 1. Initial and final colony populations and standard errors for
LARGE and SMALL population treatments.

	Initial Population	Final Population	Statistic
Treatment	(Day 0)	(Day 44)	(between days)
LARGE Population	35000 ± 1750 (N = 3)	34619 ± 3662 (N = 3)	$F_{1,4} = 0.01$ P = NS
SMALL Population	10000 ± 500 (N = 3)	18386 ± 2158 (N = 3)	$F_{1,4} = 15.1$ P = 0.017
Statistic (between treatments)		$F_{1,4} = 30.05$ P = 0.018	

Table 2. Proportion of pollen foragers, recorded during 10 minute
observation periods at 10:30 A.M., for LARGE and SMALL
population treatments.

	LARGE Population	SMALL Population	Statistic
Parameter			
Proportion Pollen Foragers	0.19 ± 0.02 (N = 12)	0.36 ± 0.05 (N = 12)	$F_{1,2} = 58.12$ P = 0.02

Note: For each treatment, sample size (N = 12) = 3 colonies x 4 observation
periods.

Table 3. Trip times, trip frequencies and hive times, during 90 minute observation periods, for pollen and non-pollen foragers from LARGE and SMALL population treatments.

Parameter	LARGE Population	SMALL Population	Statistic
Non-pollen Foragers			
Trip Time (seconds)	1667.7 ± 126.4 (N=95)	1210.8 ± 157.6 (N=33)	$F_{1,2}=47.54$ $P=0.02$
Trip Frequency (trips/90 min.)	1.23 ± 0.06 (N=81)	1.00 ± 0.00 (N=38)	$F_{1,2}=29.46$ $P=0.03$
Hive Time (seconds)	827.8 ± 66.0 (N=103)	818.8 ± 118.5 (N=25)	$F_{1,2}=1.14$ $P=0.39$
Pollen Foragers			
Trip Time (seconds)	2683.9 ± 250.7 (N=16)	1680.4 ± 212.6 (N=50)	$F_{1,2}=9.47$ $P=0.09$
Trip Frequency (trips/90 min.)	1.21 ± 0.15 (N=14)	1.41 ± 0.16 (N=46)	$F_{1,2}=0.58$ $P=0.42$
Hive Time (seconds)	849.9 ± 103.3 (N=47)	557.4 ± 57.3 (N=62)	$F_{1,2}=2.92$ $P=0.23$

Note: Sample sizes (N) are based directly on the number of complete observations throughout the experiment.

Table 4. Mean volume, concentration and sugar mass of nectar loads carried by foragers from LARGE and SMALL population treatments.

Parameter	LARGE Population	SMALL Population	Statistic
	(N=153)	(N=122)	
Volume (µl)	19.2 ± 1.0	14.6 ± 0.8	$F_{1,2}=20.14$ $P=0.04$
Concentration (mg/µl)	30.3 ± 1.3	32.6 ± 1.3	$F_{1,2}=0.08$ $P=0.80$
Sugar Mass (mg)	5.2 ± 0.3	4.7 ± 0.4	$F_{1,2}=0.78$ $P=0.47$

Note: Sample size (N ≈ 150) = 3 colonies x ≈ 10 bees x 5 sampling days. Variation around this number resulted due to unusable bees in some cases and occasionally 11 bees were trapped.

Figure 1. Brood areas, eggs and larvae, and standard errors for LARGE
and SMALL treatments. Values with the same letter are not
significantly different at P=0.05.

Figure 1:
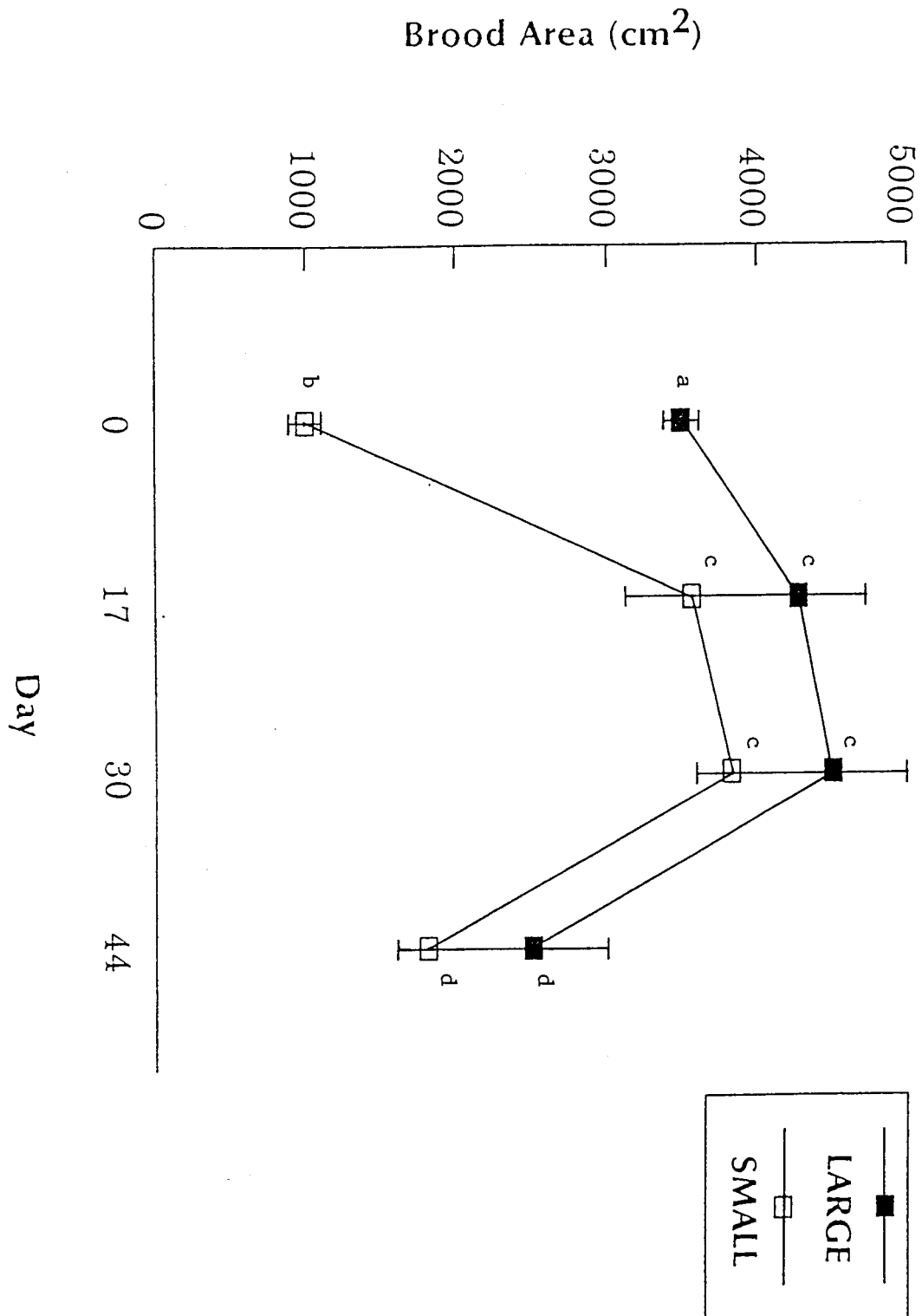
COLONIAL BROOD LEVELS AND POLLEN FORAGING

Introduction

A colony of social insects functions as an organized social unit in which individuals must not only respond to their own survival needs, but must also respond to the needs of the colony as a whole. In honey bees, research has focused on a variety of colony-level behaviours which vary in response to changes in colony state, yet little is known about how individuals vary their behaviour in response to changes in colony state. In this chapter I investigate the effect of variation in brood quantity on pollen foraging in the honey bee, *Apis mellifera*.

Pollen collection by honey bee workers provides an excellent system in which to study the integration of individual behaviours into colony functions. Pollen is collected by honey bees to satisfy their colony's protein requirements, particularly for larval stages but also for adults (Morton 1950; Winston 1987). Numerous studies have found that an increase in eggs and larvae results in an increased proportion and number of pollen foragers (Filmer 1932; Fukuda 1960; Free 1967; Todd and Reed 1970; Al-Tikrity et.al. 1972). An increase in colonial pollen stores is also associated with a decline in pollen collection (Free 1967; Barker 1971; Moeller 1972), and conversely Fewell (1990) noted an increase in the proportion of pollen foragers associated with a reduction in pollen stores.

Past research has placed a strong emphasis on nectar collection, implying that honey bee colonies are primarily "nectar-driven", and in a state in which colonial variation in nectar demand primarily influences both

colony-level and individual foraging behaviour. However, colonies are not viewed as either pollen or nectar "driven", rather the value of both pollen and nectar resources are affected by colony state, and colony-level and individual foraging behaviour reflect changes in the values of these resources.

Previously, I have shown that pollen is likely to attain a higher value in a newly-established colony working to increase growth (Chapter 2). Increased brood levels is a characteristic of a growing colony. Under these conditions, foraging behaviour consistent with an increased value of the pollen resources required for brood rearing is expected. I have investigated this relationship in the experiment presented here.

This study was designed to examine how colony state affects the foraging behavioural of individual workers. I conducted field experiments to observe the behavioural response of individual pollen foragers to high and low quantities of brood. My results show a significant colony-level response to such manipulations. But I also demonstrate that individual pollen foragers can assess the value of pollen and vary the size of their pollen loads depending on the amount of brood present in their colony.

Materials and Methods

Colony Manipulations

This study was conducted during May and June of 1989, near Abbotsford, British Columbia, Canada. I used eight honey bee colonies, *Apis mellifera* L., housed in standard deep Langstroth equipment.

Environmental (Al-Tikrity et.al. 1972) and genetic (Calderone and Page 1988) factors are known to affect pollen collection. I minimized these effects by randomizing colonies among treatments and conducting experiments within a brief period of time in the same location. Colonies were assigned randomly to one of two treatment groups; HIGH or LOW brood. Measurements of brood, honey and pollen areas were made using a frame-sized, plexiglass grid consisting of 32 squares each with an area of 25 cm^2. HIGH brood colonies were manipulated to contain similar amounts of capped and uncapped brood, totalling 9600 $\pm$ 480 cm^2, and LOW brood colonies were stocked with 1600 $\pm$ 80 cm^2 of brood, again with half capped and half uncapped. All colonies contained 9600 $\pm$ 480 cm^2 honey stores, 1600 $\pm$ 80 cm^2 pollen stores, and adult populations of 25,000 $\pm$ 1200 workers.

The day of the manipulation was considered to be 'day 0', and all colonies were censused on day 7 and day 15 to determine the amounts of capped and uncapped brood, honey and pollen.

I conducted the experiment twice, from the 4th of May to the 19th of May and then from the 20th of May to the 4th of June. To control for colony effects, all colonies were switched treatments between experiments.

Colony-level Foraging Behaviour

The total number of foragers and the proportion of pollen foragers were examined to determine if the manipulations resulted in a colony-level response. I conducted two five minute entrance observations at each hive on each day, once in the morning and again in the afternoon, during which the number of pollen carrying and non-pollen carrying foragers returning to the hive were recorded. For both colony-level and individual behaviours, observations avoided census and rainy days and were made on days 1, 2, 4, 5, 9, 10, and 11.

Individual Foraging Behaviour

The mass of individual pollen loads was used to investigate individual foraging behaviour. I collected ten returning pollen foragers from each colony about noon on each sampling day. Pollen loads were removed from the corbicula of each hind leg and the total mass (mg) of each load was recorded. I also recorded each bee's mass and extracted the crop contents using a 100 µl micropipette to compare the amounts of nectar carried by pollen foragers.

Statistics

Data were analyzed in a nested ANOVA design (Sokal and Rolff 1981, pp. 271-320), and intrinsic differences among experimental hives were accounted for using factor "HIVE" nested within "TREATMENT" to identify significant sources of variance. In all cases "TREATMENT*HIVE" was used as the error term. Proportional data were transformed using an arcsine transformation. All data were tested for the assumptions required by an ANOVA and, where the data did not meet these assumptions, the appropriate transformations were made. For all data tables, mean values are listed plus or minus standard errors. Sample sizes are noted as "N" and represent the number of observations entered into the analysis. In all cases, significance was accepted at the 0.05 level.

Results

Hive Census

Uncapped brood: The area of uncapped brood was significantly different between treatment groups only at initial manipulation; no significant differences were found at the end of weeks 1 and 2 (end of week 1, $F_{1,14} = 0.26$, $P = 0.62$; end of week 2, $F_{1,14} = 0.001$, $P = 0.96$, Fig. 1a)

Pollen stores: HIGH brood colonies exhibited a significant reduction in pollen stores during week 1, while LOW brood colonies remained constant ($F_{1,14} = 6.27$, $P = 0.03$, Fig. 1b). At the end of week 2, the treatments were not significantly different ($F_{1,14} = 0.48$, $P = 0.50$, Fig. 1b).

Honey stores: Honey stores (Fig. 1c) did not vary significantly between treatments (end of week 1, $F_{1,14} < 0.01$, $P = 0.96$; end of week 2, $F_{1,14} < 0.01$, $P = 0.98$), and within each treatment group honey levels did not vary significantly between weeks ($F_{1,2} = 2.58$ $P = 0.09$).

Colony-level Response

Proportion of pollen foragers: HIGH brood colonies had a significantly higher proportion of pollen foragers during week 1 than did LOW brood colonies (Table 1). The proportion of pollen foragers was not significantly different between treatment groups during week 2 (Table 1).

Total foragers: The total number of foragers during weeks 1 and 2, was not significantly different between treatment groups (Table 1).

Individual Response

Pollen loads: No significant relationship was found between individual bee mass and pollen load by regression analysis ($r^2 = 0.025$). There were significant differences by "DAY" for individual pollen loads and I therefore analyzed pollen load data separately for each day during weeks 1 and 2. On day 2, individuals from HIGH brood colonies collected significantly larger pollen loads than did individuals from LOW brood colonies ($F_{1,6} = 7.13$, $P = 0.03$, Fig.2). Pollen loads were not significantly different between treatment groups during week 2 ($F_{1,14} = 0.39$, $P = 0.54$).

Some pollen foragers were observed to collect both pollen and nectar on the same trip, but the frequency of this behaviour was not significantly different between treatment groups ($F_{1,14} = 1.78$, $P = 0.20$).

Discussion

In large colonies of social insects with a highly developed system for the division of labour, it is not necessary for all individuals to assess the many parameters which define the overall state of their colony. Past research focusing on variation in colony-level behaviour associated with colony state, has concluded that individuals are integrated into colony-level behaviours and directed according to colony needs. My results indicate that variation in colony state, colonial brood levels, is associated with both variation in colony-level behaviour, in the proportion of bees foraging for pollen, and variation in individual behaviour, in the size of pollen loads carried.

Colony State Development

Pollen satisfies the protein requirements of honey bee colonies, and an increase in eggs and larvae should produce an increased demand for pollen. Hive censuses confirmed that HIGH brood colonies exhibited a significant reduction in pollen stores immediately following manipulations (Fig. 1b) indicating an increased pollen demand.

Responses to variation in brood levels should be most pronounced immediately following the manipulations, since rapid egg laying by queens in LOW brood colonies and sealing of uncapped brood in HIGH brood colonies quickly equalized the two treatment groups. There were no significant differences in the areas of uncapped brood between treatment groups by the end of week 1 (Fig. 1a).

Colony-level Response

My results confirm that an increase in brood area is associated with an increased proportion of pollen foragers (Table 1) (Filmer 1932; Fukuda 1960; Free 1967; Todd and Reed 1970; Al-Tikrity et.al. 1972). These results indicate that mechanisms exist which coordinate colony-level behaviours in response to changing colony requirements.

While an increase in total foragers associated with an increased demand for pollen is expected, the colony-level behavioural response is likely constrained by an increased demand for within-hive bees to tend larval brood. I observed that HIGH brood colonies did not increase their total foragers in response to an increased demand for pollen, suggesting that colonies with medium populations may not have a large surplus of workers that can be re-allocated to foraging as colony requirements change.

Individual Response

I observed that, immediately following brood manipulations, individual pollen foragers from HIGH brood colonies carried significantly larger loads than individuals from LOW brood colonies (Fig. 2, day 2). This is consistent with the expectation that individual pollen foragers can adjust their foraging strategy depending on their colony's pollen requirements. Individuals must have some basis for assessing colony state and can use their assessment to make foraging decisions.

My observations indicate that individuals can increase their foraging effort under the stressed conditions of increased brood levels, and suggest

that individuals do not constantly forage at some maximal effort. The potential costs of increased work effort may result from an increase rate of physical deterioration (Neukirch 1982) or an increased risk of predation. However, when the immediate needs of the colony increases the value of pollen resources, the individual may bear the potential costs of an increased foraging effort to satisfy those needs.

To predict whether an individual worker is expected to vary her foraging behaviour in response to changes in colony state, the type of information available to that forager should be considered. While the mechanism for this assessment is not known, pollen foragers deliver their loads directly to pollen storage cells (Winston 1987), so that after every trip they could re-assess colonial pollen needs. Pollen foragers are thought to use brood pheromones as a signal for assessing brood levels (Free 1967; Jaycox 1970b; Scott 1986) and, in delivering their load directly to storage cells, they may be able to continually assess pollen stores relative to brood pheromone signals. In this way, individual pollen foragers could base their specific foraging strategy on a direct assessment of the colony's nutritional status. My results, which indicate that the response by individual pollen foragers to brood manipulations was immediate and did not linger after treatments had equalized, are consistent with this prediction.

Other recent studies of colony state and pollen foraging confirm that individuals are able to assess various colony state parameters and vary their foraging strategy accordingly. Higo and co-workers (1990) found that individual pollen foragers from colonies treated with the appropriate supplemental dose of synthetic queen pheromone carried significantly larger pollen loads than individuals from control colonies. Fewell (1990)

manipulated colonies to contain low pollen stores and found that individual pollen foragers from those colonies carried significantly larger loads than foragers from colonies with high pollen stores, suggesting that, while pollen foragers may use brood pheromones, they are also able to make an assessment of colonial pollen needs based on pollen stores alone. In each of these studies, the manipulations likely raised the value, or at least the perceived value in the case of synthetic queen pheromones, of pollen resources to the colony. In each case, individual pollen foragers were observed to adjust their behaviour in response to the value of the resource.

For an individual bee, the choice of what to forage for may be directed by colony-level organizing mechanisms which balance the demand for both pollen and nectar resources. However, the choice of how to forage is likely based on that individual's ability to determine the value of the resource through an assessment of colony state variables and balance its own work effort against the value of that resource to the colony.

Table 1. Mean number of total foragers and proportion of pollen foragers measured during five minute counts for HIGH and LOW brood treatments.

Treatment	Total Foragers		Proportion Pollen Foragers	
	week 1	week 2	week 1	week 2
HIGH Brood	306.3 ± 25	400.3 ± 11	0.31 ± 0.03	0.36 ± 0.02
LOW Brood	365.4 ± 35	390.3 ± 12	0.21 ± 0.02	0.34 ± 0.03
Statistic				
$F_{1,14}$	2.35	0.27	6.49	0.43
P	0.15	0.61	0.02	0.52
N	20	24	20	24

Note: In each case, sample size (N) = 4 colonies x no. of observation periods.

Figure 1:

1a. Mean area of uncapped brood, eggs and larvae, and standard errors for HIGH and LOW brood treatments for two weeks followings colony manipulations.

1b. Mean area of pollen stores and standard errors for HIGH and LOW brood treatments for two weeks following colony manipulations.

1c. Mean area of honey stores and standard errors for HIGH and LOW brood treatments for two weeks following colony manipulations.

In all cases, data points marked with the same letter are not significantly different at the $P = 0.05$ level.

Figure 2. Mean mass of individual pollen loads and standard errors for HIGH and LOW brood treatments during weeks 1 and 2. Data have been analyzed separately for each day during this period. Sample sizes, on each day for each treatment, ranged from 39 to 41, and "*" denotes significant differences at the $P = 0.05$.
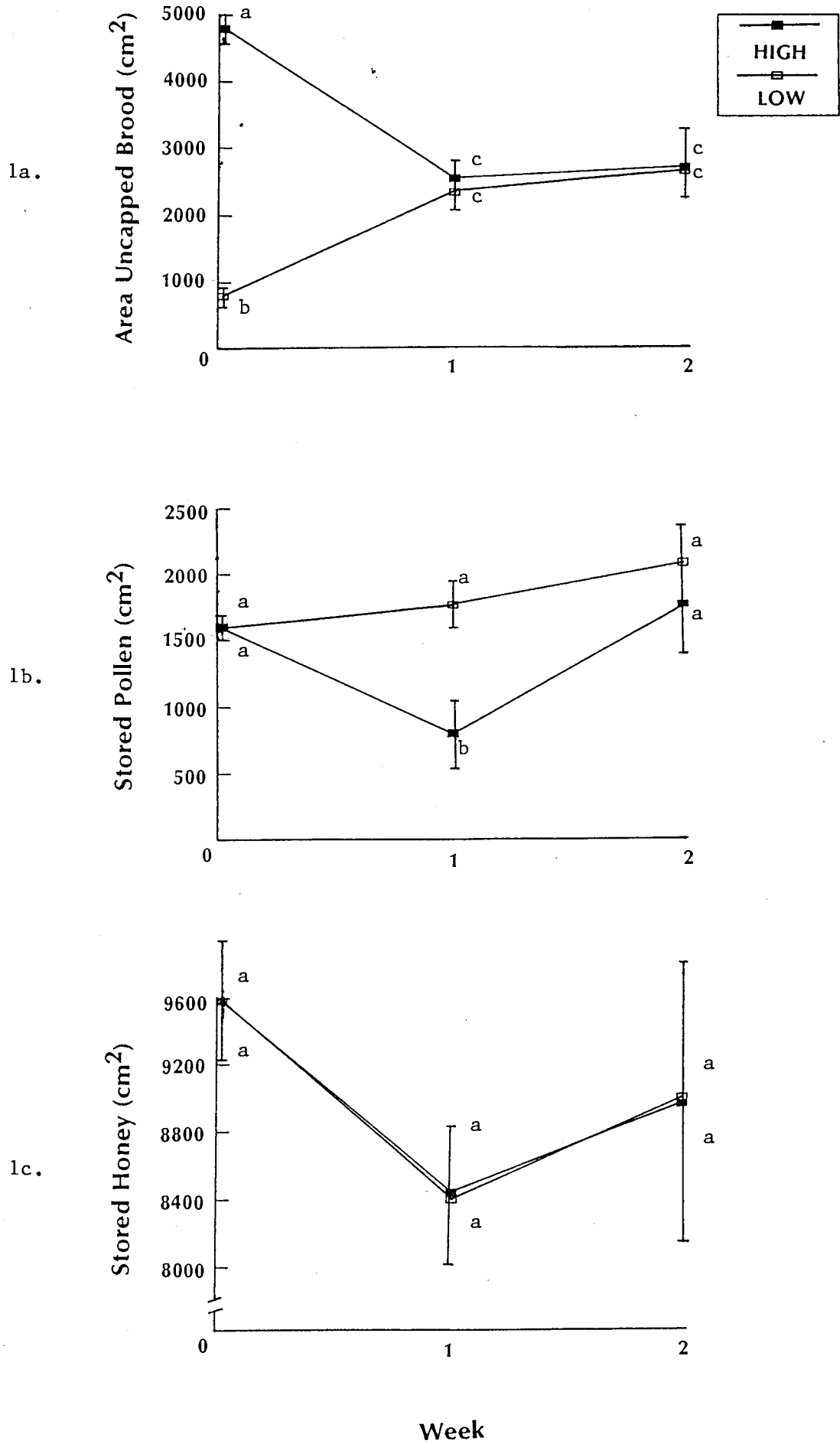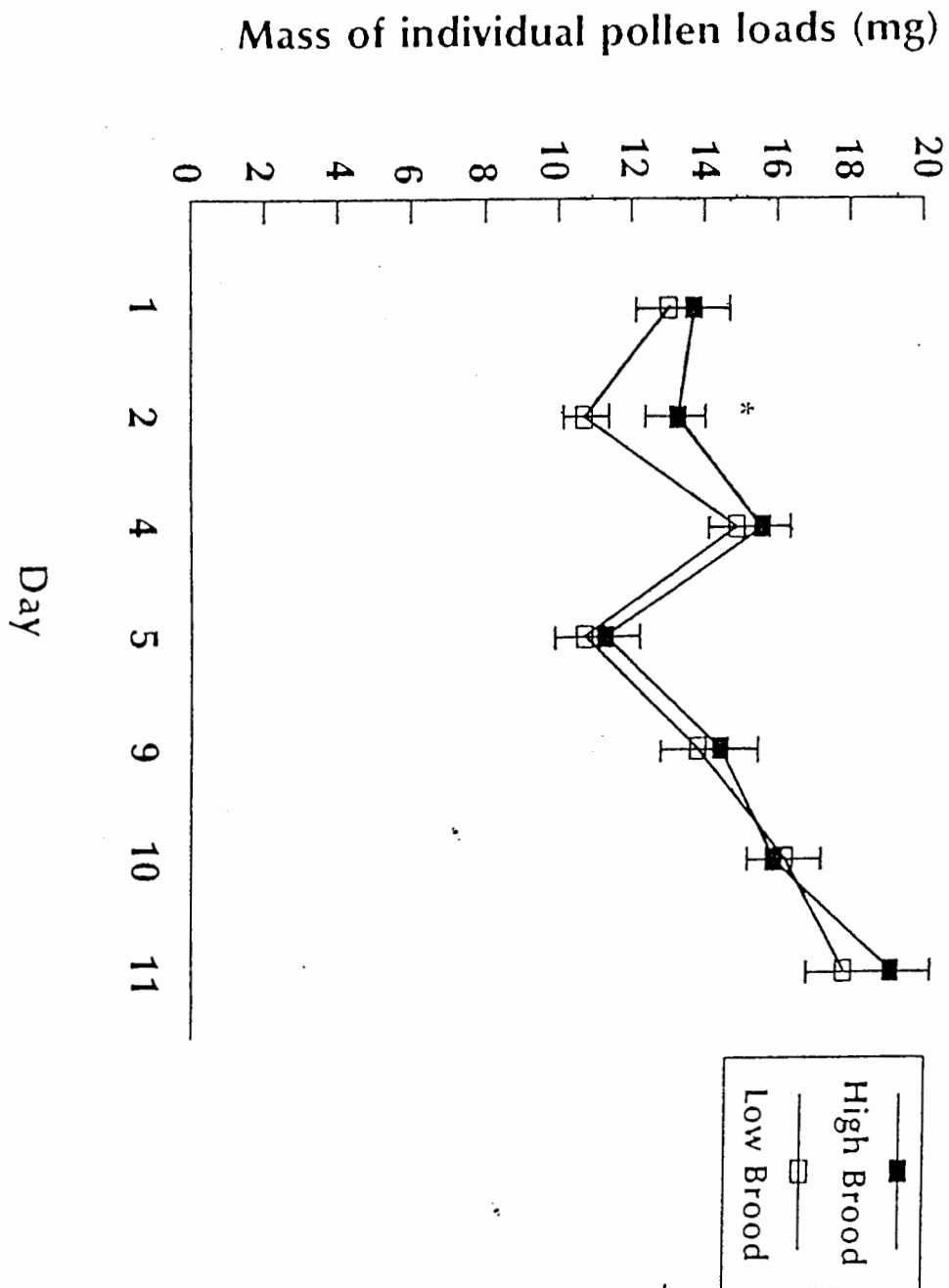
Figure 1:

Figure 2:

SUMMARY

This study has demonstrated that colony state can have a significant effect on both colony-level and individual foraging behaviour. The individual, while functioning as a part of the colony-level foraging strategy, is able to assess the nutritional status of the colony and vary her specific foraging strategy accordingly.

The Population Study, (Chapter 2), focused primarily on nectar foragers and showed that colony size affects the value of nectar resources which is reflected in the foraging effort of individuals foraging for nectar from LARGE and SMALL colonies. LARGE colonies assign a high value to nectar resources and individual nectar foragers from those colonies exhibit a greater work effort than individual foragers from SMALL colonies. However, there were no significant differences in work effort between treatments, for pollen foragers indicating that in SMALL colonies, pollen was assigned a high value compared to nectar. These results indicate that colony size can affect the values of both pollen and nectar resources; LARGE colonies placed a higher value on nectar resources than SMALL colonies, while SMALL colonies placed a higher value on pollen resources than LARGE colonies. The manipulation of colony size likely affects the perceived life cycle stage of the colonies. SMALL colonies behaved like newly-established colonies, which should place a high value on the pollen resources needed to build the population. LARGE colonies behaved like well-established colonies, which should place a high value on the nectar resources needed to over-winter successfully.

Although the primary focus of the Population Study, (Chapter 2), was on nectar foragers, this study showed that at early stages of the colony cycle, colonies tend to increase the value of pollen resources and the subsequent Brood Study, (Chapter 3), sought to examine this effect more closely.

The primary goal of a colony during early stages of the colony cycle, should be to increase its population size through an emphasis on brood rearing. It is the elevated brood levels which increases colonial pollen demands and thus the value of pollen resources. The Brood Study, (Chapter 3), confirms this as individual pollen foragers from HIGH brood colonies exhibited a significantly greater foraging effort, immediately following manipulations, than individuals from LOW brood colonies.

These two studies suggest that during the growth and development of honey bee colonies, the value of pollen and nectar resources shift. Colonies are neither pollen nor nectar "driven", rather, the values of pollen and nectar fluctuate depending on the immediate needs of the colony. There may be colony state conditions which increase the value of both pollen and nectar resources to a hive. While it is well established that a colony can adjust its overall foraging strategy in response to colony state, this study provides evidence that individual workers can assess their colony's nutritional status and vary their specific foraging behaviour according to the value of resources.

While this study increases our understanding of how colony state and foraging behaviour interacts, it also raises numerous interesting questions. Investigations into the behaviour of individual pollen foragers at the flower and its relationship to colony state would provide a better basis for

comparing pollen and nectar foragers. Observations of individual nectar and pollen foragers combined with very close monitoring of colony resources would increase our understanding of exactly how and when shifts in resource values occur. Finally, an overall recognition of the importance of the relationship between pollen resources and colony state and the behavioural variation of both individual pollen and nectar foragers, would result in a stronger basis for future investigations into these questions.

REFERENCES

Allen, M.D., and E.P. Jeffree. 1956. The influence of stored pollen and colony size on the brood rearing of honey bees. Ann. Appl. Biol. 44: 649-656.

Al-Tikrity, W.S., Benton, A.W., Hillman, R.C., and W.W. Clarke. 1972. The relationship between the amount of unsealed brood in honey bee colonies and their pollen collection. J. Apic. Res. 11: 9-12.

Barker, R.L. 1971. The influence of food inside the hive on pollen collection by a honey bee colony. J. Apic. Res. 10: 23-26.

Bolten, A.B., Feinsinger, P., Baker, H.G., and I. Baker. 1979. On the calculation of sugar concentration in flower nectar. Oecologia 41: 301-304.

Brian, M.V. 1953. Brood rearing in relation to worker number in the ant *Myrmica*. Physiol. Zool. 26: 355-366.

Brian, M.V. 1966. Inefficiency in brood-rearing in the ant *Myrmica rubra* L. Insectes Sociaux 3: 71-74.

Brian, M.V. 1983. **Social Insects**. Chapman and Hall, London.

Calderone, N.W., and R.E. Page. 1988. Genotypic variability in age polyethism and task specialization in the honey bee *Apis mellifera* (Hymenoptera: Apidae). Behav. Ecol. Sociobiol. 22: 17-26.

Cale, G.H. 1968. Pollen gathering relationship to honey collection and egg laying in honey bees. Amer. Bee J. 108: 8-9.

Cole, B.J. 1984. Colony efficiency and the reproductivity effect in *Leptothorax allardycei* (Mann). Insectes Sociaux 31: 403-407.

Darwin, C.R. 1859. **On the origin of species**. New American Library Inc., New York, N.Y.

Dyer, F.C., and J.L. Gould. 1983. Honey bee navigation. Amer. Sci. 71: 587-597.

Emerson, A.E. 1960. The evolution of adaptation in population systems. In: **Evolution after Darwin**, Vol. 1. Sol Tax, ed., pp.307-348. University of Chicago Press, Chicago, Ill.

Fergusson, L.A., and M.L. Winston. (1988). The influence of wax deprivation in temporal caste structure in honey bee (*Apis mellifera* L.) colonies. Can. J. Zool. 66:1997-2001.

Fewell, J.H.. (1989). Foraging effort and population size in the honey bee, *Apis mellifera* L. (in prep.)

Fewell, J.H. (1990). The relationship between food stores and foraging effort in the honey bee, *Apis mellifera* L. (in prep.)

Filmer, R.S. 1932. Brood area and colony size as factors in activity of pollination units. J. Econ. Entomol. 25: 336-343.

Free, J.B. 1967. Factors determining the collection of pollen by honey bee foragers. Anim. Behav. 15: 134-144.

Frisch, K. von. 1967. **The dance language and orientation of bees**. Harvard University Press, Cambridge, Mass.

Fukuda, H. 1960. Some observations on the pollen foraging activities of the honey bee, *Apis mellifera* L. (preliminary report). J. Fac. Sci. Hokkaido University (ser 6) 14: 381-386.

Gould, J.L. 1976. The dance-language controversy. Q. Rev. Biol. 51: 211-244.

Higo, H., Slessor, K., and M.L. Winston. 1990. Colony development, foraging behaviour and synthetic queen pheromones in the honey bee, *Apis mellifera*. In Prep.

Hirschfelder, H. 1951. Quantitative Untersuchungen zum Polleneitragen der Bienenv lker. Z. Bienenforsch. 1: 67-77.

Houston, A.I., Schmid-Hempel, P., and A. Kacelnik. 1988. Foraging strategies, worker mortality and the growth of the colony in social insects. Am. Nat. 131: 107-114.

Inouyé, D.W., Favre, N.D., Lanum, J.A., Levine, D.M., Meyers, J.B., Roberts, M.S., Tsao, F.C., and Y-Y Wang. 1980. The effects of nonsugar nectar constituents on estimates of nectar energy content. Ecology 61: 992-996.

Jaycox, E.R. 1970a. Honey bee queen pheromones and worker foraging behaviour. Ann. Entomol. Soc. Amer. 63: 222-228.

Jaycox, E.R. 1970b. Honey bee foraging behaviour: responses to queens, larvae, and extracts of larvae. Ann. Entomol. Soc. Amer. 63: 1689-94.

Kacelnik, A., Houston, A.I., and P. Schmid-Hempel. 1986. Central-place foraging in honey bees: the effect of travel time and nectar flow on crop-filling. Behav. Ecol. Sociobiol. 19: 19-24.

Lee, P.C. 1985. Reproduction and growth of temperate evolved bee colonies (*Apis mellifera* L.). M.Sc. Thesis. Simon Fraser University, Burnaby, B.C.

Lee, P.C., and M.L. Winston. 1985a. The influence of swarm size on brood production and emergent worker weight in newly founded honey bee colonies (*Apis mellifera* L.). Insectes Sociaux 32: 96-103.

Lee, P.C., and M.L. Winston. 1985b. The effect of swarm size and date of issue on comb construction in newly founded colonies of honey bees (*Apis mellifera*). Can. J. Zool. 63: 524-527.

Lee, P.C., and M.L. Winston. 1987. Effect of reproductive timing and colony size on survival, offspring colony size and drone production in the honey bee (*Apis mellifera*). Ecol. Entomol. 12:187-195.

Lindauer, M. 1967. Recent advances in bee communication and orientation. Ann. Rev. Entomol. 12: 439-470.

Little, M. 1979. *Mischocyttarus flayipes* in Arizona: social and nesting biology of a polistine wasp. Z. Tierpsychol. 50: 282-312,

Louveaux, J. 1958. Recherches sur la récolte du pollen par les abeilles (*Apis mellifica* L.). Ann. Abeille 1: 113-188, 197-221.

McNamara, J.M., and A.I. Houston. 1986. The common currency for behavioural decisions. Am. Nat. 127: 358-378.

Michener, C.D. 1964. Reproductive efficiency in relation to colony size in hymenopterous societies. Insectes Sociaux 11: 317-342.

Moeller, F.E. 1972. Honey bee collection of corn pollen reduced by feeding pollen in the hive. Amer. Bee J. 112: 210-212.

Morton, K. 1950. The food of worker bees of different ages. Bee World. 32: 78-79.

Neukirch, A. 1982. Dependence of life span of the honey bee (*Apis mellifera*) upon flight performance and energy consumption. J. Comp. Physiol. 146: 35-40.

Otis, G.W., Winston, M.L., and O.R. Taylor. 1981. Engorgement and dispersal of Africanized honey bee swarms. J. Apic. Res. 20: 3-12.

Oster, G.F., and E.O. Wilson. 1978. **Caste and Ecology in the Social Insects**. Princeton University Press, Princeton, N.J.

Pomeroy, N. 1979. Brood bionomics of *Bombus ruderatus* in New Zealand (Hymenoptera: Apidae). Can. Entomol. 111: 865-874.

Pyke, G.H., Pulliam, H.R., and E.L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52: 137-154.

Richards, O.W., and W.J. Richards. 1951. Observations on the social wasps of South America (Hymenoptera: Vespidae). Trans. R. Entomol. Soc. 102: 1-170.

Rinderer, T.E. 1981. Volatiles from empty comb increase hoarding by the honey bee. J. Apic. Res. 24: 161-167.

Rosov, S.A. 1944. Food consumption by bees. Bee World 25: 94-95.

Schoener, T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2: 369-404.

Scott, C.E. 1986. Biology and management of wild bee and domesticated honey bee pollinators for tree fruit pollination. Ph.D. diss., Simon Fraser University, Burnaby, B.C.

Schmid-Hempel, P. 1986. Do honey bees get tired? The effect of load weight on patch departure. Anim. Behav. 34: 1243-50.

Schmid-Hempel, P. 1987. Efficient nectar collection by honey bees. I. Economic models. J. Anim. Ecol. 56: 209-218.

Schmid-Hempel, P., Kacelnik, A., and A.I. Houston. 1985. Honey bees maximize efficiency by not filling their crop. Behav. Ecol. Sociobiol. 17: 61-66.

Seeley, T.D. 1985. **Honeybee Ecology**. Princeton University Press, Princeton, N.J.

Seeley, T.D. 1989. Social foraging by honey bees: how nectar foragers assess their colony's nutritional status. Behav. Ecol. Sociobiol. 24: 181-189.

Seeley, T.D. and P.K Visscher. 1988. Assessing the benefits of cooperation in honey bee foraging: search costs, forage quality, and competitive ability. Behav. Ecol. Sociobiol. 22:229-237.

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.

Sokal, R., and F.J. Rohlf. 1981. **Biometry**. 2nd Ed. W.H. Freedman and Comp., New York, N.Y.

Stephens, D.W., and J.R. Krebs. 1986. **Foraging Theory**. Princeton University Press, Princeton, N.J.

Todd, F.E. and C.B. Reed. 1970. Brood measurement as a valid index to the value of honey bees as pollinators. J. Econ. Entomol. 63: 148-149.

Weipple, T. 1928. Futterverbrauch und Arbeitsleistung eines Bienenvolkes im Laufe eines. Jahres. Arch. Bienenk. 9: 1-21.

Wilson, E.O. 1971. **The Insect Societies**. Harvard University Press, Cambridge, Mass.

Winston, M.L. 1987. **The Biology of the Honey Bee**. Harvard University Press, Cambridge, Mass.

Winston, M.L. and L.A Fergusson. 1986. Influence of the amount of eggs and larvae in honey bee colonies on temporal division of labour. J. of Apic. Res. 25(4);238-241.

Winston, M.L. and L.A. Fergusson. 1985. The effect of worker loss on temporal caste structure in colonies of the honey bee (*Apis mellifera* L.). Can. J. Zool. 63: 777-780.

Winston, M.L. and E.N. Punnett. 1982. Factors determining temporal division of labour in bees. Can. J. Zool. 60: 2947-52.

Wolf, T.J., and P. Schmid-Hempel. (1990). On the integration of individual foraging strategies with colony ergonomics in social insects: nectar-collection in honey bees. Behav. Ecol. Sociobiol. (in press).