

**Foraging task specialisation  
and  
foraging labour allocation  
in  
stingless bee colonies**

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# **Foraging task specialisation and foraging labour allocation in stingless bee colonies**

**Specialisatie in foerageertaken  
en de verdeling van foerageerarbeid  
in angelloze bijen kolonies**

(met een samenvatting in het Nederlands)

## **Proefschrift**

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# Chapter 1

## General introduction

### Division of labour in stingless bees

As in all eusocial insect species, one of the major features of stingless bee colonies is the division of labour among colony members. This division is thought to enhance task performance due to (temporal) specialisation on a certain task (Oster and Wilson 1978). Division of labour in social insect colonies involves primarily that between queens and workers. Stingless bee queens are morphologically and behaviourally specialised in reproductive tasks. The workers perform tasks related to colony survival and are not reproducing, or only male producing, themselves (Chinh *et al.* 2003). Queens and workers thus belong to distinctly different castes, where switches between reproductive castes in adult life are not possible.

In addition, a secondary division of labour among workers exists. In a bee colony workers can perform several tasks, from nursing to foraging. The distribution of the bee workers over the different tasks is associated with worker age, although there is high plasticity in this temporal distribution, as workers pass through age castes at different rates and individual differences occur in predisposed preferences for certain tasks (reviewed by Gordon 1996). This so-called age polyethism is influenced by environmental stimuli, as has been shown in honeybees (Gordon 1996), and probably also by the bee's own experience (Seeley 1995). In honeybees, genetic factors also strongly influence the division of labour in workers (Calderon & Page 1988). In the different temporal worker castes, a division can be made between tasks that need a physiological, morphological or learning ability specialisation, as for example nursing and foraging, and tasks that can be performed by any worker as the need arises, such as receiving nectar (Johnson 2005). Environmentally induced switches



between tasks do occur, although switches that require a type of specialisation might take several days (Johnson 2005). This makes the distribution of workers over the different tasks, especially the ones that do not need specialisation, more flexible than the division of labour concerning reproduction.

A third level of division of labour can be found within the temporal worker caste “foraging” (honeybees: Seeley 1995; stingless bees: Biesmeijer 1997). Although foragers tend to specialise on the performance of one foraging task for shorter or longer periods, workers are physically able to perform all foraging tasks. Foragers performing different tasks do not show physical differences, as in reproductive division of labour, nor do they differ in age (Free 1967, Biesmeijer & Tóth 1998), as in temporal worker castes. This results in a very flexible division of foraging labour, which does not result in different “foraging castes” but in different “foraging groups”. Participation of workers in these forager groups can differ from moment to moment and is dependent on a combination of external and internal factors (Calderon & Page 1988, Seeley 1995; Biesmeijer 1997).

External factors concern the immediate environment of the individual forager, such as behaviour of other colony members, food availability and colony needs. Honeybee foragers, for example, switch tasks as the result of changes in pollen storage, (Fewell & Winston 1992, 1996, Fewell and Bertram 1999, Johnson 2002; Rotjan *et al.* 2002).

Internal factors influence the level of response to an environmental factor or, in other words, the probability of performing a certain foraging task. The previous experience of an individual can be such an internal factor, as has been shown clearly in stingless bees (Biesmeijer *et al.* 1998). Also in bumblebees it has been observed that successful foragers are less likely to switch foraging tasks, as a result of changes in colony needs, than less successful foragers (Cartar 1992). Other internal factors that influence division of foraging tasks in social bees are rearing environment (Oster & Wilson 1978) or genetic make-up (honeybees: Robinson & Page 1989, Fewell & Bertram 2002, stingless bees: Ranger & O’Donnell 1999). Recently, much attention is given to a genetic basis for foraging performance of individual honeybees (Dreller 1998, Fewell & Bertram 2002, Ranger & O’Donnell 1999, Calderon & Page 1992, Fewell & Page 2000, Oldroyd *et al.* 1994, Page *et al.* 1995).

In *Apis mellifera* a high level of intra-colonial genetic diversity has been found, resulting from high degrees of polyandry. Workers of a honeybee colony are daughters of the same mother, but can have different fathers, since the queen mates with many drones, even exceeding the number of 30 mates (Moritz *et al.* 1996). It is assumed that genetically different individuals differ in sensitivity to external stimuli for a given task (Fewell & Roberts 2000). This would result in differences in task performance between individuals. Some



“patrilines” show a propensity to collect pollen, while others show a high degree of nectar collection. Genotypic variation results in a high number of specialised honeybee foragers, but does allow the colony to respond flexibly when external stimuli for a certain task change.

Stingless bee queens, however, are generally considered to mate with only one male (Peters *et al.* 1999), although cases of multiple mating have been reported for some species (Imperatriz-Fonseca *et al.* 1998). In one case of a polyandrous or polygynous stingless bee species, genetically based task specialisation has been found (Ranger & O’Donnell 1999). Intrinsic variation in foraging task preference, however, can also result from many other environmental factors, such as larval feeding (Oster & Wilson 1978).

Although models do exist showing that efficient foraging task allocation can emerge from systems based on identical workers following the same rules (Bonabeau *et al.* 1996), it seems safe to assume that foragers of both honeybees and stingless bees show individual variability in their tendency to perform certain foraging tasks.

## Foraging behaviour

Growth, survival and reproduction of eusocial bee colonies are all dependent on efficient resource influx. Pollen and nectar form the most important components of social bee resources, but also the collection of water, resin and mud are important for colony survival in stingless bees.

For bees, nectar serves as a source of carbohydrates for energy, and pollen as a source of protein mainly for feeding larvae. Eusocial bees are thus totally dependent on flowering plants for their food. Since food availability changes from season to season, and even within a day, food collecting behaviour of perennial colonies like those of stingless bees takes place in a very dynamic foraging environment.

Colonies should thus be able to adjust their foraging labour to changes in environmental conditions. That the dynamics in foraging environment influence colony foraging behaviour can be seen clearly in the daily foraging pattern of social bees (honeybees: Roubik & Buchmann 1984, Seeley 1995; stingless bees: Roubik 1989, Biesmeijer 1997, Bruijn de & Sommeijer 1997). Pollen is generally most abundantly available in the early morning, and becomes more scarce later in the day. Nectar on the other hand is produced throughout the day, and sugar concentration increases over the day by evaporation. Indeed, in many stingless bee species it has been found that pollen is collected earlier in the day than nectar (Bruijn de & Sommeijer 1997, Roubik 1989, Biesmeijer 1997) and nectar collection peaks around noon (Biesmeijer 1997; Bruijn de



& Sommeijer 1997). Colony foraging behaviour is not only affected by food availability patterns: food quality, climatic conditions, competition between species and colony needs can also play a major role in social bee foraging patterns (Seeley 1995, Biesmeijer 1997, Slaa 2003).

Living on an unpredictable food source may have serious implications for the survival of adult bees and a steady production of brood. To adjust foraging behaviour to the current situation, colonies have to reallocate the labour that is available for foraging over the different foraging tasks. Understanding the ways through which social bee colonies can change foraging behaviour is essential for understanding how these colonies can respond adaptively to an unpredictable environment.

There are two ways in which social bee colonies can adjust the *labour* devoted to different foraging tasks; 1) adjust the *total foraging force* allocated for a particular task and 2) adjust the *individual effort* of foragers already working on the task (Anderson & Ratnieks 1999, Johnson 2002, Rotjan *et al.* 2002). An increase in foraging force for a particular task can be attained in two ways. Firstly, individuals can switch from other foraging tasks to the required task. Switching foraging tasks is physically possible and has been observed in both stingless bee (Biesmeijer & Tóth 1998) and honeybee foragers (Ribbands 1952). Specialising on one foraging task, however, is thought to result in more efficient foraging and switching tasks might be costly (Oster & Wilson 1978). Indeed, bumblebee foragers that specialise on either nectar or pollen, contribute more to the colony's food-intake than bees that switch regularly between food commodities (O'Donnell *et al.* 2000). Another reason why switching tasks is thought to be less efficient is the loss of foraging labour directed towards the other foraging tasks, which results in a decrease of influx of that particular resource.

Apart from forager task switching, increasing the foraging force for a particular task can also be achieved by allocating new foragers to the task. This assumes a reserve supply of labour that can be allocated over foraging tasks in response to stress. Indeed, in honeybees, large numbers of unemployed workers can be found that serve as back-up forces (Seeley 1995, Kolmes 1985). Colony size, however, might play a major role in the availability of back-up forces. As stingless bee colonies are mostly significantly smaller than honeybee colonies, the presence of a large number of non-active workers seems less likely.

Adjustments in individual foraging effort can also result in changes in labour devoted to a certain foraging task. Individual foragers can adjust both their individual foraging tempo as well as the load size they carry.

Most studies on modifications in foraging labour allocation due to environmental changes focussed on pollen stress in honeybees (Fewell and Winston 1992, 1996, Fewell & Bertram 1999, Johnson 2002, Rotjan *et al.*



2002). Honeybee colonies exposed to sudden decrease in pollen stores, adjusted foraging behaviour mainly by allocating non-foragers to the task of pollen foraging (Fewell & Bertram 1999; Rotjan *et al.* 2002) and by increasing individual foraging activity for pollen collection (Fewell & Winston 1992, Rotjan *et al.* 2002). So far, only one study has addressed adjustments in foraging labour in stingless bees (Biesmeijer *et al.* 1999). This study focussed on the response of *Melipona beecheii* colonies to experimental pollen stress. The observed increase in pollen foraging was the result of intensified individual foraging activity and an increase in pollen foragers, but it was uncertain whether this increase originated from allocated non-foragers or from switching active foragers. As this study was performed in the field, influences from changes in food availability, in addition to the induced pollen stress, could not be excluded.

## Aims of this thesis

The objective of the present study was a systematic investigation of the occurrence and plasticity of foraging task specialisation and the dynamics of forager allocation in stingless bees. With the data obtained in this study I aim to offer a contribution to the basic understanding of how social insect colonies can respond adaptively to an unpredictable environment.

As a model for this study we mainly used the stingless bee *Plebeia tobagoensis* Melo. We chose this species because *P. tobagoensis* can easily be kept in climatically controlled rooms with artificial feeding and because this stingless bee species forages well under greenhouse conditions. Colonies of this species are of intermediate size (100-1500 individuals) compared to other stingless bee species, but significantly smaller than honeybee colonies.

## Outline of this thesis

As foraging behaviour is not controlled centrally, colony foraging patterns are the result of foraging choices of individual workers. Therefore, in the following three chapters of this thesis I focus on factors involved in foraging choices and foraging performance of individual foragers.

As the initial commodity choice of individuals is thought to have a major influence on their future foraging career (Biesmeijer 1997), factors involved in the foraging choice of novice stingless bee foragers are investigated in Chapter 2. In this chapter I also investigated whether initial choice indeed affects future foraging choices in *P. tobagoensis*.



During their foraging career individuals can focus on the collection of one food commodity (specialise) or switch regularly between the collection of different commodities. As specialisation is thought to enhance individual foraging efficiency, I present data on occurrence and dynamics of individual specialisation in foragers of *Plebeia tobagoensis* in Chapter 3. The second aim of this chapter was to study whether specialised individuals indeed perform better than bees that switch between commodities. In Chapter 4, more data are presented on individual foraging performance in an analysis of the effects of foraging experience on performance in *P. tobagoensis*.

Through these three chapters I aim to provide more insight in the development of individual foraging careers and the occurrence and benefits of individual specialisation.

In the remainder of the thesis I investigate colony-level foraging patterns and their relation to factors both inside and outside the nest. I aim to unravel some of the mechanisms used by colonies to adapt to changes in their environment by reducing the colony foraging pattern to changes in foraging behaviour of individual workers.

In Chapter 5, I describe the ways through which *P. tobagoensis* colonies can adjust the distribution of foraging labour over the different foraging tasks when a new foraging task is presented. In this chapter, I mainly focus on the difference in labour provided by new foragers and foragers previously engaged in collecting other commodities. In Chapter 6, I present the results of a field study on the influence of a change in food availability on the allocation of foraging labour. This study was performed with another species of stingless bee, *M. beecheii*, in El Salvador. In Chapter 7, data is presented on how changes inside the nest affect colony foraging patterns and where this extra labour devoted to foraging originates from at the individual level in *P. tobagoensis*.

The results of the studies presented in this thesis are summarised and discussed in Chapter 8.



## Chapter 2

# Influence of environmental and colony factors on initial commodity choice of foragers of the stingless bee *Plebeia tobagoensis* (Hymenoptera; Meliponini)

*With: MJ Sommeijer*

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### Summary

Novice foragers of social bees have to decide what food commodity to collect when they start foraging for the first time. In this decision making process two types of factors are involved: internal factors (the response threshold) and external factors (environmental and colony conditions). In this study we will focus on the importance of two external factors, pollen storage level and information from experienced foragers about food availability in the field, on the initial commodity choice of foragers of the stingless bee species *Plebeia tobagoensis*. We also studied the effect of the initial choice of individuals on their subsequent foraging career. This study was performed in a closed greenhouse compartment, where food availability and colony condition could be controlled. Information on food availability in the field from experienced foragers and pollen storage level both greatly influenced the initial commodity choice of individuals, with more choices for the commodity communicated by experienced foragers or lacking in storage. The initial choice of foragers is of importance for their future foraging career, although a substantial proportion of foragers did switch between food commodities. Because of the ability of novice foragers to become flexibly distributed over foraging tasks, social bees are able to respond to changes in their environment without directly having to decrease foraging effort devoted to other foraging tasks. This, in combination with individual flexibility during foraging careers makes it possible for colonies of *P. tobagoensis* to forage efficiently in an ever-changing environment.



## Introduction

Living in a dynamic environment, eusocial bee colonies need to be able to adjust to countless changes inside and outside the colony. As expected, honeybee and stingless bee colonies can adjust the allocation of foraging labour to nectar or pollen collecting in response to variation in colony condition and food availability in the field (Biesmeijer *et al.* 1999, Fewell & Winston 1992, 1996, Seeley 1995). Food collection in bee colonies is not centrally controlled. Neither the queen nor single workers possess all information needed for centralised control nor do such individuals direct the foraging behaviour of other colony members in a centralised way (Gordon 1996). Instead each foraging individual decides by itself when, where and what to collect on every foraging trip it makes.

Two factors are involved in the foraging decision making process of individual workers (summarised in concept of Biesmeijer & de Vries 2001): 1) internal factors; the memory of the bee and the response threshold, that determine the response to foraging stimuli and 2) external factors; environmental and colony conditions, which determine the degree of exposure to stimuli associated with the decision (Biesmeijer & de Vries 2001, Fewell & Bertram 1999, Fewell & Page 2000, Gordon 1996, Robinson & Page 1989, Seeley 1995, Biesmeijer *et al.* 1998).

Experienced foragers of stingless bees (Biesmeijer *et al.* 1998) and honeybees (von Frisch 1967, Seeley 1995, Biesmeijer & Seeley 2005), for example, mainly use information from their own previous foraging trips (internal information) to decide what and where to collect, while information from nest mates (external information) is mainly used to decide when to initiate foraging.

Because an individual forager tends to revisit the same food source after having been successful on it (Biesmeijer *et al.* 1998, Seeley 1995), the initial choice for collecting a certain type of commodity has a major influence on future foraging choices, and consequently on the colony foraging behaviour. To understand the organisation of colony foraging behaviour, it is therefore important to study how commodity choice is regulated in novice foragers.

### **Internal factors involved in initial commodity choice of foragers**

Novice foragers do not have a memory on previous foraging conditions yet. But there are various other intrinsic factors that might play a role in commodity choice of these individuals. The preceding in-hive tasks do not seem to play a role in initial commodity choice of stingless bee foragers (Biesmeijer & Tóth 1998) nor does the age of the individual (honeybees: Ribbands 1952; stingless bees: Biesmeijer *et al.* 1998, Sommeijer *et al.* 1983).



Although genetic effects on food commodity choice have been indicated for honeybees (Fewell & Page 2000, Robinson & Page 1989), the influence of genes on foraging choices in stingless bees is still largely unknown. Genetically based commodity preference has been demonstrated in one polygynous or polyandrous species of stingless bees, *Partamona bilineata* (Ranger & O'Donnell 1999). Since stingless bees are generally known to be monogynous and monoandrous, within-colony diversity is expected to be lower in most other species. However, since intrinsic variance can also arise from environmental factors, e.g. larval food composition (Oster & Wilson 1978), intrinsic factors can not be ruled out as an influence on initial commodity choice in stingless bee foragers.

### **External factors involved in initial commodity choice of foragers**

Although various studies have shown that environmental and colony conditions influence colony foraging behaviour and foraging of experienced foragers both in honeybees and stingless bees (Biesmeijer *et al.* 1999, Seeley 1995), the influence of such factors on the initial foraging choice of foragers has not been studied before.

Information on environmental conditions can be obtained from returning foragers. In both honeybees (Seeley 1995) and stingless bees (Biesmeijer *et al.* 1998) returning successful foragers have a positive influence on the reactivation of experienced foragers. Studies on recruitment behaviour indicate that returning successful foragers can recruit large numbers of previously non-active foragers in most stingless bees (Aguilar 2004, Nieh 2004, Aguilar *et al.* 2005). This probably includes the recruitment of novice foragers. Information on the availability of specific food sources could thus be transferred and thereby influence the initial commodity choice of foragers.

Colony condition influences both colony and individual foraging behaviour of honeybees (Camazine 1993, Fewell & Bertram 1999, Fewell & Winston 1992) and stingless bees (Biesmeijer *et al.* 1999). The degree of pollen storage, for example, is known to affect both the number of pollen foragers and the activity of individuals (Biesmeijer *et al.* 1999, Camazine 1993, Fewell & Winston 1992, Rotjan *et al.* 2002). It is not known, however, if and to what extent this factor influences the initial commodity choice of foragers.

In this study we focus on the *initial* commodity choice of stingless bee foragers. To improve the insight in the organisation of colony foraging behaviour in stingless bees we investigated whether colony storage level (colony condition) and information from experienced foragers on food availability in



the field (environmental condition) influence the initial commodity choice of novice foragers of the stingless bee *Plebeia tobagoensis*. We also compared the initial choice of bees with their subsequent foraging career.

## Materials and methods

### Bee colonies and experimental conditions

The experiments were conducted in a closed greenhouse compartment (15m×5m×4m) in the botanical gardens of Utrecht University, The Netherlands. Inside the compartment, no other food sources were present besides the ones we used for the experiments. As a pollen source, ten flowering plants of *Spathiphyllum sp.* were installed in a group formation. A feeder, consisting of a plate (15 cm × 10 cm) with fifty small holes filled with sucrose solution (50% w/w, with vanilla essence (5 µl/100 ml)), served as a nectar source. These food sources (nectar and pollen) were placed next to each other at a distance of three meters from the entrance tube of the colony. Both food sources were novel to the bees, as they were different from the pollen and syrup fed to the colonies before the start of the experiment. The minimum temperature in the greenhouse compartment was set at 20°C.

Six stingless bee colonies of *Plebeia tobagoensis* Melo (2003), originating from Tobago (Trinidad and Tobago, West Indies), were used for the experiments. Colonies consisted of 700–1200 individuals and a physogastric and productive queen. Each colony was first kept for 10 months in a climate room at the Utrecht University. During this period, the colonies were fed daily with syrup (unscented sucrose solution 50% w/w) and pollen (originating from *Melipona favosa* colonies of Tobago). The syrup and pollen were placed directly into the storage area of the hive and bees sometimes covered the provided food with wax, leaving a small hole open at the top, as if it were a storage pot. Because of this way of feeding and because individuals were not able to forage outside of the hive in this period, we defined the individuals of every colony as a novel forager at the start of the experiments in the greenhouse compartment.

In each colony, at least 100 individuals were marked with UniPosca water-based odourless paint markers one day before the start of the experiment. In order to mark individuals that had a foraging tendency, we first placed the colony in a small room with natural light but without any food. Here the colonies were opened only for a short period and all individuals that flew out were captured and marked with individual colour combinations on the thorax. From previous experiments it is known that these paint marks last for at least 6 days.



**Table 1:** Summary of procedure for all experiments. Indicated are the conditions of all experiments on both days and the colonies used for each experiment.

Experiment:	Day 1	Day 2	Colonies
Pollen storage	Low pollen storage High nectar storage	High pollen storage High nectar storage	Colony 1 and 2
Information on food availability	Information on nectar No information on pollen	Information on nectar Information on pollen	Colony 3 and 4
Information on food availability	Information on pollen No information on nectar	Information on nectar Information on pollen	Colony 5 and 6
Control	High pollen storage High nectar storage Information on nectar Information on pollen	High pollen storage High nectar storage Information on nectar Information on pollen	Colony 4 and 2

### Experimental procedure on initial commodity choice of foragers

To study the influence of external factors on the initial commodity choice of foragers, we designed experiments in which we could examine individual responses in respect to different conditions inside the colony and to different information levels on food availability in the field (Table 1).

Each experiment designed for this study lasted two days. On the first day of each experiment, we either induced a difference in the degree of the pollen storage compared to nectar storage (colony condition) or in the information on pollen availability in the field compared to nectar availability (environmental condition). On the second day, both the degree of nectar and pollen storage and the information on nectar and pollen sources were equalised again. In addition, we designed a control experiment without differences between pollen and nectar storage or differences between information on nectar and pollen availability in the field. A control experiment that did not allow any information flow from returning foragers was practically not possible, as all bees (novice and experienced) stopped foraging when the majority of foragers did not return from foraging trips.

Comparing the distribution of initial choices for nectar or pollen between those two days with the Chi-square test with Yates' Correction for Continuity, made it possible to determine the effect of these factors on the



initial commodity choice of individuals. The Chi-square test for goodness of fit was used to test if there was a preference for one of the commodities as initial choice within one day.

Each experiment was performed twice with a different colony (Table 1). The control experiment was performed with two colonies already used in these experiments (colony 4 and colony 2), but because more than 8 months were between these experiments it was certain that all experienced foragers had died. Each experiment started at 09:30 and observations stopped at 15:00, after which all foragers were returned to the colony and the hive entrance was closed.

**Degree of pollen storage:** To induce a difference between pollen and nectar storage, the used colony was deprived of pollen feeding for one week before the start of the experiment. In both colonies used in this experiment the deprivation resulted in brood-cannibalism before the start of the experiment. Brood-cannibalism also occurred in pollen-stress experiments with the stingless bee *Melipona beecheii* and might be a common response of stingless bees to pollen stress (Biesmeijer *et al.* 1999).

One hour before the start of the experiment, one colony was placed in the greenhouse compartment. The experiment started as soon as the hive entrance was opened. Marked individuals visiting the food sources were recorded. Unmarked individuals visiting the food sources were captured and kept in separate glass jars for each food source. In this way the initial choice of marked and unmarked novice foragers could be observed. At the end of the first day the unmarked individuals were counted, marked and returned to the colony. After this we restored pollen stores by placing 5 plastic tubes (5 ml) filled with pollen (originating from *Melipona favosa* colonies of Tobago) in the hive.

On the second day of the experiment (now without pollen stress), the initial choice of foragers (that had not been foraging on day 1) was recorded in the same way. This experiment was carried out twice with different colonies (colony 1 and colony 2).

**Information on food availability in the field:** By preventing successful foragers of one of the food sources (either nectar or pollen) from returning to the hive, novice foragers inside the hive could obtain information only about one of the two available food sources. To avoid contamination of this experimental set-up by large differences in colony stores as a result of a difference in influx of nectar and pollen on the first day, it was made certain that storage of both nectar and pollen was present in large quantities before the start of the experiment.



The first choice of all marked individuals was recorded and unmarked foragers visiting the food sources were captured and marked. On the second day (information on both food sources), all successful foragers were allowed to return to the hive and the initial choice of foragers was recorded in the same way. This experiment was carried out twice with only information on nectar presence in the greenhouse compartment (colony 3 and colony 4) and twice with only information on pollen presence in the greenhouse compartment (colony 5 and colony 6).

### **Experimental procedure on influence of initial choice on subsequent careers**

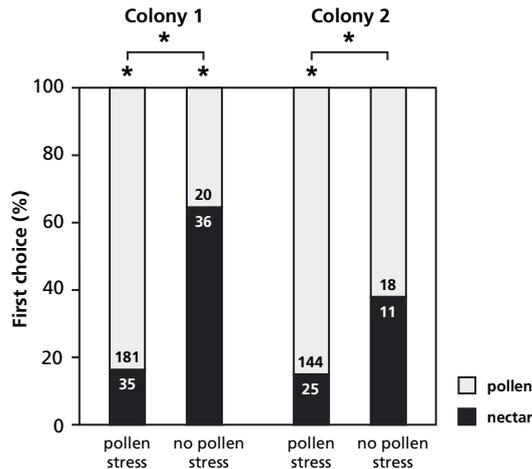
To study the influence of the initial choice on future foraging careers of the individuals, the first choice of marked individuals was compared with the commodity choices on subsequent flights on both experimental days. Observations on commodity choices of these individuals were made continuously on the food sources between 9:30 and 15:00 on both days after which all foragers were returned to the colony and the hive was closed. The careers of the marked individuals on the two days of the experiment were characterised as pollen-specialist, nectar-specialist or flexible (Biesmeijer & Tóth 1998). Foragers were regarded as specialists when they foraged for more than 80% on one food commodity (Biesmeijer & Tóth 1998). Only marked individuals foraging on both experimental days were included in the analysis. In order to test the effect of the first choice on future foraging careers of the individuals, the number of foragers in each category was compared using the Chi-square test for goodness of fit.

## **Results**

### **Influence of pollen storage level on the initial commodity choice of foragers**

When pollen stores were low, the vast majority of novice foragers in both colonies chose pollen collection (colony 1: pollen=84%, nectar=16%;  $\chi^2=98.69$ ,  $df=1$ ,  $p<0.001$ ; colony 2: pollen=85%, nectar=15%;  $\chi^2=83.79$ ,  $df=1$ ,  $p<0.001$ ) (Fig. 1). When pollen storage was restored, novice individuals of one colony more often chose nectar collection (colony 1: pollen=36%, nectar=64%;  $\chi^2=4.57$ ,  $df=1$ ,  $p=0.03$ ) while novice individuals of the other colony chose equally often for pollen and nectar collection (colony 2: pollen=62%, nectar=38%;  $\chi^2=1.69$ ,  $df=1$ ,  $p=0.19$ ) (Fig. 1). In both colonies a much higher percentage of novice individuals chose pollen collection during pollen stress compared to the situation when pollen storage was restored (colony 1: pollen





**Figure 1:** The proportion of novice foragers choosing nectar or pollen on their first collection flight, with pollen stress (day 1) and without (day 2) for Colony 1 (left side) and Colony 2 (right side). Asterisk (\*) indicate significance level  $p < 0.05$ .

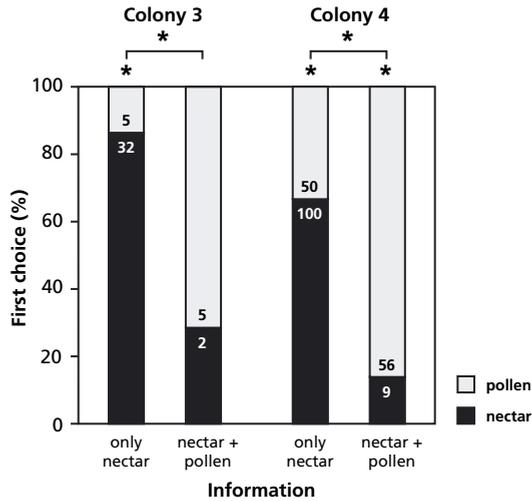
stress: 84%, no pollen stress: 36%;  $\chi^2$ -test with Continuity Correction:  $\chi^2 = 50.836$ ,  $df = 1$ ,  $p < 0.001$ ; colony 2: pollen stress: 85%, no pollen stress: 62%;  $\chi^2$ -test with Continuity Correction:  $\chi^2 = 7.421$ ,  $df = 1$ ,  $p < 0.01$ ) (Fig. 1).

#### **Influence of information on food availability in the field on initial commodity choice of foragers**

**Nectar:** When only information on nectar availability could be transferred in the hive, most novice individuals of both colonies started collecting nectar instead of pollen (colony 3: nectar=86%;  $\chi^2 = 19.70$ ,  $df = 1$ ,  $p < 0.01$ ; colony 4: nectar=67%;  $\chi^2 = 16.67$ ,  $df = 1$ ,  $p < 0.001$ ) (Fig. 2). When information on both food sources could be transferred, no significant difference in commodity preference could be found for novice individuals of the first colony (colony 3: pollen=71%;  $\chi^2 = 1.29$ ,  $df = 1$ ,  $p = 0.26$ ) while in the other colony most novice foragers chose pollen collection (colony 4: pollen=86%;  $\chi^2 = 33.99$ ,  $df = 1$ ,  $p < 0.001$ ), (Fig. 2). In both colonies a much higher percentage of novice foragers chose nectar collection when information from returning foragers indicated only nectar presence, compared to the situation when information on presence of both components was available (colony 3: only nectar information: 86%, information on both sources: 29%;  $\chi^2$ -test with Continuity Correction:  $\chi^2 = 8.19$ ,  $df = 1$ ,  $p < 0.01$ ; colony 4: only nectar information: 67%, information on both sources: 14%;  $\chi^2$ -test with Continuity Correction:  $\chi^2 = 48.53$ ,  $df = 1$ ,  $p < 0.001$ ) (Fig. 2).

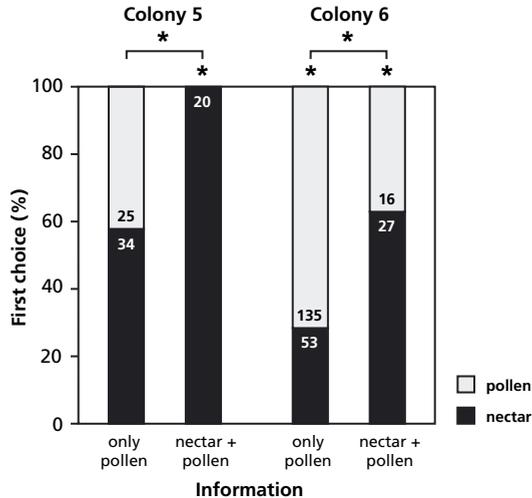
**Pollen:** Novice foragers of the first colony chose equally for pollen and nectar when only pollen information was available (colony 5: pollen: 42%;





**Figure 2:** The proportion of novice foragers choosing either nectar or pollen on their first collection flight, with experienced foragers offering only nectar information (day 1) and experienced foragers offering nectar and pollen information (day 2) for Colony 3 (left side) and Colony 4 (right side). Asterisk (\*) indicate significance level  $p < 0.05$ .

$\chi^2 = 1.37$ ,  $df = 1$ ,  $p = 0.24$ ) (Fig. 3). When successful foragers on both pollen and nectar returned to the hive, however, all novice individuals of this colony chose nectar collection (colony 5: nectar 100%;  $\chi^2 = 18.18$ ,  $df = 1$ ,  $p < 0.001$ ) (Fig. 3). Most novice individuals of the second colony chose pollen collection when returning foragers only could transfer information on pollen availability (colony

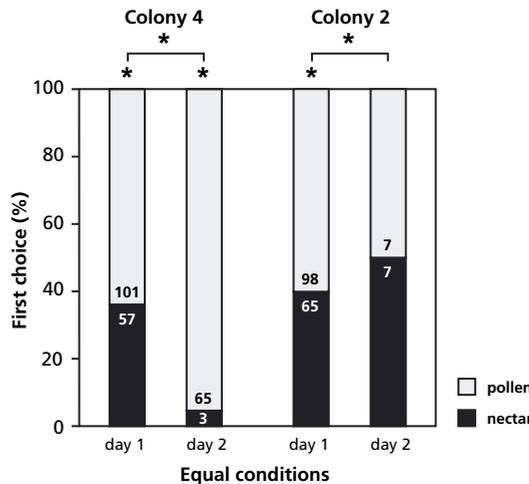


**Figure 3:** The proportion of novice foragers choosing nectar or pollen on their first collection flight, with experienced foragers offering only pollen information (day 1) and experienced foragers offering nectar and pollen information (day 2) for Colony 5 (left side) and Colony 6 (right side). Asterisk (\*) indicate significance level  $p < 0.05$ .



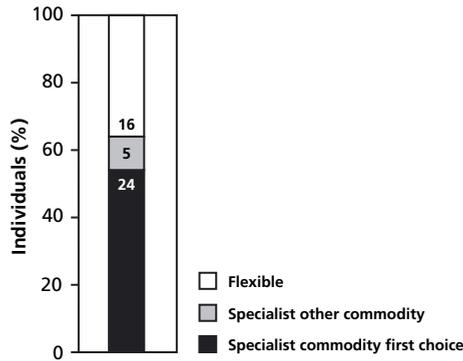
6: pollen: 72%;  $\chi^2=35.77$ ,  $df=1$ ,  $p<0.001$ ) (Fig. 3). When information on both commodities was available most novice individuals chose equally for pollen and nectar collection (colony 6: nectar: 63%;  $\chi^2=2.81$ ,  $df=1$ ,  $p=0.09$ ). Novice individuals had a significantly higher tendency to collect pollen instead of nectar when only information on pollen presence was available, compared to when information on both nectar and pollen presence was available (colony 5: only pollen information: 42%, information on both sources: 0%;  $\chi^2$ -test with Continuity Correction;  $\chi^2=8.86$ ,  $df=1$ ,  $p<0.01$ ; colony 6: only nectar information: 72%, information on both sources: 37%;  $\chi^2$ -test with Continuity Correction;  $\chi^2=17.01$ ,  $df=1$ ,  $p<0.001$ ) (Fig. 3).

**Control:** When intranidal stores and information on food availability in the field were kept constant for two days, a significant difference was found in pollen and nectar choice between the days in the first colony (colony 4: pollen day 1: 64%; pollen day 2: 96%;  $\chi^2$ -test with Continuity Correction;  $\chi^2=22.85$ ,  $df=1$ ,  $p<0.001$ ), but on both days individuals chose mostly pollen (day 1:  $\chi^2=12.25$ ,  $df=1$ ,  $p<0.001$ ; day 2:  $\chi^2=56.53$ ,  $df=1$ ,  $p<0.001$ ) (Fig. 4). For the second colony there was no significant difference in nectar and pollen choice between these days (colony 2: pollen day 1: 60%; pollen day 2: 50%;  $\chi^2$ -test with Continuity Correction; colony 2:  $\chi^2=0.21$ ,  $df=1$ ,  $p=0.65$ ) (Fig. 4).



**Figure 4:** The proportion of novice foragers choosing nectar or pollen on their first collection flight, with equal colony conditions and equal information on pollen and nectar from experienced foragers (day 1 and day 2) for Colony 4 (left side) and Colony 2 (right side). Asterisk (\*) indicate significance level  $p<0.05$ .





**Figure 5:** The influence of the initial commodity choice of novice foragers on their future foraging career. The category “specialist commodity first choice” includes individuals that specialised for more than 80% on the same commodity as their first commodity choice. The category “specialist other commodity” includes individuals which specialised for more than 80% on a food commodity other than their first commodity choice. The category “flexible” includes individuals which did not specialise for 80% on one of the food commodities.

### *Influence of first choice on subsequent foraging careers*

Few individuals specialised on a material different from their first choice (11%) (Fig. 5). Most individuals continued to forage on the material of their first choice (53%) (first choice vs. other commodity:  $\chi^2=12.448$ ,  $df=1$ ,  $p<0.001$ ) or did not specialise on any of the commodities available (36%)(flexible vs. other commodity:  $\chi^2=5.762$ ,  $df=1$ ,  $p=0.016$ ) (Fig. 5).

## Discussion

Colony foraging in stingless bees is based on individual decision making. To make these decisions, individuals use a variety of information sources from both inside and outside the hive (Biesmeijer *et al.* 1998, Biesmeijer & Slaa 2004). In this study we investigated the effect of two external information sources on the initial commodity choice of foragers of the stingless bee *Plebeia tobagoensis*. We found that both within-colony food storage as well as transferred information on food availability in the field greatly influenced the foraging choices of novice individuals, with, in total, more choices for the commodity lacking in storage or mostly communicated.

The need for a certain food commodity can increase due to weather conditions or long absence of this type of commodity in the field. It seems highly adaptive to the colony to be able to adjust its foraging efforts towards this commodity. The fact that initial commodity choice of individuals is influenced by food storage conditions in this study first of all indicates that individuals



are able to perceive this condition inside the colony. Honeybee foragers assess pollen storage in the nest through trophallactic interactions with nurse bees (Camazine 1993, Seeley 1995). Stingless bee foragers could obtain information about pollen stores through direct perception or through interactions with nest mates, which in either way could influence their way of foraging. Secondly, the fact that the initial commodity choice of individuals is influenced by the colony condition indicates that novice individuals actually use the information on pollen storage in their decision making process.

Novice stingless bee foragers clearly use, in addition to information on food storage, information obtained from successful foragers about commodity availability. It is known from many species of stingless bees that successful foragers can provide non-foraging nest mates with information about quality, direction and distance of the food source (Aguilar 2004, Biesmeijer & Slaa 2004, Nieh 2004). Although it is not known if foragers of *P. tobagoensis* communicate detailed location information, returning successful foragers do influence the initial commodity choice of individuals. This property may allow colonies to respond adaptively to a sudden increase of a specific food commodity in the field.

In principle, there are three ways in which social bee colonies can change the foraging effort devoted to a particular foraging task; 1) allocate non-foragers to the task (including novice foragers), 2) reallocate active foragers (individual switching), and 3) intensify the activity of foragers already working on the task to work harder (Anderson and Ratnieks, 1999; Rotjan *et al.*, 2002). Honeybee colonies exposed to a sudden decrease in pollen stores provide additional labour for pollen foraging, mainly by recruiting non-foragers (Fewell & Bertram 1999, Rotjan *et al.* 2002) and by increasing individual foraging activity (Fewell and Winston 1992). It may be advantageous for a colony to rely mainly on the recruitment of non-foragers when a change in foraging focus is needed. Firstly, recruiting non-foragers to a task does not decrease foraging effort devoted to other foraging tasks. This can be seen in honeybees where overheating of the brood nest results in an increase of water collection, without decrease of nectar collection (Kuhnholz & Seeley 1997). Secondly, recruiting non-foragers to a task might be less costly than having individuals switching from other tasks. Specialists are known to perform better in foraging (e.g. collect bigger loads, more foraging flights per day, less unsuccessful flights per day) compared to individuals that switch between foraging tasks (Chittka & Thomson 1997, O'Donnell *et al.* 2000, Chapter 3).

In our study the initial choice of foragers seems of importance for their further foraging career, at least for the first two days of foraging. Most foragers that specialised on one food commodity hold on to their first choice during



the experiments. A substantial proportion of foragers (36%), however, did not specialise on any of the food components. After their initial commodity choice, based on pollen shortage or information from other foragers, these bees switched to other food components when food stress was eliminated or when information on other food sources entered the hive.

Novice foragers of *P. tobagoensis* appear to be highly sensitive to information on food storage and food availability in the field. By being able to allocate available novice foragers flexibly over foraging tasks, *P. tobagoensis* colonies are able to respond to changing food conditions in and outside the colony, without directly having to decrease foraging effort devoted to other foraging tasks. The additional possibility of reallocating foragers to collection of other food commodities (individual switching) provides these bees with a flexible system of foraging behaviour.

The fact that individual commodity choices are influenced by external factors does not imply that internal factors are non-existent or of no importance in *P. tobagoensis*. Many studies have shown the importance of internal factors, such as genetic composition and juvenile hormone levels, on task regulation (Robinson 1987, Robinson & Page 1989). In honeybees and stingless bees intrinsic factors, however, do not result in rigid behaviour preventing individual switching between foraging tasks.





## Chapter 3

# Effect of food availability on individual foraging specialisation in the stingless bee *Plebeia tobagoensis* (Hymenoptera; Meliponini)

With: MJ Sommeijer

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### Summary

Individual specialisation in foraging behaviour of social bees is thought to enhance foraging performance, increasing colony fitness. In a dynamic environment, however, colonies have to be able to respond to short-term changes in food availability. As a result, costly switches in individual foraging behaviour might be necessary for colony flexibility. Here we test the hypothesis that in a stable environment task specialisation in foraging is preferred, but that individuals switch to other foraging tasks when changes in food availability occur. This study, using the stingless bee species *Plebeia tobagoensis*, was performed in a greenhouse compartment, where food availability could be controlled. When all food commodities were present in the compartment, most individuals collected only one commodity. When this food commodity was removed in the deprivation period half of the earlier specialists switched to another material, while the specialists from which the preferred commodity was not removed did not switch foraging tasks. When comparing foraging performance of flexible and specialised individuals we found that specialised bees performed more and shorter flights and collected bigger pollen loads compared to flexible foragers. After a provoked switch in foraging task the number of unsuccessful flights of former specialists increased drastically. However, most specialised foragers do make a costly switch to another food commodity when a change in food availability occurs. It seems likely that this high flexibility is adaptive for relatively small social bee colonies, living under variable foraging conditions.



## Introduction

Eusocial bee colonies require large amounts of food for daily survival and to build up stores to survive dearth periods. Influx of food, mainly nectar and pollen, is therefore a major factor in colony fitness and survival (Roubik 1989). Finding and collecting food in the field is, however, a complex and unpredictable process. Flowers vary in their mechanisms for release of pollen and nectar and foraging bees need different techniques to collect, transport and store these different food commodities. Focussing on the collection of one particular food commodity by different individuals (foraging task specialisation) is therefore expected to increase individual foraging performance (Oster & Wilson 1978). Indeed bumblebee foragers that specialise on either nectar or pollen contribute more to the colony's food-intake than bees that switch regularly between food commodities (O'Donnell *et al.* 2000). Although specialisation on the collection of one food commodity is thought to increase foraging performance, not all foragers in social bee colonies are specialists. To be able to collect sufficient food from a dynamic environment, social bee colonies need to be able to respond flexibly to short-term changes. Apart from responding to these changes by flexibly allocating new foragers, changes in colony foraging behaviour can also result from changes in individual foraging behaviour (Fewell & Winston 1992).

Few studies have been done on the proportions of specialised and flexible foragers in social bee colonies. In honeybees about 40% of the freely foraging individuals specialised in the collection of one food commodity during their foraging career (Ribbands 1952). In a study on bumble bees 30-40% of the foragers behaved as specialists (O'Donnell *et al.* 2000). In the stingless bee *Melipona beecheii* about 50% of the foragers specialised on one food commodity during their foraging career (Biesmeijer & Tóth 1998), while more than 70% of *Melipona favosa* (Sommeijer *et al.* 1983) and *Trigona minangkabau* (Inoue *et al.* 1985) foragers collected only one type of material over a sequence of days.

Although these differences in proportions might indicate interspecific differences in mechanisms for forager allocation, the proportion of flexible and specialised individuals in a colony is probably not fixed. Various factors may influence the possibilities for individual bees to behave as specialised foragers. Variability in food availability and colony state are probably the most important factors affecting the degree of task specialisation of individual foragers. Although previous studies described the presence of specialised and flexible foragers in social bee colonies (Ribbands 1952, Sommeijer *et al.* 1983, Inoue *et al.* 1985, Biesmeijer & Tóth 1989, O'Donnell *et al.* 2000), nothing is known about



proportional changes in specialised and flexible foragers resulting from changes in food availability.

In this study we investigated the occurrence and dynamics of foraging task specialisation in colonies of the stingless bee *Plebeia tobagoensis* in a controlled environment, that allowed us to manipulate food availability. It is expected that individuals, in order to forage efficiently, tend to behave as specialists, and thus focus on the collection of one food commodity, when the opportunity is there (all food commodities reliably available). When this food commodity is removed from the environment, however, individuals of *P. tobagoensis* are expected to respond by making a costly switch in foraging behaviour (Dukas & Visscher 1994).

The second aim of this paper is to test whether specialised individuals of the stingless bee *P. tobagoensis* do perform better in foraging than flexible individuals, and if switches as a result of the removal of the preferred food source influence foraging performance of individuals.

## Materials and methods

### Bee colonies and experimental conditions

The stingless bee *Plebeia tobagoensis* is common on Tobago, West Indies. Melo & Alves-dos-Santos (2003) recently described this species. Two colonies of *P. tobagoensis* were studied under controlled conditions in a greenhouse of Utrecht University, The Netherlands. Colony 1 contained approximately 1300 workers and colony 2 about 700 workers. The colonies were first kept for 6 months in a room with climate control at Utrecht University. One day before the start of each experiment one colony was placed in a closed experimental greenhouse compartment (15 m × 5 m × 4 m) in the botanical gardens of Utrecht University. All food sources used in the experiment were installed before the introduction of the bees. The minimum temperature in the greenhouse was set at 20°C (natural temperature range: 23°C - 31°C).

Hundred flowering strawberry plants (*Fragaria x ananassa*, var. Elan) were used as a nectar and pollen source. As an additional pollen source ten flowering spathiphyllum plants (*Spathiphyllum sp.*) were installed. Fifty small nectar feeders (sucrose solution, 50% w/w, with vanilla essence (5 µl/100 ml)), placed 3 cm apart in a “patch” arrangement, served as an additional nectar source. We also installed one small pine tree (*Pinus sp.*) with damaged bark as a resin source. Water was available from a dripping tap. The resin and pollen plants were inspected twice daily to ensure availability of these commodities. Every hour the syrup in the feeders was renewed to ensure constant availability and sucrose concentration.



### Marking procedure

On the day before the start of the experiment we captured bees foraging on the available food sources and marked their thorax with an individual two-colour combination (UniPosca water based odourless paint markers). In each experiment at least 50 individuals were marked. We tried to mark equal numbers of foragers on each food source (but in practice this was not always possible).

### Experimental procedure

To create a stable food availability period followed by a change in food availability, the experiments consisted of 3 pre-deprivation days and 3 deprivation days. On pre- deprivation days all food commodities were present in the greenhouse compartment. During the deprivation period we removed either nectar (nectar deprivation experiment) or pollen (pollen deprivation experiment). For the nectar deprivation experiment all sucrose solution feeders were removed and the nectaries of the strawberry plants were sealed with glue. For the pollen deprivation experiment the anthers of the strawberry flowers were cut away and the spathiphyllum plants were removed.

Both colonies were subjected to a nectar- and a pollen deprivation period. As there was no significant difference in frequencies of flexible and specialised foragers between the colonies during the pre-deprivation period the results of the two colonies were pooled (Fisher's exact test,  $p=0,111$ ) (see also Fig. 1).

### Behavioural observations

**Observations on foraging behaviour:** Incoming individuals and the materials collected were identified by the use of a video camera (Sony CCD-TV228) placed above the nest entrance. For this, the nest entrance had a glass lid. As a confirmation of the video-data, the presence of marked bees on the food sources was visually scanned every hour during the experiments. Water and nectar foragers could be discriminated on video, since the abdomen of returning nectar foragers is clearly less swollen compared to that of water foragers. Resin and pollen foragers could, in these experiments, be distinguished by the colour of the load carried. When bees returned to the hive with no visible pollen- or resin load on the corbiculae and without swollen abdomen, this flight was defined as unsuccessful.

An individual bee was considered to be a specialist when she collected the same material on more than 80% of her foraging flights in the pre-deprivation period (Biesmeijer & Tóth 1998). All bees performing at least one successful flight in the pre-deprivation period were included in the analysis. The number of specialised versus flexible individuals in the pre-deprivation period was compared using the Chi-square test for goodness of fit. The proportion of



specialised bees in the pre-deprivation period that switched to another food commodity when their preferred commodity was removed in the deprivation period was compared with the proportion of specialised bees that switched when their preferred commodity was not removed with the Chi-square test for independence.

**Measuring individual foraging performance:** To compare the individual foraging performance of individuals that focussed on the collection of one food commodity (specialists) during the pre-deprivation period with that of individuals that collected different commodities (flexible foragers) in this period, we calculated the total number of flights, the mean duration of each flight, the mean load size (only for pollen) and the proportion of unsuccessful flights of the first three days of the experiment from the video recordings. Pollen load size was estimated by categorising loads as small (loads flat) (1), medium (loads round) (2) or large (loads oval) (3). Individual performance was calculated by averaging these category scores. Due to the small sample size for some collected materials, the mean flight duration could only be calculated for foragers on sugar solution and strawberry pollen. The mean load size could only be established for pollen foragers. The individual foraging performance of specialised and flexible individuals was compared using the Mann Whitney U test.

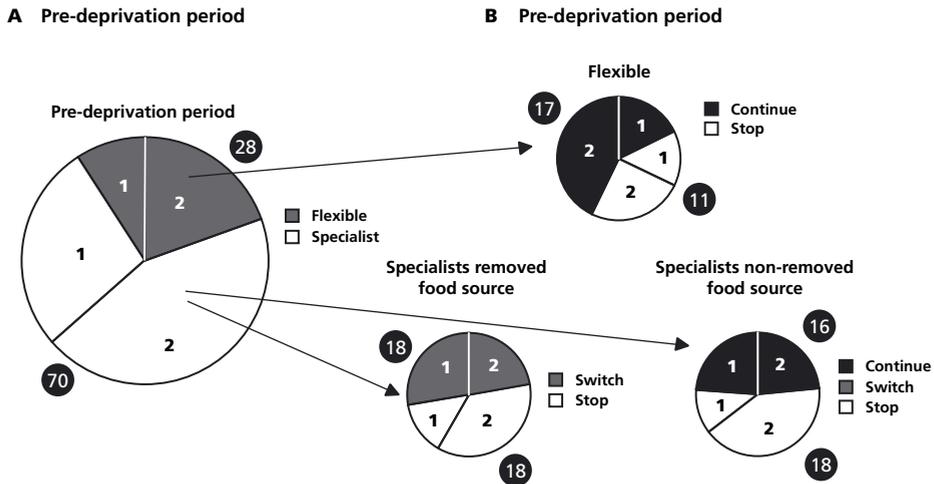
In addition, in order to get an indication of the costs of a provoked switch when the preferred food commodity was removed, we compared the difference in foraging performance between the pre-deprivation period and deprivation period of individuals that switched and individuals that did not switch with the Wilcoxon Signed Ranks Test. Because of natural differences in duration for the collection of the different commodities, no comparison could be made in flight duration or number of flights before and after switching. Foraging performance could in this case only be reflected by the proportion of unsuccessful flights.

## Results

### Individual task specialisation under different food availability conditions

In the pre-deprivation period 71% (N=98, n=70) of the foragers focussed on the collection of one food commodity (nectar, pollen, resin or water) (Fig. 1A). When one food commodity was removed in the deprivation period, 50% (N=36, n=18) of the specialists formerly foraging on this food source switched to another food commodity (Fig. 1B). Eight of these former



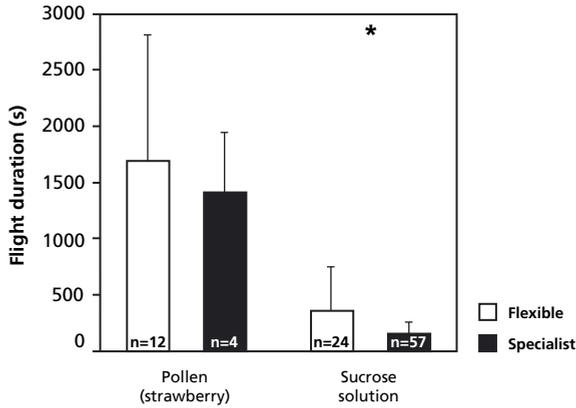


**Figure 1: (A)** Proportion of specialised compared to flexible foragers when all food sources were available in the greenhouse compartment (pre-deprivation period). Specialised bees collected the same material on more than 80 % of their flights. Sample size numbers are indicated in the graph. **(B)** Proportion of individuals that stop or continue foraging after one of the food sources was removed (deprivation period). The foragers are divided in three categories; “flexible” consists of individuals foraging on more than one material in the pre-deprivation period, “specialists removed food source” consists of individuals that collected the same material on more than 80 % of their flights in the pre-deprivation period, but from which the preferred food source was removed in the deprivation period, “specialists non-removed food source” are individuals that collected the same material on more than 80 % of their flights in the pre-deprivation period, but from which the preferred food source was not removed in the deprivation period. Sample size numbers are indicated in the graph. Although data of both colonies is pooled, colonies can be separated by the numbers in the figures.

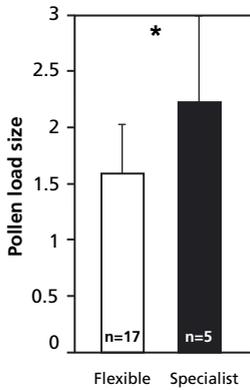
specialists switched to a food commodity they had never collected before, while ten bees switched to a food commodity they had collected to a minor extent (< 20% of their flights) in the pre-deprivation period. From the 18 former specialists that stopped foraging in the deprivation period (and thus did not switch to another food commodity), fourteen were never seen again, while only four restarted foraging on their former food commodity after the end of the deprivation period (data not shown). From the bees that specialised in the pre-deprivation period but from which the preferred food commodity was not removed in the deprivation period (n=34), no individuals switched but 18 bees stopped foraging. This shows that significantly more individuals switch foraging tasks when their preferred food commodity is removed in the deprivation period compared to when the preferred commodity is available in both periods ( $\chi^2=11.75$ ,  $df=1$ ,  $p<0.01$ ).

Seventeen of the 28 flexible individuals continued foraging, whereas eleven stopped foraging altogether. The proportion of active bees in the pre-deprivation period that stopped in the deprivation period is equal for specialists from which the preferred food commodity was removed, specialists from which





**Figure 2:** Mean duration of foraging flights in seconds on artificial flowers for sugar solution collection and on strawberry for pollen collection of specialised and flexible forager in the pre-deprivation period. The mean duration + SE and sample sizes are given in each bar. Results were tested using the Mann-Whitney-U test. Asterisk indicates significant difference ( $p < 0.05$ ).



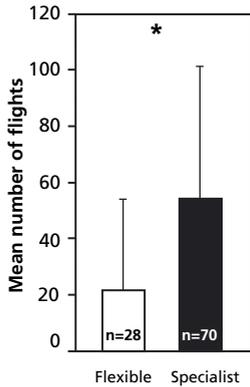
**Figure 3:** Mean pollen load size of specialised and flexible foragers in the pre-deprivation period. Load size categories were estimated from video recordings. The mean pollen load sizes + SE are given in each bar; sample sizes are indicated on the x-axis. Results were tested using the Mann-Whitney-U test. Asterisk indicates significant difference ( $p < 0.05$ ).

the preferred commodity was not removed and flexible individuals ( $\chi^2=1.2$ ,  $df=2$ ,  $p=0.54$ )

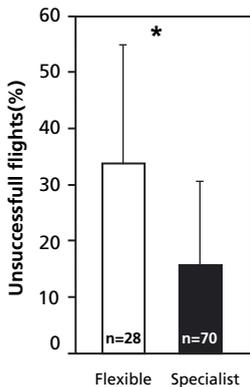
### Individual foraging performance of specialised and flexible foragers

**Pre-deprivation period:** Individuals focussing on one food commodity made shorter flights than flexible individuals collecting syrup from the feeders (Mann-Whitney  $U=333.50$ ,  $Z=-3.63$ ,  $n=81$ ,  $P<0.01$ ) (Fig. 2) in the pre-deprivation period. There was no significant difference between flexible individuals and specialists in flight duration when collecting pollen (Mann-Whitney  $U=24.00$ ,  $Z=0.00$ ,  $n=16$ ,  $P=1.00$ ) (Fig. 2). However, specialised pollen collectors carried bigger pollen loads than flexible foragers (Mann-Whitney  $U=15.50$ ,  $Z=-2.12$ ,  $n=14$ ,  $P=0.03$ ) (Fig. 3).





**Figure 4:** Mean number of flights of specialised and flexible foragers in the pre-deprivation period. The mean number of flights + SE are given in each bar; sample sizes are indicated on the x-axis. Results were tested using the Mann-Whitney-U test. Asterisk indicates significant difference ( $p < 0.05$ ).

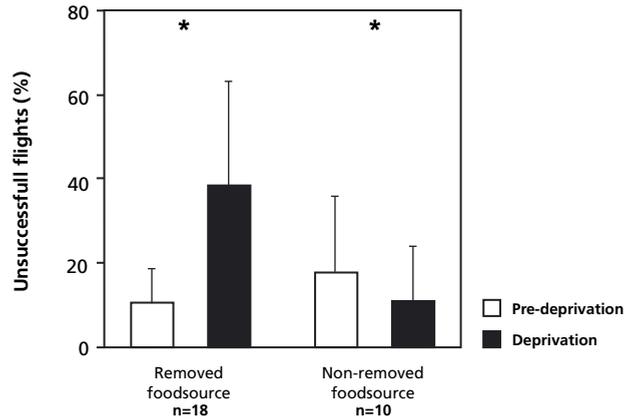


**Figure 5:** Mean percentage of unsuccessful flights for specialised and flexible foragers in the pre-deprivation period. Flights were indicated as unsuccessful when no visible load was present when entering the hive. The mean number of flights + SE are given in each bar; sample sizes are indicated on the x-axis. Results were tested using the Mann-Whitney-U test. Asterisk indicates significant difference ( $p < 0.05$ ).

The total number of flights during the pre-deprivation period was smaller in flexible foragers than in specialists (Mann-Whitney  $U=519.50$ ,  $Z=-3.62$ ,  $n=98$ ,  $P<0.01$ ) (Fig. 4). In addition, flexible foragers performed more unsuccessful flights (flights without a load) compared to specialised foragers (Mann-Whitney  $U=445.00$ ,  $Z=-4.21$ ,  $n=98$ ,  $P<0.01$ ) (Fig.5).

**Deprivation period:** Specialists that switched foraging task because of the removal of their preferred food commodity in the deprivation period performed more unsuccessful flights after their switch (deprivation period) compared to before (pre-deprivation period) (Wilcoxon Signed Rank test:  $Z=-3.51$ ,  $n=18$ ,  $p<0.01$ ) (Fig. 6). Specialists from which the preferred food commodity was not removed performed fewer unsuccessful flights in the deprivation period compared to the pre-deprivation period (Wilcoxon Signed Rank test:  $Z=-1.99$ ,  $n=10$ ,  $p=0.47$ ) (Fig. 6). So specialists that had to switch tasks in the deprivation period performed a higher proportion of unsuccessful flights compared to specialists that could continue collecting the same commodity ( $\chi^2=12.7$ ,  $df=1$ ,  $p<0.01$ ) (Fig. 6).





**Figure 6:** Mean percentage of unsuccessful flights in the pre-deprivation and deprivation period, both for specialised sucrose solution foragers that could continue foraging on sucrose solution in the deprivation period and for specialised individuals that switched to another food source in the deprivation period. The mean number of flights + SE are given in each bar; sample sizes are indicated on the x-axis. Results were tested using the Wilcoxon Signed Rank test. Asterisk indicates significant difference ( $p < 0.05$ ).

## Discussion

### Individual task specialisation under different food availability conditions

In order to improve their individual foraging performance, foragers of social bees are generally assumed to specialise in the collection of one type of commodity (Oster & Wilson 1979). We found support for this hypothesis in the stingless bee *Plebeia tobagoensis*, where 71% of the foragers focussed on the collection of one food commodity when the commodity was always available. Lower percentages of specialists were found in other studies on foraging task specialisation in stingless bees and other social bee species (30–70% specialists (Ribbands 1952, O'Donnell *et al.* 2000, Biesmeijer & Tóth, 1998, Inoue *et al.* 1985)). Those other studies were performed on foraging bees in their natural habitat where food availability fluctuates. Our study was conducted under specified foraging conditions where food availability could be controlled. The high percentage of specialists in this study is probably the result of this highly stable and confined environment. The experimental scheme in this study is comparable to a natural situation of high food availability, such as mass-flowering periods, followed by the depletion of this source after several days.

The removal of one of the food commodities in the deprivation period, thereby artificially changing food availability, caused former specialists to



readily switch to the collection of other food components. From the eighteen specialists that actually stopped foraging in the deprivation period, fourteen individuals were never seen again, indicating that they probably died during the experiment. This results in only a very small number of *P. tobagoensis* foragers (4 individuals) that really stopped foraging when their preferred food commodity was no longer available (and actually restarted when this food commodity was re-introduced). These specialists can be considered as “obligate” specialists. Even when the food commodity in which they were specialised was no longer available, they did not switch to the collection of another food commodity, but ceased foraging altogether. Similarly, specialised honeybee foragers, that major on the collection of one specific material, temporarily stop foraging when this material is not available anymore (Free 1993, Seeley 1995). This is thought to prevent foragers from spending energy when food availability is low (Gordon 1996), in this way increasing their longevity. It has indeed been confirmed that an unexpectedly high rate of inactive bees can be found in honeybee colonies (Seeley 1995). These bees might serve as “backup” foraging forces in times of great mortality or opportunity (Michener 1974, Anderson & Ratnieks 1999).

Allocating non-foragers to a new foraging task may be less costly than switching of foragers to this task (Rotjan *et al.* 2002). Colony size might be one of the factors that facilitate the existence of these back-up forces. Large colonies, such as in the honeybee, can afford to have back-up forces and in this way can dynamically allocate specialised bees among food sources (Seeley 1995). Smaller colonies, such as in *Plebeia tobagoensis* (100-1500 individuals, own observation), may have to rely more on flexible individuals when colony elasticity is needed. Additional support for this hypothesis can be found in data on flower constancy. Bumblebees (*Bombus terrestris*, colony size  $\pm$  250 individuals, pers. comm. MJ Duchateau) and stingless bees (*Trigona spp.*) are found to be more flexible in visiting different flower types than honeybees are (Free 1970, Slaa *et al.* 1998).

Although specialisation seems to result in higher individual foraging performance, not all individuals in this study focussed on the collection of only one food component. About 19% of the individuals switched regularly between resources, even when food availability was stable. Small changes in colony condition might have triggered the changes in foraging behaviour of these individuals, but flexible individuals may also play a crucial role for efficient foraging organisation in a stable environment. Although the individual foraging performance of these flexible individuals is not high, colonies might benefit from having some foragers that explore the environment and locate the resources (explorers or scouts (von Frisch 1967)), after which other individuals can be recruited to the food source (exploiters or recruits (von Frisch 1967)).



### Causes of task specialisation in social bees

Theoretical models and observational studies on bees suggest that task specialisation can result from a combination of factors, such as experience and physiological and genetic make-up (Speathe & Weidenmuller 2002, Thomson & Chittka 2001, Robinson & Page 1989, Fewell & Page 1993, Fewell & Bertram 2002, Ranger & O'Donnell 1999, Biesmeijer 1997). Task specialisation based on foraging experience results in a relatively flexible task allocation mechanism, where individuals can still switch between foraging tasks. Physiologically based task specialisation, such as seen in certain ant species (e.g. *Dorylus spp.*, Breandle *et al.* 2003), and genetically based task specialisation result in a more rigid task allocation mechanism, where individual switching is impossible or less likely to occur. Genetic effects on foraging task allocation have been demonstrated clearly in the polyandrous honeybee (*Apis mellifera*) (Robinson and Page 1989, Fewell & Bertram 2002) and in the polygynous or polyandrous stingless bee *Partamona bilineata* (Ranger & O'Donnell 1999). Stingless bees are generally known to be monogynous and it is assumed that most species have singly mated queens (Roubik 1989), reducing genotypic diversity. Although Ranger & O'Donnell (1999) state that high rates of recombination of the mother queen's genome can contribute to genotypic diversity even in these stingless bee species, Peters *et al.* (1999) found a much higher genetic similarity in stingless bee colonies than in honeybee colonies. However, genotypic variability is not a necessary condition for a more "programmed" form of task specialisation, because variance in foraging task preference can arise from environmental factors, such as differences in larval food composition, as well (Oster & Wilson 1978).

Although the mechanistic basis for task specialisation in *Plebeia tobagoensis* remains unclear, a rigid task allocation mechanism seems unlikely as many individuals switch readily between food commodities when food availability changes. Knowledge on factors involved in task specialisation in monogynous and monoandrous stingless bee species might give more insight on the mechanistic bases and evolution of task specialisation in social bee species.

### Foraging performance of specialised and flexible foragers

Our results support the hypothesis that task specialisation increases individual foraging performance (Oster & Wilson 1978). Low sample sizes, however, did not allow for comparisons in all food components available. Specialised sucrose solution foragers needed less time per flight than bees that collected other food commodities as well. Specialised pollen foragers did not show significantly shorter flight durations, but collected bigger loads in the same time as flexible foragers did. In addition, specialised bees performed more



foraging flights and had fewer unsuccessful flights. After a provoked switch in foraging task the number of unsuccessful flights of former specialists increased drastically. Unsuccessful flights might be caused by difficulties in finding the new resource when switches are made.

Our data on higher individual foraging performance in specialised foragers is in agreement with results obtained for bumblebees (O'Donnell *et al.* 2000, Cartar 1992). However, in a field study on the stingless bee *Melipona beecheii* a relationship between specialisation and performance was not found (Biesmeijer & Tóth 1998). In this study flexible foragers followed the patterns of pollen and nectar presentation by plants in the study area. Some flexible foragers “specialised” on collecting pollen (P) in the early morning and after a switch “specialised” on collecting nectar (N) during the rest of the day (e.g. PPPNNN) (Biesmeijer & Tóth 1998). This type of switching might be more efficient than the more irregular switching seen in our study (e.g. NPPNNP), explaining the differences in results on foraging performance.

The higher foraging performance of specialised individuals is thought to be caused by limitations of memory for motor patterns and/or sensory stimuli (Waddington 1983, Waser 1986, Lewis 1986, Heinrich 1976). However there is no agreement on which specific limitations of memory and learning are responsible and the data of observational studies is ambiguous. Honeybees, at least, can store more than one odour and colour in their memory (Menzel *et al.* 1993, Reinhard *et al.* 2004) and bumblebees can store and retrieve information on flowers which require different motor patterns, although the best performance is reached by bees that focus on a single task (Chittka & Thomson 1997). The stingless bee species *Trigona dorsalis* and *Oxytrigona mellicolor* visit different flower types when the perceptual similarity is high, when flower types are more dissimilar, however, individuals restrict their visits to one of the two flower types available (Slaa *et al.* 2003).

The lower foraging performance for bees collecting various food commodities might be the result of a negative transfer effect, in which bees use some characteristics of the first learned motor pattern for the second learned task, where it is interfering with foraging performance (Chittka & Thomson 1997). Retroactive interference, meaning that individuals fail to perform a learned task appropriately after they have learned a second task, might be another factor in the lower foraging performance of bees that are involved in more than one foraging task (Adams 1987).

Learning different sensory stimuli and motor patterns at the flowers is not the only difficulty bees encounter when they switch from the collection of one food commodity to another. Upon arrival at the nest, pollen and nectar foragers follow completely different procedures to unload. Pollen foragers enter the hive, go to the storage area and deposit their load directly in storage cells.



Nectar foragers, on the other hand, regurgitate the collected nectar to one or more hive bees near the hive entrance. Thus, also in unloading the different food commodities learning constraints might play a role in foraging performance differences between flexible and specialised foragers.

## Conclusions

In colonies of *Plebeia tobagoensis* most foragers tend to specialise in the collection of one food commodity when all commodity types are reliably available. This seems to increase colony food influx because of higher individual foraging performance. However, when changes in food availability demand for changes in foraging behaviour, former specialists of *P. tobagoensis* do switch to the collection of other food commodities. For social bee species with a relatively small numbers of foragers, such as *P. tobagoensis*, flexible behaviour of the individuals is likely to be adaptive for the colony. Our results show that foraging task specialisation in colonies of *P. tobagoensis* is a very dynamic property and is probably not regulated by “programmed” mechanisms such as physiological or genetic make-up.

Colony size and mating frequency might be important factors in the occurrence of more rigid task specialisation in eusocial colonies, indicating that forager task specialisation in social bees might have evolved in concert with increase in colony size.





## Chapter 4

# Effect of experience on foraging performance in the stingless bee *Plebeia tobagoensis* (Hymenoptera; Meliponini)

*With: MJ Sommeijer*

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### Summary

Although foraging performance of bees is generally assumed to improve when experience is gained, not many long-term studies have been done on the development of foraging performance in social bees. In this study, we analysed the effect of experience on performance in novice foragers of the stingless bee *Plebeia tobagoensis* over two successive days. Foraging performance, computed as the total foraging trip time and the load size, improved significantly with increased experience, mostly already after the first few foraging trips. The improvement in foraging trip time was mainly the result of a decrease in flower handling time and time necessary to find the food source. There was a decrease in foraging performance following the night and the highest foraging performance level of all studied aspects was already reached on the first foraging day. This specific foraging performance pattern might be adaptive for social bee species with relatively small colony sizes, foraging in a dynamic foraging environment.



## Introduction

Foraging performance of bees, collecting nectar or pollen, is generally assumed to improve when experience is gained. Although many studies have been done on development of foraging performance (Menzel *et al.* 1974, Heinrich 1979, Gould & Gould 1988), most of these studies focused on learning and cognitive abilities of bees and studied development of foraging performance only during a single observation session, instead of during several days.

Dukas and Visscher (1994), in a field study on honeybees (*Apis mellifera*), were the first to show an increase in foraging performance over a period of several days. However, because they focused on long-term improvement patterns, the development of the foraging performance within one day was not studied. A second study on long-term foraging performance patterns in bees was done on bumble bees (*Bombus terrestris*) (Kearar *et al.* 1996). This study showed that foraging skills of individual bumble bees, such as approaching and probing of flowers, increased rapidly on the first foraging day (Kearar *et al.* 1996), but decreased again following a night. Nothing is known, however, on long-term foraging improvement patterns of stingless bees.

Information on development of foraging performance in relation to foraging experience can improve our knowledge on the evolution of foraging strategies, such as flower constancy and task specialisation in social bee species, as these strategies are thought to increase efficiency in locating and exploiting food sources (Oster & Wilson 1978). In the present study, the development of foraging performance in marked, novice foragers of the stingless bee species *Plebeia tobagoensis* was followed over a period of two days. To investigate which part of a single foraging trip is responsible for the increase in foraging performance we divided each foraging trip in several parts: departure from hive to arrival at food source, flower handling at the food source and departure from food source to arrival at hive.

## Materials and methods

The experiment was carried out in a closed greenhouse compartment (15 m × 5 m × 4 m) of the Botanical Gardens of Utrecht University, the Netherlands. The temperature during the experiments ranged from 25 to 35°C and relative humidity was 40–70%. The maximum temperature difference between morning and afternoon measurements was 5°C. Observation periods were continuous and took place between 10.30 and 15.30 h. Foragers were prevented from leaving the hive outside observation periods.



Three colonies of the stingless bee species *Plebeia tobagoensis* Melo were obtained from Tobago, West Indies. The colonies contained approximately 400–500 individuals. The colonies were first kept for 6 months in a chamber with climate control at the Utrecht University (25°C and 65% relative humidity). Before the start of the experiment, between 130–190 individuals of each colony were marked with individual colour codes on the thoracic dorsum (UniPosca water-based odourless paint markers). Because only very few marked individuals started foraging on the first day of our experiment, we recorded data on 13 novice individuals making 20 foraging flights on the first day of the experiment and 8 of these 13 individuals making 20 foraging flights on the second day of the experiment.

During the research period, individuals were allowed to forage on an artificial nectar source, consisting of 10 glass capillaries filled with sucrose solution (1.6 M), placed at 150 cm from the nest. The capillaries, inclined to 20°, were glued on paper with a graduated scale in millimetres to allow recording of the amount of sucrose solution imbibed by individual foragers. A black dot indicated the opening. Capillaries were replaced when less than 10  $\mu$ l remained in the capillaries to avoid forced interruptions in sucrose uptake. Marked bees were allowed to forage freely on the food source but were captured when they had performed 20 foraging flights on a foraging day. Unmarked bees were removed from the experimental set-up.

Foraging experience of individual foragers was measured as the number of foraging trips. Foraging performance was computed using total foraging trip time (time between departure from the hive and arrival at the hive with a full load) and load size (amount of sucrose solution uptake at the artificial flower). The total foraging trip time was divided in 1) time between departure at the hive and arrival at the food source, 2) flower handling time (time spent on the artificial food source from the moment of arrival until departure) and 3) time between departure from the food source and arrival at the hive.

To test whether an increase in foraging experience increased foraging performance the one-way repeated-measures ANOVA was used (with degrees of freedom adjusted according to Greenhouse-Geisser). The simple within-subject contrast ANOVA (each foraging trip compared to the first foraging trip) was used to test whether increasing foraging experience increased foraging performance compared to the first trip.

To test if foraging performance had decreased following the first night, we used a paired sample t-test or Wilcoxon signed rank test to compare foraging performance of the end of the first foraging day (mean last five foraging trips of each bee separately) with the foraging performance at the start of the second foraging day (mean first five foraging trips of each bee separately). To test if foraging performance reached its peak after one foraging day we used a paired



sample t-test or Wilcoxon signed rank test to compare foraging performance at the end of the first foraging day (mean last five foraging trips of each bee separately) with the end of the second foraging day (mean last five foraging trips of each bee separately).

## Results

### Foraging experience and performance

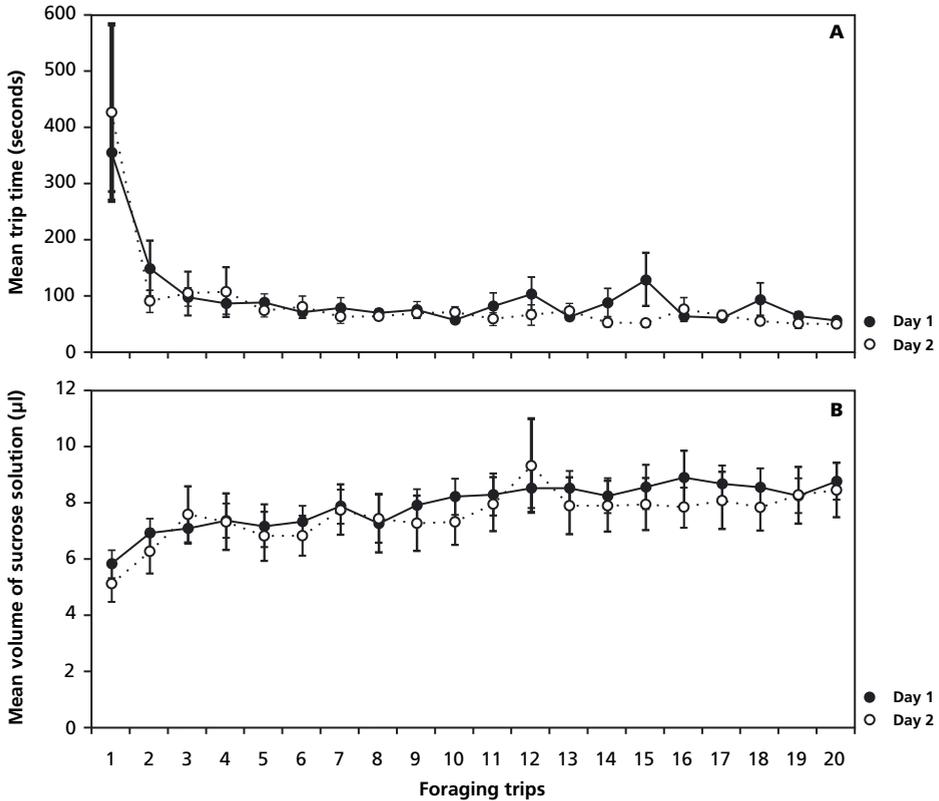
The mean foraging trip time significantly decreased with foraging experience on the first day of foraging ( $F_{3,498, 41.978}=6.451$ ,  $p<0.01$ ) and on the second day of foraging ( $F_{1,366, 9.564}=4.835$ ,  $p=0.045$ ) ( Fig.1A). Compared to the first trip the mean trip time significantly decreased already from the 3<sup>rd</sup> trip onward on both days (simple within-contrast ANOVA trip 1 vs trip 3: day 1:  $F=11.485$ ,  $p<0.01$ ; day 2:  $F=5.583$ ,  $p=0.05$ ). There was a difference in total foraging trip time between the end of the first day and the start of the second ( $Z=-2.100$ ,  $N= 8$ ,  $p=0.036$ ). No difference was found between the end of the first day and the end of the second day ( $Z=-0.560$ ,  $N=8$ ,  $p=0.575$ ).

In addition, an increase in volume of sucrose solution uptake with foraging experience could be found on the first ( $F_{5,444, 65.331}=4.231$ ,  $p<0.01$ ) and second day of foraging ( $F_{3,060, 21.421}=3.409$ ,  $p=0.035$ ) (Fig.1B). There was no difference in uptake between the last foraging trips on the first foraging day and the first foraging trips on the second foraging day ( $t_7=1.899$ ,  $p=0.099$ ) or between the last foraging trips of both days ( $t_7=0.444$ ,  $p=0.671$ ).

**From hive to food source:** The time between departure from the hive and arrival at the food source decreased with foraging experience on the first day of foraging ( $F_{2,262, 22.619}=4.214$ ,  $p=0.024$ ,  $n=11$ ) but not anymore on the second day ( $F_{2,157, 12.941}=1.126$ ,  $p=0.358$ ,  $n=7$ ) (Fig. 2A). There was a slight difference between the end of the first day and start of the second day in flight time from hive to food source ( $t_6=-2.453$ ,  $p=0.05$ ). No difference could be found between the last foraging trips on both days ( $t_6=-0.256$ ,  $p=0.806$ ).

**Flower handling time:** Because 2 bees ( $n=12$ ) showed extreme high flower handling times on the 15<sup>th</sup> foraging trip compared to the rest of their career, the handling time did not seem to decrease with foraging experience on the first ( $F_{2,623, 26.228}=2.425$ ,  $p=0.095$ ,  $n=12$ ) or second day ( $F_{1,085, 7.592}=3.628$ ,  $p=0.094$ ,  $n=8$ ) (Fig. 2B) of foraging. When these outliers were removed from the data a decrease in handling time on the first day of foraging could be found ( $F_{2,102, 16.818}=3.731$ ;  $p=0.044$ ,  $n=10$ ).





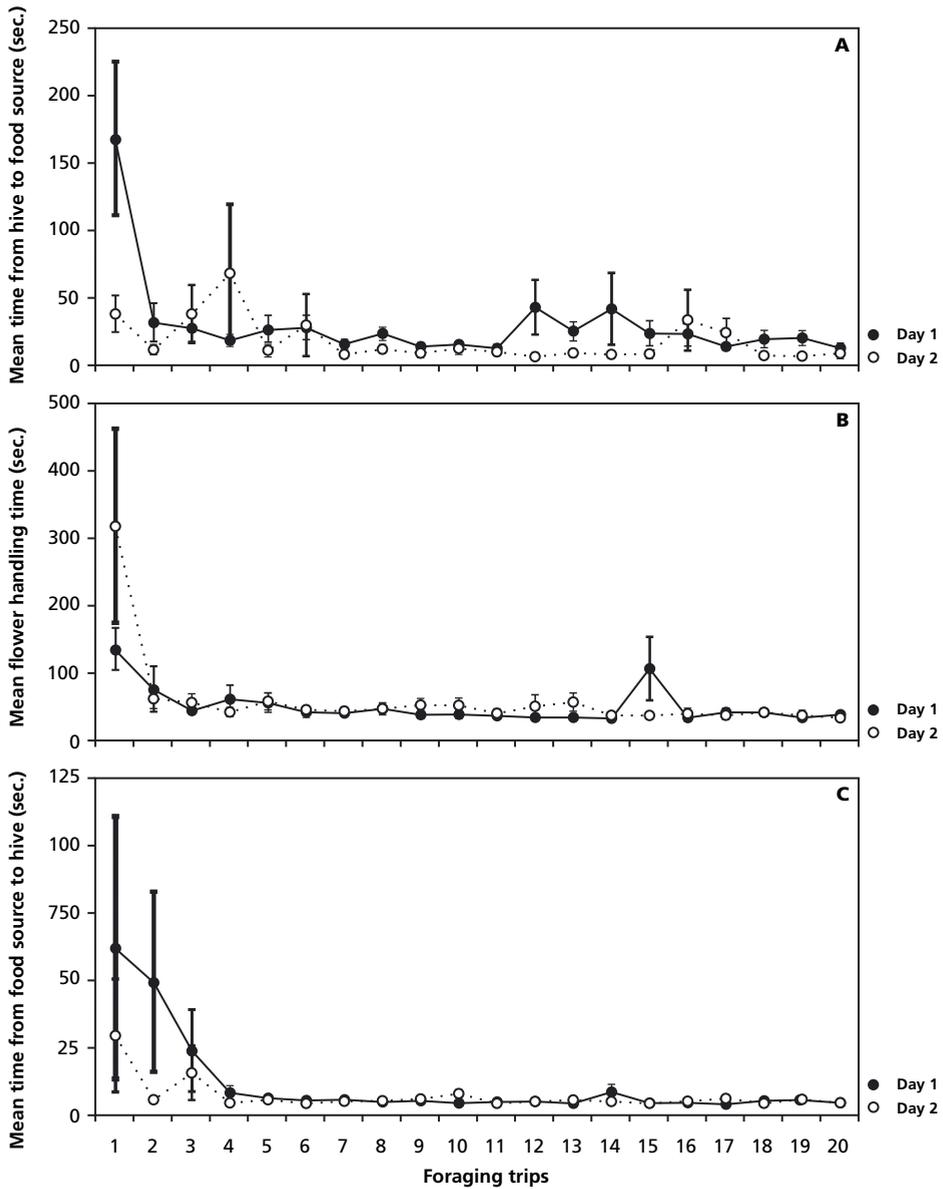
**Figure 1:** Foraging performance pattern in the stingless bee *Plebeia tobagoensis*. Mean total foraging trip time ( $\pm$ SE) (A) and mean volume of sucrose solution uptake per foraging trip ( $\pm$ SE) (B) as a function of foraging experience on the first ( $n=13$ ) and second foraging day ( $n=8$ ).

There is no difference between the last foraging trips of the first foraging day and the first trips on the second foraging, although a trend towards a difference can be found ( $t_7=-2.132$ ,  $p=0.07$ ). The last foraging flights on both foraging days show no difference in handling time ( $t_7=-0.914$ ,  $p=0.391$ ).

**From food source to hive:** On both foraging days no decrease in time between departure from the food source and arrival at the hive could be found (day 1:  $F_{1.830, 18.297}=1.374$ ,  $p=0.276$ ; day 2:  $F_{1.427, 8.563}=1.277$ ,  $p=0.310$ ) (Fig 2C).

There was no difference in time between departure and arrival between the last foraging trips of the first day and the first foraging trips of the second day ( $Z=-1.690$ ,  $N=7$ ,  $p=0.091$ ) or between the last foraging trips of both days ( $t_6=-1.527$ ,  $p=0.178$ ).





**Figure 2:** To find out which part of the total foraging trip is most responsible for foraging performance increase, foraging trip time was subdivided in; time from hive to food source, flower handling time and time from departure from the food source to arrival at hive. Mean time between departure from the hive until arrival at the food source ( $\pm$  SE) (A), mean flower handling time ( $\pm$  SE) (B) and mean time from departure of the food source until arrival at the hive ( $\pm$  SE) (C) as a function of foraging experience on the first (n=11) and second foraging day (n=8).



## Discussion

In this study, the development of the foraging performance of novice foragers of the stingless bee species *Plebeia tobagoensis* was followed over a period of two days.

We found a decrease in foraging trip time and an increase in load size with increasing experience. The decrease in foraging trip time already occurred after about 3 foraging trips. After these first few trips foraging performance seemed to reach a plateau. The decrease in foraging trip time was mainly the result of a decrease in the flower handling time and of the time necessary to reach the food source and not of the time necessary to fly back home.

The performance level on total foraging time that was obtained at the end of the first foraging day reduced after a night, since trip times were again longer at the start of the following morning. The performance levels of all studied foraging aspects on the end of both foraging days did not differ, indicating that the highest level of foraging performance was already reached on the end of the first foraging day. These results seem to coincide with those found in bumble bees (Kearse *et al.* 1996).

Increase in foraging performance with experience can be the result of several factors involved in foraging. First of all, learning might play a role. Learning the exact location of a food source and learning how to handle the flower can improve foraging performance. Several studies on both honey bees and bumble bees have indeed shown that bees are able to learn food source location, flower features, and other factors involved in foraging performance (Menzel *et al.* 1974, Gould & Gould 1988, Papaj & Lewis 1993). The results of our study would in that case indicate that stingless bees forget part of their learned abilities overnight.

However, there are other factors that might play a role in foraging performance improvement as well. One such factor might be the presence of scent-marks on the food source. The use of food source marking pheromones has been found in honey bees (von Frisch 1967), bumble bees (Schmitt & Bertsch 1990) and stingless bees (Lindauer & Kerr 1960, Aguilar & Sommeijer 2001, Schmidt *et al.* 2003, Jarau *et al.* 2004). It has been shown that the scent-marks produced by the forager itself or by foragers of the same colony can attract bees to revisit the food source. The scent-marks might as well give information on the exact landing place on the food source, in this way increasing foraging performance of individuals that use these marks when revisiting the source. Neither our experimental set-up, nor the set-up of Kearse *et al.* (1996), can exclude the use of own scent marks by individual foragers when revisiting the



food source, although flower handling time and sucrose solution uptake did improve as well and these are probably not affected by the presence of scent marks.

Irrespective of the way it is realised, the overnight decrease in foraging performance may be an important foraging strategy for bees living in relatively small colonies in a dynamic environment. This would facilitate individual flexibility in food source collection, instead of complete forager specialisation. In smaller sized social bee colonies, such as those of bumble bees and some stingless bees, foragers may have to visit many different food sources and collect different food components during their foraging career in order to allow the colony to respond to extra- and intra-nidal changes. In such species it may pay off to forget or to be able to ignore faded information of scent marks of the previous day.



## Chapter 5

# The allocation of foragers to a new foraging task in the stingless bee *Plebeia tobagoensis* (Hymenoptera; Meliponini)

*Proc. Exper. Appl. Entomol., NEV, Amsterdam: 16 (2005)*

### Summary

Social insect colonies can adjust the distribution of forager labour over different foraging tasks in three ways; 1) unemployed or new foragers can be allocated. 2) workers that are employed in certain tasks can be allocated to other tasks. 3) workers already foraging on a task can be activated to work harder. In this study we examined how colonies of the stingless bee *Plebeia tobagoensis* adjust their foraging forces when a new foraging task occurs. So far, only one study has been done on ways of adjusting foraging labour devoted to certain foraging tasks in stingless bees. The increase in foraging labour directed to, in this case, pollen foraging was the result of intensified individual foraging activity and an increase in pollen foragers, but it was uncertain whether this increase originated from allocated non-foragers or switched active foragers. We found that most of the labour for the new task was supplied by allocating non-foragers to this task. In the stingless bee *Plebeia tobagoensis* the flexibility of colony foraging behaviour seems to be largely dependent on the allocation of non-active foragers and not on the flexible behaviour of individual active foragers. When we assume that the allocated foragers were mostly unemployed before, the activation of these foragers seems to be an economic solution for forager allocation in the case of the occurrence of a new foraging task.



## Introduction

Stingless bees, like other social insects, can adjust their colony foraging activity in response to changes in resource availability (Seeley 1995, Biesmeijer 1997, Gordon 1996). Not only foraging activity in general, but also the distribution of workers over different foraging tasks, e.g. nectar or pollen collection, can be modified to the actual foraging situation (Seeley 1995, Biesmeijer 1997). Pollen and nectar are generally not equally available during the day, which results in a difference in allocation of foragers over these resources over the day in both honeybees and stingless bees (Seeley 1995, Biesmeijer 1997).

There are three ways in which a colony can adjust the foraging activity devoted to different foraging tasks (Rotjan *et al.* 2002); 1) new or unemployed foragers can be allocated to a task, 2) workers that are employed in a task can be allocated to another task (switching), 3) workers already working on a certain task can be activated to work harder.

In honeybees it was found that the increase in pollen foraging activity, caused by experimentally induced pollen stress, was mostly the result of the allocation of new foragers to the task of pollen foraging (Rotjan *et al.* 2002). Similarly, the increase of water collection in case of brood overheating in honeybees seemed to be the result of the allocation of new foragers to the task of water foraging instead of, for example, reallocating nectar foragers to this job (Seeley 1995)

In stingless bees only one study has been performed on mechanisms used to adjust foraging labour devoted to certain foraging tasks in stingless bees (*Melipona beecheii*: Biesmeijer *et al.* 1999). The increase in foraging labour directed to pollen foraging was the result of intensified individual foraging activity and an increase in pollen foragers. In this study on *Melipona beecheii* it remained uncertain however, if these foragers originated from allocated non-foragers or active foragers that switched to the collection of pollen.

In this study we examined how colonies of the stingless bee *Plebeia tobagoensis* adjust their foraging forces when a new food source becomes available. Since, the introduction of this new food source resulted in a new foraging task, only the first two processes (allocation of non-foragers or task switching of active foragers) can result in adjustments of forager allocation.

## Materials and Methods

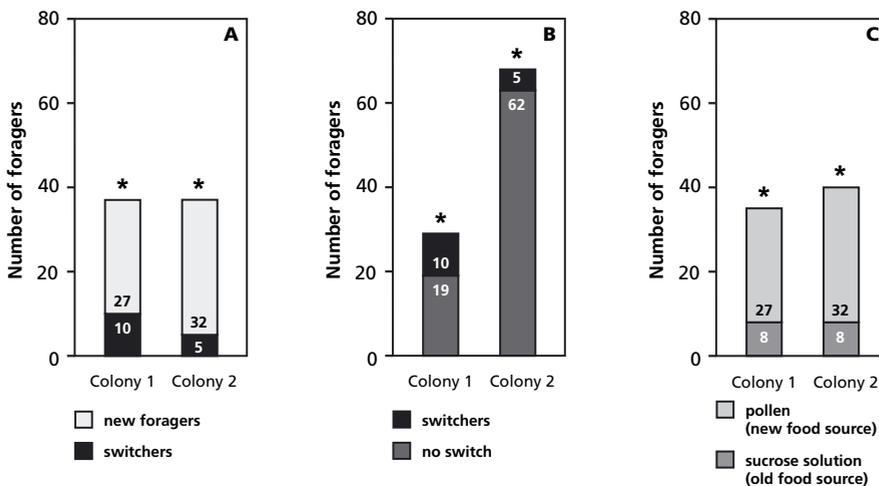
The experiment was performed in a climate controlled greenhouse compartment of the Utrecht University Botanical Gardens. We used two colonies of the stingless bee *Plebeia tobagoensis* Melo (2003), with colony



sizes of around 800 bees. On the first day of the experiment only sucrose solution (60% w/w, with vanilla essence (5 $\mu$ l/100 ml) feeders were placed in the compartment. Bees foraging on this food source were colour marked and counted. On the second day of the experiment we introduced, next to the sucrose feeder, a new source which contained pollen (5 *spathiphyllum* flowers (which offer exclusively and abundantly pollen). Bees visiting the food sources were colour marked and counted. To analyse which foragers were visiting the new food source, the history of each forager visiting this source was taken into account (new foragers or old forager from the first day of the experiment)). The experiment was performed once with each *P. tobagoensis* colony.

## Results

When the new food source was introduced on the second day of the experiment we found that most of the foragers on this source were new foragers that had not foraged on the first day of the experiment (col. 1: 73%;  $\chi^2=7,81$ ,  $p<0.01$ ; col. 2: 86%;  $\chi^2= 47.68$ ,  $p<0.01$ ) (Fig. 1A). From the bees that foraged on the first day of the experiment (before the introduction of the new food source) only a small proportion switched to the new food source (pollen) on the second day of the experiment (col.1: 34%; col.2: 7%) (Fig. 1B). From the bees that started foraging on the second day of the experiment, the vast



**Figure 1:** The allocation of switchers (bees collecting sucrose solution on the first day of the experiment) and new foragers (unemployed foragers on the first day of the experiment) over a newly introduced food source (pollen) on the second day of the experiment (A). Proportion of foragers that switched from collecting sucrose solution on the first day of the experiment to pollen collection (newly introduced food source) on the second day of the experiment (B). Allocation of new foragers (unemployed foragers on the first day of the experiment) over the old (sucrose solution) and new food source (pollen) on the second day of the experiment (C).



majority was allocated to the new food source (pollen) (col. 1: 77%:  $\chi^2=10.31$   $p<0.01$ ; col. 2: 80%:  $\chi^2= 14.40$ ,  $p<0.01$ ) (Fig. 1C).

## Discussion

In social bee colonies the allocation of workers is dynamic, meaning that the individuals can switch foraging tasks, and the distribution of foragers over different foraging tasks can change with environmental conditions (Gordon 1996).

In this study, on the stingless bee *Plebeia tobagoensis*, we analysed the processes which are involved in the reallocation of foragers when a new food source becomes available. We found that most of the labour for the new task was supplied by allocating non-foragers to this task. This agrees with the back-up found in honeybees by Rotjan et al (2002) and Seeley (1995). It should be noted, however, that the occurrence of new foragers on the second day of the experiment could also be the result of “nest-bees” becoming older and shifting to the task of foraging. But the difference in the number of new pollen foragers and new sucrose foragers on the second day of foraging suggests that most of the new foragers were allocated because of the occurrence of a new foraging task.

Although some individuals switched from sucrose solution collecting to pollen collecting, this seemed not nearly as important for the allocation of foragers to the new food source as allocation of non-foragers. When we assume that the non-foragers of the second day were mostly unemployed on the first day of the experiment, which has been found in honeybees (Seeley 1997), this seems to be a low cost solution. Switching is costly (Chapter 3), especially when foragers are successful on the first day of the experiment, as is the case in our study. By allocating unemployed foragers, the other foraging tasks can continue without interruption. Allocating unemployed foragers is only possible, however, when a colony has a reserve supply of labour. This might be the case in eusocial insect colonies or when foraging activity is low. These unemployed bees might serve as “labour in stock” for situations when sudden changes in colony needs or food availability occur.



## Chapter 6

# The effect of mass flowering on food storage and foraging behaviour of the stingless bee *Melipona beecheii* (Hymenoptera; Meliponini)

With: SM Schaafsma, M Sandker & MJ Sommeijer  
Submitted to *Ecological Entomology*

### Summary

Mass flowering plant species offer a great amount of food over a relatively short period of time. In order to benefit from this sudden increase in food availability social bees have to increase their foraging activity and direct it towards this rich food source. In this study we investigate the influence of blooming mass flowering plants on the foraging behaviour and the colony's food storage of the stingless bee *Melipona beecheii* in El Salvador. Knowledge on flexibility of foraging behaviour and the effect of this flexibility on colony condition when food availability in the field suddenly increases is essential for understanding how social insect colonies can respond adaptively to a dynamic environment.

We found a positive relationship between the number of mass-flowering plants in bloom and colony weight, which was at least partly the result of an increase in nectar storage. The increase in nectar foraging was probably the result of an increase in individual foraging activity but there was also an indication of reallocation of pollen foragers towards nectar foraging. *M. beecheii* colonies thus are able to benefit from the surplus of food available due to blooming mass flowering species and rely partly on flexibility of individual foraging behaviour in order to respond to an unpredictable environment.



## Introduction

Bees require two food components: nectar, as a source for carbohydrates for energy, and pollen, as a source of protein mainly for feeding larvae. For bees, which are thus totally dependent on plants for their food, periods of high food availability are often followed by periods of meagre foraging conditions (Seeley 1985). Social bee colonies with perennial nests have to survive in such a dynamic foraging environment for longer periods. As survival of adult bees and a steady production of brood depend on constant food availability, all highly social bees store nectar and pollen reserves for periods with low food influx.

In the tropics, the habitat of stingless bees, two extreme patterns of flower appearance can be distinguished (Gentry 1974): 1) steady state, where the individual plant produces small numbers of new flowers almost daily over an extended period, 2) mass-flowering (big bang), where an individual plant produces large numbers of new flowers each day over a short period (often less than one week). Mass-flowering periods offer great opportunity for social bees to hoard large amounts of pollen and nectar.

From many social bee species it is known that they profit from mass-flowering periods (Appanah 1993). Giant honeybees (*Apis dorsata*), for example, migrate to the site of mass flowering plants and populations increase rapidly in response to mass flowering (Itioka *et al.* 2001). In addition, bumblebee densities increase with an increase in mass-flowering crops in their surroundings (Westphal *et al.* 2003). Although stingless bees are mentioned as major pollinators of mass-flowering species (Augspurger 1980, Nagamutsi & Inoue 2002), little is known about how stingless bees respond to this sudden increase in food availability. In a study on the response of stingless bees (*Trigona spp.*) on general flowering in Malaysia, the frequency of forager returns increased during the general flowering event (Nagamitsu & Inoue 2002), indicating an increase in food influx during this period of high food availability.

There are two ways in which bee colonies can boost foraging activity when mass flowering occurs; 1) increase the number of foragers and 2) activate foragers to work harder (Anderson & Ratnieks 1999, Rotjan *et al.* 2002). Most studies on environmental cues influencing foraging labour reallocation in social bees, have been directed to changes in food stores inside the colonies (stingless bees: Biesmeijer *et al.* 1999, bumblebees: Cartar 1992, Landry *et al.* 2000; honeybees: Fewell & Winston 1996, 1992, Fewell & Bertram 1999, Rotjan *et al.* 2002). In honeybee colonies exposed to a sudden decrease in pollen stores, for example, additional labour for the task of pollen foraging can be the result of allocating non-foragers to the task (Fewell & Bertram 1999, Rotjan *et al.* 2002) but also of an increase in individual foraging activity (Fewell &



Winston 1992). In a study on pollen stress in *Melipona beecheii* in Costa Rica, no increase in the total number of foragers was found, but the number of pollen foragers increased and there were indications of increased individual foraging activity (Biesmeijer *et al.* 1999). In stingless bee colonies extra non-foragers might not be as massively available as in honeybee colonies since colony sizes of most stingless bee species are smaller than those of honeybees. In that case increase in individual foraging activity might be an important factor in increasing colony foraging activity.

Not much is known about the effect of an increase in food availability in the field on the recruitment of foraging labour in social bees. Núñez (1970) reported an increased allocation to feeders with high nectar flow rates compared to feeders with low flow rates in honeybees. Inoue *et al.* (1985) revealed a negative correlation between the amounts of resources and the flight duration in the stingless bee *Trigona minangkabau*, which might indicate an increase in the number of foraging flights per individual per day.

More information on the dynamics of foraging behaviour and effect on colony condition as a result of a surplus of food availability in the field in social bees is essential for understanding how these colonies can respond adaptively to a dynamic environment.

In this study we will focus on three hypotheses:

- 1) Colony food storage; when blooming mass-flowering plants have a positive effect on food storage of stingless bees, we expect the weight and number of storage pots to increase with increasing mass-flowering.
- 2) Colony foraging activity; an increase in pollen and nectar flights is expected when stingless bees utilise the increase in food availability due to mass-flowering.
- 3) Individual foraging activity; because of low colony sizes in *M. beecheii*, a possible increase in foraging activity during mass-flowering is expected to be at least partly the result of increased individual foraging activity. Thus, we expect individual foraging activity to increase with an increase in mass flowering.

## Methods

### Study area and bee colonies

This study was performed in Caballero, Chalatenango (UTM-coordinates: 0269351-1582671); a mountain village at approximately 1400 m. asl. in the Neotropical forest in the north of El Salvador. The observations took place from December 2003 to April 2004. In total, three colonies of the stingless bee



species *Melipona beecheii* Bennett with colony sizes of 500–1000 individuals were used in this study. The colonies were housed in wooden hives (60 × 20 × 20 cm) which were placed 1.30 m. above the ground. A plastic tube with two blockades, placed in front of the original entrances, slowed the bees down when entering the hive, making observations on the loads of the bees possible.

### Mass-flowering

All mass-flowering species in the circumference of 500 meters from the colonies were counted and localised with the help of a Global Positioning System (GPS). Although *Melipona spp.* can forage up to 4 km from the hive (Roubik & Aluja 1983, van Nieuwstad & Iraheta 1996), most foraging is concentrated close to the hive (Roubik & Aluja 1983). The mass-flowering species present in the study area and flowering during the observation period were *Vernonia patens* (a shrub providing both nectar and pollen), *Cordia alliodora* (a tree providing both nectar and pollen), and *Gliricidium sepium* (a tree providing only nectar). During this study, *M. beecheii* did forage mainly on the mass-flowering species *C. alliodora* and *V. patens* (data PROMABOS), but food was also collected from the non-mass flowering species *Myriocarpa sp.*, *Tibouchina longifolia* and *Liquidambar styraciflua* (data PROMABOS).

Each week the number of mass-flowering plants in bloom was recorded per species. The number of mass-flowering plants in bloom within the circumference of 500 meter added up for all species is “the number of mass-flowering plants in bloom” which is used as a weekly measurement (Table 1).

### Experimental procedures

**Colony food storage:** Changes in colony weight are a reliable indicator of changes in colony storage (Seeley 1995). Colony weight was measured weekly at the end of a foraging day for colony 1, 2 and 3 from January 28 until April 21. The weight was measured with an accuracy of 100 grams. The weight of colony 1 at the start of the experiment was 7.2 kg, colony 2 weighted 10.5 kg and colony 3 weighted 7.6 kg. The weight increase per week of the three colonies was checked for similarities of slopes with an R squared change linear regression. Because the slopes of the weight increase were equal for all three colonies, the data on these colonies was pooled (F change<sub>removed</sub> = 1.447, P=0.253, df=2,13). A partial correlation was used to test the relationship between the increase in weight and the number of mass-flowering plants in bloom.

The nectar pots of colony 1 were counted weekly from March 3 until April 7. At the end of a foraging day the hive in which the colony was housed was opened and all visible nectar pots were counted. At the start of



**Table 1:** Mass flowering plants in the research period in the circumference of 500 meters around the *M. beecheii* hives. Plants were counted as parts of a whole plant when only part of the tree was flowering.

Date	number of trees flowering			total
	<i>C. alliodora</i>	<i>G. sepium</i>	<i>V. patens</i>	
17/12/03	0	0	0	0
19/12/03	0	0	0	0
08/01/04	0	0	0	0
14/01/04	23	0	0	23
21/01/04	23	3	0	26
28/01/04	23	6	0	29
04/02/04	11.5	6	0	17.5
11/02/04	5.75	6	5	16.75
18/02/04	1.15	4.5	5	10.65
25/02/04	1.15	4.5	15.15	20.8
03/03/04	1.15	1.5	25.25	27.9
10/03/04	0	0	60.6	60.6
17/03/04	0	0	101	101
24/03/04	0	0	50.5	50.5
31/03/04	0	0	25.25	25.25
07/04/04	0	0	5	5
14/04/04	0	0	0	0
21/04/04	0	0	0	0

the experiment, 16 nectar pots were present. Because of an invasion of phorid flies (*Pseadohypocera kerteszi*), a serious pest of stingless bee colonies, it was not possible to count the nectar pots more than 6 times during the research period. Pollen pots were not counted as they were located deeper into the nest. A Pearson product-moment correlation was used to test the relationship between the weekly increase in nectar pots and the number of mass-flowering plants in bloom.

**Colony foraging activity:** Observations on colony foraging activity were made weekly for colony 1 from December 19 until April 20 and for colony 2 from February 11 until April 20. For both colonies, the number of departures, pollen trips and nectar trips were counted for ten minutes every hour from 7:00 until 17:00. A Pearson product-moment correlation or Spearman's Rank order correlation was used to test the relationship of the different variables of colony foraging activity against the number of mass-flowering plants in bloom.



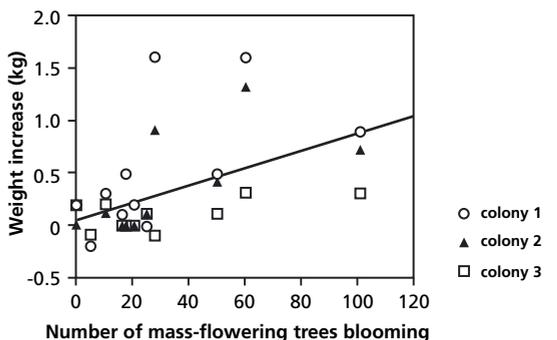
**Individual foraging activity:** The individual foraging activity was analysed by marking foragers and recording their flight behaviour by the use of video. Foragers of colony 1 were observed weekly from February 17 until April 21. Two days before the start of every observation foraging bees were captured between 10:00 and 17:00 and marked with numbered paper tags. On observation days a video camera was placed above the plastic entrance tube. Recordings were made from 9:00 until 12:00. The personal identification number and the departure time were noted down for every marked forager. The individual foraging frequency was calculated as the number of times a forager left the colony within the 3 hours recorded. A Spearman's Rank order correlation was used to test the relationship between the individual foraging frequency and the number of mass-flowering plants in bloom.

## Results

### Colony food storage

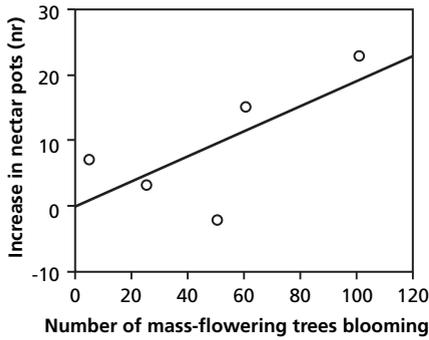
There was a strong positive correlation between the number of mass flowering plants in bloom and the weight increase of the colonies ( $r^2=0.551$ ,  $P = 0.001$ ,  $n=33$ ), with high numbers of mass flowering plants associated with high levels of weight increase (Fig. 1). This correlation coefficient indicates a substantial relationship between mass-flowering and colony weight (Martin & Bateson 1993).

The correlation coefficient for the relationship between the number of mass-flowering plants and the increase in number of nectar pots indicates a marked relationship between the two values ( $r^2=0.699$ ,  $P = 0.189$ ,  $n=5$ ) (Fig. 2). It should be noted, however, that this correlation is not statistically significant, which might be due to the low sample size.

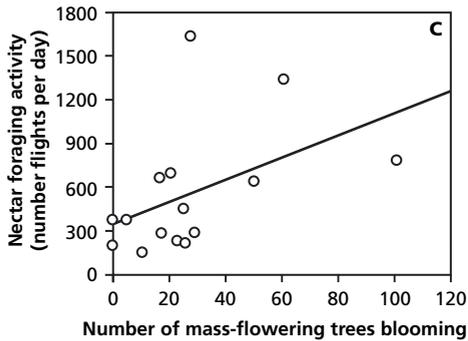
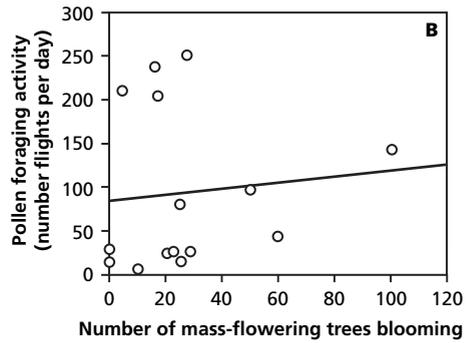
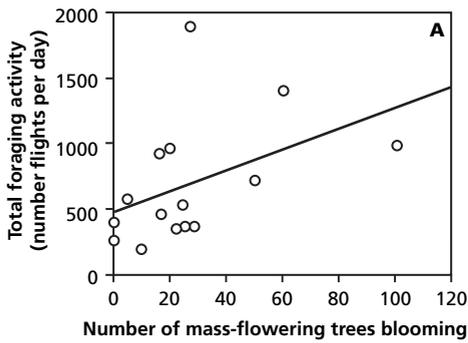


**Figure 1:** Weight increase compared to the number of mass-flowering plants in bloom for three colonies of *Melipona beecheii*. Correlation for total population:  $r=0.581$ ,  $p<0.001$ ,  $n=33$ .





**Figure 2:** Increase in number of nectar pots, compared to number of mass-flowering plants in bloom for colony 1 of *Melipona beecheii*. Correlation:  $r=0.699$ ,  $p=0.189$ ,  $n=5$ .

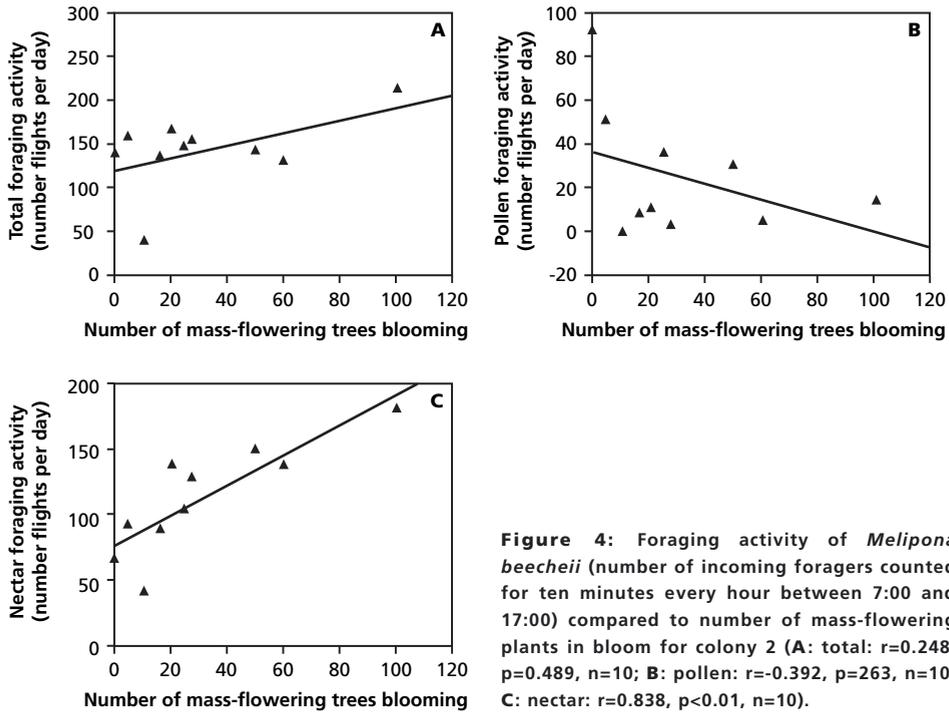


**Figure 3:** Foraging activity of *Melipona beecheii* (number of incoming foragers counted for ten minutes every hour between 7:00 and 17:00) compared to number of mass-flowering plants in bloom for colony 1 (A: total:  $r=0.522$ ,  $p=0.046$ ,  $n=15$ ; B: pollen:  $r=0.213$ ,  $p=0.446$ ,  $n=15$ ; C: nectar:  $r=0.542$ ,  $p=0.037$ ,  $n=15$ ).

### Colony foraging activity

Because foraging patterns did differ significantly between the colonies, both colonies observed in this study were treated separately (total foraging activity:  $\chi^2_9 = 259.774$ ,  $P < 0.001$ ; nectar:  $\chi^2_9 = 168.660$ ,  $P < 0.001$ ; pollen:  $\chi^2_9 = 388.344$ ,  $P < 0.001$ ). Total foraging activity of colony 1 was positively correlated with the number of mass-flowering plants in bloom ( $r_s = 0.522$ ,  $P = 0.046$ ,  $n = 15$ ) (Fig. 3A), indicating a substantial relationship (Martin & Bateson 1993). Total foraging



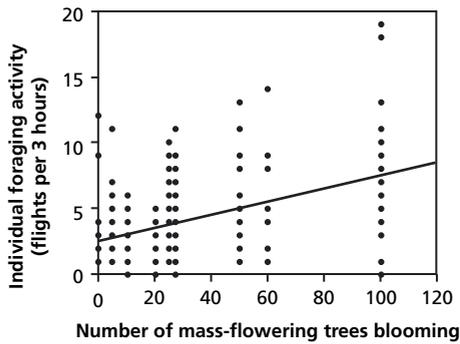


activity of colony 2, however, did not increase significantly with increased mass-flowering ( $r_s=0.248$ ,  $P=0.489$ ,  $n=10$ ) (Fig. 4A). The collection of nectar increased significantly with increased mass-flowering in both colonies (colony 1:  $r_s=0.542$ ,  $P=0.037$ ,  $n=15$ ; colony 2:  $r^2=0.838$ ,  $P<0.01$ ,  $n=10$ ) (Fig. 3C and 4C), indicating a substantial to marked relationship (Martin & Bateson 1993). Pollen collection, on the other hand did not show a significant positive correlation with mass-flowering (colony 1:  $r_s=0.213$ ,  $P=0.446$ ,  $n=15$ ; colony 2:  $r^2=-0.392$ ,  $P=0.263$ ,  $n=10$ ) (Fig. 3B and 4B).

### Individual foraging activity

The increase in total foraging activity in colony 1 was at least partly the result of an increase in individual foraging activity, as the number of flights per individual forager increased with the number of mass-flowering plants in bloom ( $r_s=0.405$ ,  $P<0.01$ ,  $n=205$ ). The correlation coefficient indicates a substantial relationship between mass-flowering and individual foraging activity in *Melipona beecheii* (Martin & Bateson 1993) (Fig. 5).





**Figure 5:** Individual foraging activity (number of flights per three hours) compared to the number of mass-flowering plants in bloom for one colony of *Melipona beecheii*. Correlation:  $r=0.405$ ,  $p<0.01$ ,  $n=205$ .

## Discussion

In this study we investigated the relationship between the number of mass-flowering plants in bloom and the foraging behaviour and condition of colonies of the stingless bee species *Melipona beecheii*.

The availability of blooming mass flowering plants clearly improved foraging conditions for *M. beecheii* colonies. In all colonies studied we found that an increase in mass flowering resulted in an increase in colony weight. This increase was most probably the result of the increase in the number of nectar pots, as the number of nectar pots seemed to increase in colony 1 and nectar collection increased in the two studied colonies. Colony weight and nectar storage are strong indicators of colony survival. In addition, a surplus of food is needed for colony reproduction (swarming): food stores and food availability in the field are related to the production of sexuals in both honeybees and stingless bees (Roubik 1982, van Veen 1999, Chinh 2004). Brood production, however, did not seem to correlate with foraging conditions in *M. beecheii* (van Veen 1999). In our study brood production could not be monitored because of the danger of infestation of the colonies with phorid flies (*Pseudohypocera kerteszi*) and further research is needed to investigate the importance of mass-flowering on colony reproduction in *M. beecheii*.

In order to be able to respond to the opportunity mass flowering plants offer, social bees have to increase foraging activity directed towards the collection of food provided by mass flowering plant species. This study showed that *M. beecheii* colonies respond to variation in mass-flowering plants in bloom by adjusting their colony foraging behaviour. In both studied colonies, nectar collection increased significantly with increased mass flowering, whereas pollen collection was independent of mass flowering. The increase in nectar collection can be the result of increase in individual foraging activity or of an increase



in the number of foragers directed towards nectar collection. The positive relationship between individual foraging activity and mass flowering indicates that at least part of the increase of labour devoted to food collection from mass-flowering plants is the result of an increase in individual foraging activity. Food availability in the field is known to be an important factor influencing individual foraging activity (honey bees: Núñez 1982, Seeley 1995; stingless bees: Biesmeijer *et al.* 1999).

Clearly, variation in individual foraging activity can contribute significantly to colony foraging flexibility. Colony flexibility can, however, also be the result of an increase in the number of bees foraging on a certain food source. This can, in this case, either be by allocating non-foragers to the source or by redirecting foragers already collecting other food components. In one of the two studied colonies the correlation between pollen collection and mass flowering showed a negative correlation-coefficient (although not significant), which might indicate that foraging effort of pollen collection was directed to nectar collection in this colony. In a field study in Costa Rica on pollen stress in *Melipona beecheii*, it was found that colonies did not increase their overall foraging force in this situation but did increase the number of pollen foragers (Biesmeijer *et al.* 1999). Although allocation of non-foragers in this case can not be ruled out, the lack of increase in overall foraging force might indicate individual switching of nectar foragers to the task of pollen foraging.

The lack of a positive relationship between pollen collection and mass-flowering in both colonies may have two reasons, either these mass-flowering species in the studied area are no pollen sources for *M. beecheii*, or the collection of pollen in periods of high food availability is of less importance for these bees than the collection of nectar. Pollen, however, was collected from two mass flowering species in the study area (*Vernonia patens* and *Cordia alliodora*), although the most important pollen source was *Liquidambar styraciflua*, which is not a mass-flowering species (data PROMABOS). An increase in pollen foraging could have been expected, thus, unless a constant pollen flow might not be as important in stingless bees as the collection of nectar. In contrast to honeybees, stingless bees provide their brood with enough food for complete development and close the cells until the adult emerges (mass-provisioning). Low pollen reserves will result in low brood production but not directly in brood loss, as is the case in honeybees, thus having no short-term negative effects. In addition, small pollen reserves may also decrease the chance of a phorid fly attack as they breed in the pollen, both in storage and brood cells, collected by the bees.

Overall, this study indicates that *Melipona beecheii* colonies are able to benefit from the surplus of food available due to mass flowering species. They



do rely at least partly on flexibility of individual foraging behaviour in order to respond to the boom and bust cycles of floral food. Individual foraging activity increased when food availability increased and there were indications of switching between foraging tasks. Although it does not seem likely that *Melipona* colonies hold large back-up forces, because of small colony sizes and low production levels, increasing foraging forces by allocating non-foraging bees when great opportunity arises might still be of importance in these stingless bees.





## Chapter 7

# Foraging labour reallocation as a result of pollen stress in the stingless bee *Plebeia tobagoensis* (Hymenoptera; Meliponini)

*With: EF Rooijackers & MJ Sommeijer*

*Submitted to Behavioral Ecology and Sociobiology*

### Summary

Pollen storage levels in bee colonies can change rapidly and this can have major fitness consequences. In order to respond adaptively to changes in storage levels, colonies have to match their foraging behaviour accordingly, either by adjusting the foraging force or the individual foraging effort. From honeybees it is known that, as a result of low pollen storage levels, they increase foraging labour by allocating non-foragers to pollen foraging and by increasing individual pollen foraging effort. Stingless bees, however, differ in brood provisioning system and colony size from honeybees and this could lead to different mechanisms used to adjust foraging behaviour. In order to understand more about the dynamics of foraging labour allocation in stingless bee colonies, we studied four colonies *Plebeia tobagoensis* under different pollen storage levels (high pollen storage levels versus pollen stress). When pollen stores were removed, the changes in colony foraging behaviour of *Plebeia tobagoensis* were mainly achieved by the allocation of unexpectedly large numbers of non-foragers to pollen collection. Switching between foraging tasks and adjusting individual foraging effort played a minor role in foraging labour reallocation as a result of pollen stress. The mass-provisioning system in brood rearing of stingless bees might make it unnecessary for pollen foragers to run high mortality risks by increasing individual foraging effort during short periods of pollen stress. The ability to allocate large groups of non-foragers by *P. tobagoensis* colonies allows these colonies to respond rapidly and economically to changes in their environment.



## Introduction

In order to survive in an ever-changing environment, social bee colonies adjust their foraging behaviour to changes in resource availability (*Apis mellifera*: Seeley 1985, 1986 Sanders & Gordon 2002 *Melipona beecheii*: Chapter 6) and colony parameters (*Apis mellifera*: Fewell & Winston 1992, 1996 Fewell & Bertram 1999 Johnson 2002 Rotjan *et al.* 2002 *Bombus spp.*: Cartar 1992 *M. beecheii*: Biesmeijer *et al.* 1999). Understanding the ways through which social bee colonies can change foraging behaviour is essential for understanding how these colonies can respond adaptively to a dynamic environment.

There are two ways in which social bee colonies can adjust the labour devoted to different foraging tasks (Anderson & Ratnieks 1999 Johnson 2002 Rotjan *et al.* 2002); 1) adjust the foraging force for a particular task by either allocating non-foragers to the task or by reallocating already active foragers (individual task switching) to the needed task, and 2) adjust the individual effort of foragers already working on the task either by changes in the activity level or load.

Most studies on foraging labour reallocation in response to environmental changes have addressed pollen stress in honeybees (Fewell & Winston 1992, 1996 Fewell & Bertram 1999, Johnson 2002, Rotjan *et al.* 2002). Pollen is mainly used as a protein source for developing brood and adequate pollen supply is pivotal to colony growth. Because pollen, in general, is stored in lower quantities than honey (honeybees: Seeley 1995; *Plebeia tobagoensis*: Hofstede own observation), a decrease in pollen storage levels can occur when brood producing colonies are not able to collect pollen due to adverse weather conditions (Seeley 1995) or when pollen is not available in the field (Biesmeijer *et al.* 1999). In honeybees, larvae are fed progressively and lack of pollen can result in brood loss plus the loss of investments that were already made in the rearing of these larvae. Honeybees should thus respond quickly to decrease in pollen stores to avoid these losses.

Honeybee colonies experiencing a sudden decrease in pollen stores adjusted foraging behaviour mainly by allocating non-foragers to the task of pollen foraging (Fewell & Bertram 1999, Rotjan *et al.* 2002, Fewell & Winston 1992) and by increasing individual foraging effort for pollen collection (Fewell & Winston 1992, Rotjan *et al.* 2002).

Increasing individual foraging effort is thought to be costly, as longevity is negatively correlated with individual foraging activity (honeybees: Neukirch 1982, stingless bees: Biesmeijer & Tóth 1998) and with load size (honeybees: Wolf & Schmid-Hempel 1989). Increasing foraging forces for a certain foraging task by allocating non-foragers is thought to be more efficient than attaining this by reallocating already active foragers (task switching). By reallocating



foragers to a needed task, labour devoted to other foraging tasks is lost. In addition, individual task switching is costly because of increased handling times and higher numbers of unsuccessful flights after a change in foraging task (Cartar 1992, Chapter 3). Because honeybees are generally composed of tens of thousands of workers, it is generally assumed that honeybee colonies hold large groups of back-up forces that can be activated in response to stress (Kolmes 1985, Seeley 1995). Differences in biology and colony characteristics between the different groups of social bees, however, might result in differences between honeybees and stingless bees in the mechanisms used to adjust colony foraging behaviour.

Stingless bees, in contrast to honeybees, mass provision their brood. All food necessary for the development from larvae to adult bee is already added to the cell before the egg is laid. The lack of pollen will therefore not immediately result in the loss of existing brood and investments. This raises the question if costly adjustments of foraging behaviour, like individual task switching and adjusting individual foraging effort, in response to removal of pollen stores should be expected in stingless bees. Besides differences in brood provisioning system, there are also differences in colony characteristics between stingless bees and honeybees that might influence the mechanisms used to adjust colony foraging behaviour. Because of smaller colony sizes and lower brood production levels compared to honeybees (Velthuis 1997), stingless bee colonies might not be able to hold large back-up forces. A previous study on forager reallocation in *Plebeia tobagoensis* (100-1500 individuals) indicated, however, that the allocation of non-foragers can play a major role in the adjustment of foraging labour in stingless bees when new foraging tasks appear (Chapter 5). It is not known, however, if and to what extent allocation of non-foragers plays a role when the need for an already existing task increases, and the supposedly small back-up forces of *P. tobagoensis* might not be enough to adjust colony foraging behaviour.

So far, only one study has been published on changes in foraging behaviour due to pollen stress in stingless bees (Biesmeijer *et al.* 1999). During the first 10 days after the reduction of pollen reserves in *Melipona beecheii* colonies, pollen availability in the field was low and pollen foraging almost stopped. *M. beecheii* did not seem to increase pollen foraging as long as pollen foraging was costly. When pollen availability in the field increased again, *M. beecheii* did increase pollen foraging significantly compared to the period prior to the removal of pollen stores. This increase in pollen foraging was the result of an increase in pollen foragers and probably also partly of intensified individual foraging activity. As the total foraging force did not increase, it remained uncertain whether the increase in pollen foragers originated from allocated non-foragers or switched active foragers.



In order to understand more about the dynamics of foraging labour allocation as a result of induced pollen stress in stingless bee colonies, we studied colonies of *P. tobagoensis* foraging in a closed greenhouse compartment under different pollen storage levels. We tested the hypothesis that colonies of *P. tobagoensis* mainly respond by allocation of non-foragers to pollen foraging and that the less economic changes in individual foraging behaviour, like increasing individual foraging effort and individual task switching, will play a minor role.

## Methods

To study the response of stingless bee colonies to induced pollen stress, the colony and individual foraging behaviour of four *P. tobagoensis* colonies were recorded on two subsequent days. On the first day colonies held large pollen stores (no pollen stress), on the second day all pollen stored in the colonies was removed (pollen stress). Each day the bees foraging on the provided pollen and nectar sources were marked and observed.

### Bee colonies and experimental conditions

Four colonies of *Plebeia tobagoensis* Melo were used (further referred to as SB1 to SB4). Colony sizes ranged from 300–800 individuals and in all colonies a physogastric queen was present (Table 1).

The experiments took place in a closed greenhouse compartment (15 m × 5 m × 4 m) of the Botanical Gardens of Utrecht University, The Netherlands. The temperature in the compartment was kept at a minimum of 20°C and the humidity was set at 70%. Inside the compartment two food sources were presented next to each other, one pollen source and one artificial nectar source. The pollen source consisted of six pollen bearing *Spathyphillum* flowers in a vase. The artificial nectar source consisted of 20 small cups (∅ 1 cm) glued on a yellow board (10 × 10 cm) filled with 40% sucrose solution with anise essence (5 µl/100 ml). Experiments were conducted from October

**Table 1:** Characteristics of the *Plebeia tobagoensis* colonies used in the experiments.

Colony ID	Colony size	Queen	Brood production
SB1	± 800	Yes	Yes
SB2	± 700	Yes	Yes
SB3	± 600	Yes	Yes
SB4	± 300	Yes	Yes



2004 to January 2005. Each colony was tested separately, and measurements took place from 11:00 until 14:00. The bees were not able to forage outside observation periods.

### Experimental set-up

The experiments consisted of two days. On the first day, colonies held large pollen stores, on the second day there was an absence of stored pollen. Large pollen stores were created by introducing 3 plastic tubes (5 ml) filled with pollen in the storage area of the colonies four days before the start of the experiment. Pollen stress was created by removing these tubes and other pollen pots from the storage area at the end of the measurements on day 1. During the experiment there was always a high level of nectar storage. Due to orientation problems of returning foragers in the greenhouse many individuals were lost on the first foraging day, resulting in a lower number of participating foragers during pollen stress for almost all colonies (Chi-square test for goodness of fit: SB1:  $\chi^2=0.45$ ,  $df=1$ ,  $p=0.52$ ; SB2:  $\chi^2=7.86$ ,  $df=1$ ,  $p<0.01$ ; SB3:  $\chi^2=3.57$ ,  $df=1$ ,  $p=0.06$ ; SB4:  $\chi^2=19.66$ ,  $df=1$ ,  $p<0.001$ ) (Table 2).

On both days the numbers of bees collecting nectar, pollen or both were counted. Every bee was marked according to the source(s) visited. Simultaneously, we video-recorded the hive entrance to count the number of incoming pollen-loads and to estimate the size of the pollen loads.

From the number of pollen trips and the number of pollen foragers the number of pollen trips per pollen forager was determined (Rotjan *et al.* 2002).

We discriminated three size categories for the pollen loads based on their shape: 1) small (loads flat), 2) medium (loads round) and 3) large (loads oval) (Chapter 3)

### Marking procedure

Bees foraging on the food sources were marked using UniPosca water-based odourless markers. The marks were applied on the thorax and colours were used according to the resource visited. Three colours were used on the first day for respectively bees foraging on pollen, on nectar and bees visiting both resources, on the second day three other colours were used. If a marked bee visited a source not matching to the mark already present, it was marked with a second (the colour for bees visiting both resources) over the already present mark. Marking took place when the bee was exploiting the food source.

### Behavioural categories

To be able to analyse a possible reallocation of foragers during induced pollen stress, we used the categorisation of Rotjan *et al.* (2002). Bees were



collecting either P (pollen), N (nectar), NP (pollen and nectar) or X (nothing) on day 1 and day 2. Combining of both foraging days resulted in bees belonging to the category “continuers” when they collected P or NP on day 1 and P or NP on day 2. Bees were placed in the category “switchers” when they collected N on day 1 and collected P or NP on day 2. The category “novice” consisted of bees that did not forage on day 1 (and thus without a mark on day 2) and collected P or NP on day 2.

The categories correspond with the two ways of increasing foraging force as is described in the introduction; the category “novice” corresponds with allocated non-foragers and the category “switchers” corresponds with individuals switching foraging tasks.

### **Statistical Analysis**

To test if the number or percentage of pollen foragers and incoming pollen loads did differ between the situation of large pollen stores (day 1) and the situation of pollen stress (day 2) a Chi-square test for goodness of fit was performed for every colony separately.

In order to analyse a possible reallocation of foragers during pollen stress, the distribution of the three pollen forager categories (novices, switchers, continuers) during pollen stress was compared using a Chi-square test for goodness of fit for every colony separately. The difference in this distribution between the colonies was tested with a Chi-square test for independence. In addition, the number of non-foragers allocated to nectar or pollen during pollen stress was compared using a Chi-square test for goodness of fit. Because the number of bees switching from pollen to nectar during pollen stress was zero in three cases, no statistical tests could be performed on differences in numbers of bees switching from pollen to nectar and from nectar to pollen during pollen stress.

The difference in individual foraging effort between the situation of large pollen stores (day 1) and the situation of pollen stress (day 2) was tested by comparing both the number of foraging trips per day per bee and the size of the incoming pollen loads on the two days using a Chi-square test for independence.

## **Results**

### **Colony response to pollen stress**

Notwithstanding the decrease in foraging force, the number of pollen foragers increased significantly in two colonies (SB1 and SB4) when pollen stores were removed (Chi-square test for goodness of fit: SB1:  $\chi^2=28.27$ ,  $df=1$ ,



**Table 2:** Response of colonies to the removal of pollen stores. Between brackets the percentages of pollen foragers compared to nectar foragers and percentages of incoming pollen loads compared to nectar loads are indicated.

	Total number of foragers		Number (percentage) of pollen foragers		Number (percentage) of incoming pollen loads	
	Day 1: No pollen stress	Day 2: Pollen stress	Day 1: No pollen stress	Day 2: Pollen stress	Day 1: No pollen stress	Day 2: Pollen stress
<b>SB1</b>	93	102	26 (28%)	81 (79%)	26 (3%)	93 (11%)
<b>SB2</b>	56	30	17 (30%)	23 (77%)	89 (4%)	125 (8%)
<b>SB3</b>	49	32	10 (20%)	15 (45%)	9 (1%)	42 (3%)
<b>SB4</b>	74	29	39 (53%)	23 (79%)	129 (12%)	108 (26%)

$p < 0.001$ ; SB2:  $\chi^2 = 0.9$ ,  $df = 1$ ,  $p = 0.34$ ; SB3:  $\chi^2 = 1.00$ ,  $df = 1$ ,  $p = 0.32$ ; SB4:  $\chi^2 = 4.13$ ,  $df = 1$ ,  $p = 0.04$ ) (Table 2). Although the actual number of pollen foragers did not increase following pollen deprivation in colonies SB2 and SB3, the proportion of pollen foragers did increase significantly (Chi-square test for goodness of fit: SB2:  $\chi^2 = 20.65$ ,  $df = 1$ ,  $p < 0.001$ ; SB3:  $\chi^2 = 9.62$ ,  $df = 1$ ,  $p < 0.01$ ) (Table 2).

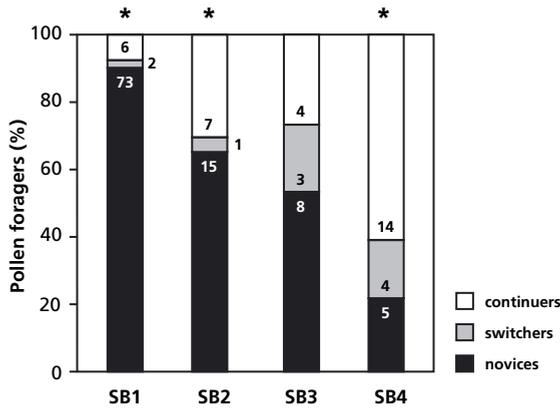
The number of incoming pollen loads also increased after removal of the pollen stores in three out of four colonies (Chi-square test for goodness of fit: SB1:  $\chi^2 = 37.72$ ,  $df = 1$ ,  $p < 0.001$ ; SB2:  $\chi^2 = 6.10$ ,  $df = 1$ ,  $p = 0.01$ ; SB3:  $\chi^2 = 21.35$ ,  $df = 1$ ,  $p < 0.001$ ; SB4:  $\chi^2 = 1.86$ ,  $df = 1$ ,  $p = 0.17$ ) (Table 2). Although the actual number of incoming pollen loads did not increase in colony SB4, the proportion of incoming pollen loads did increase significantly (Chi-square test for goodness of fit: SB4:  $\chi^2 = 5.16$ ,  $df = 1$ ,  $p = 0.02$ ) (Table 2).

### Reallocation of foragers

During pollen stress most pollen foragers belonged to the category “novice” (individuals not foraging on day 1) in colonies SB1 and SB2 (Chi-square test for goodness of fit novices vs switchers: SB1:  $\chi^2 = 67.21$ ,  $df = 1$ ,  $p < 0.001$ ; SB2:  $\chi^2 = 12.25$ ,  $df = 1$ ,  $p < 0.001$ ) (Fig. 1). In colony SB3 there was no difference between the number of novices, switchers and continuers (Chi-square test for goodness of fit  $\chi^2 = 2.80$ ,  $df = 2$ ,  $p = 0.25$ ) (Fig. 1). In colony SB4 most pollen foragers during pollen stress were continuers (foragers already collecting pollen on day 1) (Chi-square test for goodness of fit novices vs continuers:  $\chi^2 = 4.26$ ,  $df = 1$ ,  $p = 0.04$ ) (Fig. 1).

The distribution of these three categories differed significantly between the four colonies (Chi-square test for independence:  $\chi^2 = 47.21$ ,  $df = 6$ ,  $p < 0.001$ ) (Fig. 1).





**Figure 1:** Origin of pollen foragers after pollen stores were removed (day 2). The pollen foragers were divided in three categories: novices (individuals that were not seen foraging on day 1), switchers (individuals that were collecting nectar on day 1) and continuers (foragers that were already collecting pollen on day 1)

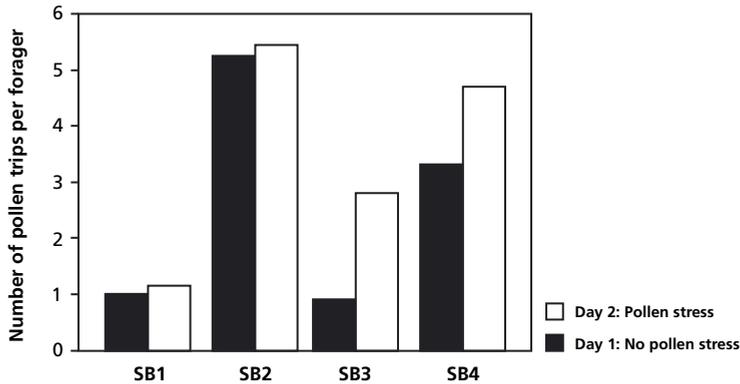
When the number of novices for either nectar or pollen during pollen stress is compared, a significantly higher number of non-foragers for pollen can be found for three out of four colonies (Chi-square test for goodness of fit: SB1:  $\chi^2=31.70$ ,  $df=1$ ,  $p<0.001$ ; SB2:  $\chi^2=5.00$ ,  $df=1$ ,  $p=0.03$ ; SB3:  $\chi^2=5.44$ ,  $df=1$ ,  $p=0.02$ ) (Table 3). Colony SB4 did not allocate non-foragers to nectar collection during pollen stress at all.

Most experienced foragers that did switch, switched from collecting nectar to collecting pollen during pollen stress and only a single forager switched from pollen to nectar collection (Table 3).

**Table 3:** Comparison between the number of non-foragers (novices) for either nectar or pollen and the number of foragers switching from sucrose solution to pollen or vice versa during pollen stress. Between brackets the percentage of novice bees allocated for sucrose solution or pollen are indicated

	Novices		Switchers	
	Pollen	Nectar	To Pollen	To Nectar
SB1	73 (79%)	19 (21%)	2	0
SB2	15 (75%)	5 (25%)	1	0
SB3	8 (89%)	1 (11%)	3	0
SB4	5 (100%)	0 (0%)	4	1
<b>Total</b>	<b>101 (80%)</b>	<b>25 (20%)</b>	<b>10</b>	<b>1</b>





**Figure 2:** Number of pollen trips per pollen forager on day 1, when pollen stores were present, and on day 2, when pollen stores were removed, for all colonies separately.

### Adjustment of individual foraging effort

There are two ways through which foragers can increase their individual pollen foraging effort: by increasing the number of pollen trips per day and by increasing the size of the pollen loads.

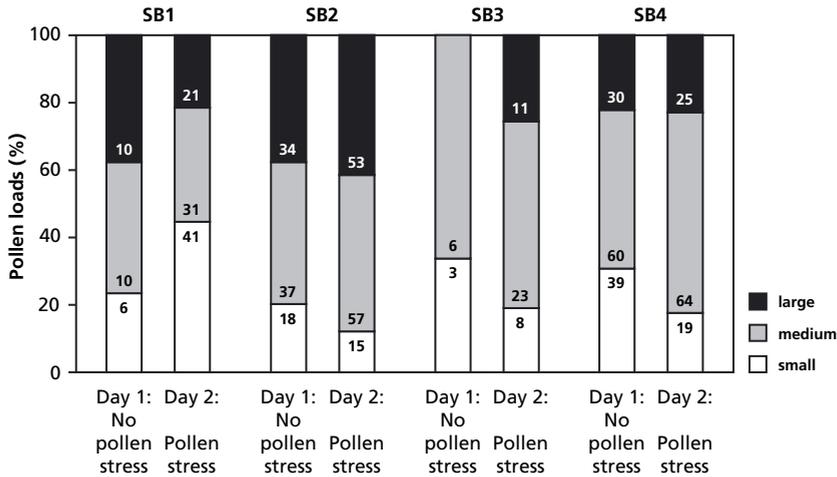
The number of pollen foraging trips per pollen forager did increase slightly, but not significantly, in all colonies during pollen stress (Chi-square test for goodness of fit: SB1:  $\chi^2=0.00$ ,  $df=1$ ,  $p=1.00$ ; SB2:  $\chi^2=0.00$ ,  $df=1$ ,  $p=1.00$ ; SB3:  $\chi^2=1.00$ ,  $df=1$ ,  $p=0.32$ ; SB4:  $\chi^2=0.50$ ,  $df=1$ ,  $p=0.48$ ) (fig 2). In addition, the distribution of incoming pollen loads for the different size categories did not change in any of the colonies, although in SB4 there seems to be a trend towards a lower percentage of small loads on day 2 (Chi-square test for independence: SB1:  $\chi^2=4.393$ ,  $df=2$ ,  $p=0.11$ ; SB2:  $\chi^2=2.70$ ,  $df=2$ ,  $p=0.26$ ; SB3:  $\chi^2=1.42$ ,  $df=2$ ,  $p=0.49$ ; SB4:  $\chi^2=5.66$ ,  $df=2$ ,  $p=0.06$ ) (Fig. 3)

## Discussion

### Colony response to pollen stress

Colonies of *Plebeia tobagoensis* responded to pollen stress by increasing influx of pollen immediately after the removal of pollen stores. Colony pollen collection has been shown to be stimulated by a decrease in pollen storage levels in honeybees (Free 1967, Fewell & Bertram 1999), bumblebees (Cartar 1992) and the stingless bee *Melipona beecheii* (Biesmeijer *et al.* 1999), indicating that this is a general trait in social bees, irrespective of the way they provision their brood. Pollen is not only important for the maintenance of brood, but also for ensuring colony growth, which is needed to produce new colonies, in both honeybees and stingless bees.





**Figure 3:** Size distribution of incoming pollen loads on day 1, when pollen stores were present, and on day 2, when pollen stores were removed, for all colonies separately. Pollen loads were divided by sight into categories small, medium and large

The observation that the removal of pollen stores resulted in an increase in pollen influx in all colonies of *P. tobagoensis* indicates that foragers somehow assess pollen storage levels and adjust their behaviour accordingly. This assessment can be made using either cues or signals (Seeley 1998, Biesmeijer & Slaa 2004). Honeybee pollen foragers obtain information on pollen storage levels through trophallaxis with nurse bees in the hive (Camazine 1993). Here the level of pollen in the trophallactic liquid is an indicator of the status of the pollen stores and thus the need for pollen collection. It is unknown whether a similar mechanism is involved in information transfer on pollen stores in *P. tobagoensis* as well, as *Melipona* nurse bees never offer food to nest mates (Sommeijer *et al.* 1985, Sommeijer & de Bruin 1994). Alternatively, workers may pick up cues directly from the nest environment, e.g. from the pollen pots or the brood combs.

### Reallocation of foragers

*P. tobagoensis* increases pollen influx mainly by allocating non-foragers to pollen foraging. In agreement with our hypothesis, switching foraging tasks and increasing individual foraging effort played a minor role in foraging labour reallocation as a result of pollen stress. The ability to allocate large groups of non-foragers by *P. tobagoensis* colonies allows these colonies to respond rapidly and economically to changes in their environment. Allocation of non-foragers as a mechanism to adjust colony foraging, has also been found for honeybees under pollen stress (Fewell & Bertram 1999, Rotjan *et al.* 2002) and for *P.*



*tobagoensis* responding to the introduction of a new foraging task (Chapter 5). Because of relatively low colony sizes and brood production levels we expected the potential back-up force of *P. tobagoensis* colonies to be small. In this study, however, we found that, at least for one of the studied colonies a relatively large number of non-foragers could be allocated. This colony, SB1, started on day 1 with 93 foragers and on day 2 allocated an additional 73 non-foragers (78%) to the task of pollen foraging.

The source of the allocated novice foragers of *P. tobagoensis* remains unclear. It is known from honeybees that large numbers of unemployed workers are present as a reserve labour force (Kolmes 1985, Seeley 1995). In *P. tobagoensis* nests, groups of inactive bees can be found as well, although sex and age of these individuals are unknown. Non-foraging workers involved in pre-foraging hive tasks, however, might be another source for an increase in foraging force. Indeed, in *M. beecheii* foraging was started at a younger age during pollen stress (Biesmeijer *et al.* 1999). In that case, allocation of non-foragers goes at the expense of in-hive tasks. The switching of individual workers between in-hive- and foraging tasks and vice-versa is an important factor in foraging force adjustments in bumblebees (Cartar 1992). Although switches from foraging tasks back to in-hive tasks have never been reported for honeybees or stingless bees, on the basis of our results this source of extra labour can not be completely excluded. To understand social bee foraging dynamics and place the mechanisms of colony foraging flexibility in an evolutionary context, it would be extremely important, however, to determine the origin of novice foragers in stingless bees.

The low contribution of switcher bees to pollen collection when pollen stores were absent may have been influenced by the high death rate on the first foraging day. The death rate (proportion of foragers that had disappeared on day 2 compared to day 1) for the studied *P. tobagoensis* colonies has been estimated at 51% - 89%, while the death rate of *M. beecheii* foragers in their natural habitat ranged from 15% to 54% (Biesmeijer & Tóth 1998). As a result of the high death rate on the first day of our experiments only a small proportion of foragers from day 1 returned on day 2, and many of these returnees (24%) switched from nectar to pollen collection. This might indicate that, when death rates would have been at normal levels, switching foraging tasks could have played a more important role in the increased pollen influx than is shown in our results.

Switching tasks also played an important role in the behavioural response of *Melipona favosa* workers to a wax-deprived period (Kolmes & Sommeijer 1992). When the authors compared their study on *Melipona favosa* with a related study on *Apis mellifera*, they concluded that the reallocation of labour



between tasks (task switching) seemed very important for the wax stress response of *Melipona favosa*, but did not occur in *Apis mellifera* (Kolmes & Sommeijer 1992).

### **Adjustment of individual foraging effort**

The removal of pollen stores in our study did not result in a significant increase in individual foraging effort in *P. tobagoensis*. The results of other studies on increase in individual foraging effort as a result of removed food stores in social bees are contradictory. In studies on honeybees with extremely different pollen treatment levels, individual pollen foraging effort was significantly higher with low pollen storage levels (Fewell & Winston 1992, Rotjan *et al.* 2002). In a study on honeybees where foragers were subjected to graded changes in pollen stores, however, no influence on individual foraging effort could be found (Fewell & Bertram 1999). When nectar reserves were depleted in wild bumblebee colonies, individual foraging effort was only significantly higher for one of the three studied bumblebee species (Cartar 1992). In a study on the response of the stingless bee *M. beecheii* to experimental pollen stress, only individuals of one of the two studied colonies showed a significant change in individual foraging activity (Biesmeijer & Tóth 1998). These results indicate that individuals can indeed change their rate of foraging activity, but apparently not always do so. The cost of shorter worker longevity might only be justified when extreme situations occur. In honeybees this situation might occur when pollen storage levels are not sufficient to feed the existing larvae. As stingless bees are mass-provisioners, the lack of pollen will not immediately result in the loss of existing brood and investments. The mass-provisioning system might make it unnecessary for pollen foragers to run high mortality risks by increasing individual foraging effort during short periods of pollen stress.



## Chapter 8

# **General summary and discussion: foraging task specialisation and foraging labour allocation in stingless bee colonies**

In this thesis, I investigated the occurrence and plasticity of foraging task specialisation and the mechanisms of foraging labour allocation in a stingless bee species with medium sized colonies. These studies show how social insect colonies can respond adaptively to an unpredictable environment.

### **Individual foraging careers**

Because colony foraging patterns are the result of the actions of individuals, in the first part of this thesis, I focussed on factors involved in foraging choices and foraging performance of individual foragers. As successful foragers tend to revisit the same food sources on following flights (Biesmeijer & Tóth 1998), the initial commodity choice is thought to have a major influence on the future foraging career of foragers. Therefore, factors involved in the foraging choice of novice stingless bee foragers were studied in Chapter 2. The initial choice of foragers was found to be greatly affected by returning successful foragers



and by the level of food storage in the nest. These factors were already found to be of influence on experienced foragers in both honeybees (Seeley 1995) and stingless bees (Biesmeijer 1997). The influence of these factors on the foraging choices of novice individuals appears to be adaptive for colony food collection as colonies can distribute new labour over the tasks that have the highest priority or that offer the greatest opportunity. As most foragers in this study collected the commodity of their first choice throughout the experiment, the first choice indeed seemed to be important for future foraging choices in *Plebeia tobagoensis*.

In order to analyse subsequent choices during individual foraging careers, I studied the occurrence and dynamics of individual specialisation in foragers of *P. tobagoensis* (Chapter 3). Foraging task specialisation can be a means of economising flight and foraging time by searching for commodities that a bee has learned to manipulate. Most individuals specialised on one food commodity as long as this commodity remained available. Specialised individuals collected more and bigger loads compared to bees that switched regularly between food components. When the preferred commodity was removed, half of the foragers switched to the collection of other commodities, although the number of unsuccessful flights increased significantly after this switch. Few individuals only restarted foraging when their original commodity became available again. Thus, although foragers preferred to specialise, when foraging conditions changed individuals were able to switch to other foraging tasks.

As foraging performance of individuals that specialised seemed greater than that of individuals that switched regularly between commodities, I studied the effect of experience on foraging performance of *P. tobagoensis* in Chapter 4. Flower handling time and time necessary to find the food source decreased significantly with experience. The highest performance level was already reached on the first foraging day, as there was a decrease in performance following a night. This specific performance pattern might make switching to other food sources at the start of a new day less costly.

When combining these studies, individual task specialisation seems rather plastic in the stingless bee *P. tobagoensis*. Although individuals seem to prefer to specialise and do show higher foraging performance when specialising, they readily switch to other foraging tasks. Foraging task specialisation in social insects is generally thought to increase individual performance, but it might hamper colony flexibility. Small colonies might lack the “manpower” to be flexible with specialised individuals, and individual task switching might be an important mechanism to reallocate foraging labour. This hypothesis is supported by the fact that age polyethism and division of labour are better developed in swarm founding social bees (Robinson 1992) with mostly larger colony sizes, compared to independent-founding species (Plowright & Lavery 1984).



## Foraging labour reallocation

To study the importance of individual switching between foraging tasks for flexible colony foraging responses in stingless bees we analysed foraging labour reallocation as a result of changes in colony stores or food availability in the field (Chapters 5, 6 and 7).

The need for labour in a certain task is determined by the difference between supply and demand for this labour. Changing the labour devoted to a task with regard to its urgency enables a colony to respond adaptively to changes in intranidal and environmental conditions. When a new foraging task was presented to *P. tobagoensis* (Chapter 5), most labour allocated to this task resulted from the allocation of new foragers. This seems a low costs solution in this, non-stressful, situation as foraging on the other food sources can continue without interruption and the number of individuals making costly switches between foraging tasks can be minimised.

Changes in foraging labour devoted towards a foraging task can also result from changes in individual foraging effort. This was found in *Melipona beecheii*, where individuals increased the number of flights per hour when confronted with an increase in food availability in the field (Chapter 6). Increase of individual foraging effort has costs attached to it, as high daily foraging activity and carrying heavy loads decrease survival probability in both honeybees (Wolf & Schmid-Hempel 1989) and stingless bees (Biesmeijer & Tóth 1998). However, in situations of high opportunity, increase in individual foraging effort seems to be an important way to increase the influx of food by the colony.

When pollen stores were removed from colonies of *P. tobagoensis* (Chapter 7), allocation of non-foragers played an important role in increasing pollen influx. This coincides with responses to pollen stress (Rotjan 2002) and heat stress (Johnson 2001) in honeybees. Notable is, however, the lack of a significant increase in individual foraging effort in the response of *P. tobagoensis*. In other studies on pollen stress in social bees, increase in individual foraging effort did play an important role in the colony response (honeybees: Rotjan 2002, Fewell & Winston 1992; bumblebees: Landry *et al.* 2000; Plowright *et al.* 1993). The lack of a strong increase in individual foraging effort in stingless bees compared to honeybees might be the result of differences in brood provisioning between stingless bees and honeybees. The mass-provisioning system of stingless bees might make it unnecessary for pollen foragers to run high mortality risks by increasing individual foraging effort during short periods of pollen stress.

The analysis of foraging labour reallocation in a dynamic environment, as described in this thesis, showed that, although individual switching does occur and contributes to foraging labour allocation in stingless bees, this is



not as important as was expected as a result of the plasticity of forager task specialisation. Foragers seem to be only receptive for information on other food sources when their own foraging efficiency declines (Biesmeijer 1997, Cartar 1992). When their own foraging success is still high, individuals are less likely to switch between foraging tasks, even though the demand for another foraging task has increased. Colony foraging adjustments during food stress thus seems to result mainly from the allocation of non-foragers.

Allocation of these non-foragers, if available, seems a low cost solution for changes in foraging labour allocation. By avoiding task switching, the collection of other food sources can continue without interruption and successful individuals do not have to waste time and energy on learning other locations and handling methods. In honey bees large numbers of non-active workers can be found in the hive. These workers serve as back-up forces and allow for high numbers of new foragers in periods of high needs. Bumblebees, however, with much smaller colony sizes (approximately 150 individuals), cannot afford groups of inactive back-up forces. In this case, allocated new foragers originate from the pool of workers active in in-hive tasks (Cartar 1992) and the increase in foraging labour interrupts labour devoted to in-hive tasks. When the urgency for foraging tasks decreases again, these workers switch back to in-hive tasks (Cartar 1992). Switching back and forth between foraging and in-hive tasks has never been observed in honeybees or stingless bees and the stronger worker task specialisation in these social bee groups makes the occurrence of these switches unlikely. Although groups of inactive bees can also be found in stingless bees, the origin of the allocated non-foragers in the present studies remains unclear. It may be possible that the allocated non-foragers originate from the normal turnover of foragers. In that case, the increase in foraging labour towards a foraging task is the result of a change in proportion of new foragers allocated to the occurring tasks. This hypothesis is supported by the results of Chapter 3, where the distribution of novice foragers was strongly influenced by changes in colony needs and information about food availability. The high number of new foragers allocated to a needed task in Chapter 7, however, is not consistent with this hypothesis. The increase in foragers in that case might not have resulted from natural turnover alone. Apparently, colonies of *P. tobagoensis* are large enough to hold some extra back-up forces. The ability to allocate large groups of non-foragers by *P. tobagoensis* colonies allows these colonies to respond rapidly and economically to changes in their environment.



## General conclusions

The results of this thesis show that the adaptive tuning of the colony foraging behaviour of stingless bees can involve changes in the total number of foragers allocated to a foraging task and changes in the individual foraging effort. The importance of each mechanism to adjust colony foraging behaviour seems to depend very much on the circumstances. Increase in individual foraging effort seems to occur mainly in situations when large amounts of food are available. Eventhough increase in foraging effort decreases longevity, in periods of high opportunity, when food is available in large quantities close to the hive, this might be worth the offer. Switching between foraging tasks can be mainly observed when foraging success declines. Succesfully employed bees probably do not switch easily to other foraging tasks. As switching is costly, switches between tasks can be economically made when the succes of the original task declined. Allocation of new foragers occurs mainly in situations of food stress or when new foraging tasks appear. By allocating non-foragers, foraging on other tasks can continue without interruption, avoiding consequent decrease in storage levels of the other commodities.

The present study contributes to the identification of the mechanisms used by stingless bee colonies to adjust colony foraging activity under different conditions and makes clear the complexity of the organisation of foraging in stingless bees. A number of questions remain unanswered, however. Comparisons between and within different groups of social bees could elucidate the influence of specific characteristics, such as brood provisioning system or colony size, on specific mechanisms used for the allocation of foraging labour. Although many studies have been performed on the occurrence of one of the mechanisms of foraging labour reallocation in honeybees, only one study has shown explicitly how all three processes can function together (Rotjan *et al.* 2002). In addition, all studies on foraging labour reallocation in social bees have been performed in the field, where many other factors, apart from the one studied, can influence colony foraging behaviour. This makes comparisons between groups, on the basis of these studies, difficult.

The group of stingless bees itself is comprised of about 400 different species. These species all live in complex colonies with elaborate social behaviour. They differ, however, in colony sizes, foraging strategies (Slaa 2003), reproductive characteristics (Chinh 2004), communication and recruitment mechanisms (Aguilar 2004) and many other features. It would be interesting to see if and how these species differ in mechanisms used for foraging labour reallocation and if these differences correspond with other interspecific differences.





## Samenvatting

### Algemene inleiding

Angelloze bijen zijn, net als honingbijen, hoogsociale bijen. Dit houdt onder andere in dat zij in kolonieverband leven met een duidelijke verdeling van taken. Er is bijvoorbeeld een verdeling in de reproductieve taken, waarbij één individu, de koningin, de meeste nakomelingen produceert en de andere individuen in de kolonie, de werksters, deze nakomelingen verzorgen en onderhoudstaken aan het nest uitvoeren.

Werksters specialiseren zich allemaal tijdelijk op deze verschillende werkstertaken en verrichten zo dus een reeks van taken in het nest. De laatste taak die een werkster van een bijenkolonie vervult is het verzamelen van voedsel buiten het nest (foerageren).

Angelloze bijen verzamelen allerlei soorten materialen als voedsel en als bouwstoffen voor het nest. De belangrijkste voedselmaterialen zijn nectar en stuifmeel. Nectar dient als energiebron voor de volwassen bijen en stuifmeel wordt vooral gebruikt om de larven te voeren. Angelloze bijen verzamelen ook water, fruitsap, wax, modder en hars. Ondanks het feit dat foerageersters zich vaak voor langere tijd richten op het verzamelen van een bepaald materiaal (en dus op één foerageertaak), zijn zij niet lichamelijk (zoals bij de reproductieve



taakverdeling) of door leeftijd (zoals bij de werkstertaakverdeling) gespecialiseerd in een bepaalde taak. Dit maakt de verdeling over foerageertaken erg flexibel.

De verdeling van foerageersters over de verschillende foerageertaken is niet centraal georganiseerd en elk individu moet dus voor zichzelf beslissen welk materiaal ze gaat verzamelen. Deze beslissing maakt zij aan de hand van interne en externe factoren. Externe factoren zijn invloeden van buitenaf, zoals bijvoorbeeld informatie van ervaren bijen, de hoeveelheid voorraden in de kolonie, de temperatuur of de aanwezigheid van andere bijen op een voedselbron. De interne factoren bepalen de gevoeligheid voor de externe factoren en betreffen bijvoorbeeld de ervaringen uit het verleden van de bij of de genetische opmaak van een individu.

Een juiste verdeling van de werksters over de verschillende foerageertaken is van groot belang voor het voortbestaan van de kolonie, aangezien deze afhankelijk is van het voedsel dat binnenkomt voor reproductie en voor de overleving van de individuen. Het is dan ook bekend dat kolonies hun algemene foerageeractiviteit, en daarmee de verdeling van werkkrachten over de verschillende foerageertaken, kunnen aanpassen aan omstandigheden in en buiten het nest. De foerageeractiviteit van een kolonie, en daarmee dus de arbeid gericht op een bepaalde foerageertaak, kan op twee manieren aangepast worden:

- 1 door verandering in het aantal individuen in een bepaalde foerageertaak
- 2 door verandering in foerageerprestatie van de individuele bijen in een bepaalde foerageertaak.

Verandering in het aantal individuen in een bepaalde foerageertaak kan ontstaan doordat individuen van foerageertaak wisselen of doordat nieuwe foerageersters ingezet worden.

Ondanks het feit dat over het algemeen wordt gedacht dat het specialiseren op de verzameling van een bepaald materiaal de individuele prestatie verhoogt, kan het de flexibiliteit van de kolonie tegenwerken.

## Doelstelling van dit proefschrift

De belangrijkste doelstelling van dit proefschrift is het systematisch bestuderen van het voorkomen van taakspecialisatie, de flexibiliteit daarvan en de dynamiek in de verdeling van foerageerarbeid over de verschillende foerageertaken bij angelloze bijen. Met de data die voor dit proefschrift verkregen zijn, wordt gestreefd naar een bijdrage aan het beantwoorden van de vraag hoe sociale insectenkolonies adaptief kunnen reageren op een steeds veranderende omgeving. Als model voor dit onderzoek is vooral gebruik gemaakt van de angelloze bij *Plebeia tobagoensis* Melo.



## Dit proefschrift

### Individuele foerageercarrières

Het eerste gedeelte van dit proefschrift richt zich op factoren die van invloed zijn op foerageerkeuzes en prestaties van individuen. Omdat succesvolle foerageersters de neiging hebben om een eenmaal bezochte voedselbron te blijven bezoeken, wordt over het algemeen gedacht dat de eerste keus van een individuele foerageerster van groot belang is voor haar verdere carrière. Daarom kijken we in hoofdstuk 2 naar de factoren die van invloed kunnen zijn op de eerste materiaalkeus van een nieuwe foerageerster.

De eerste materiaalkeus van een nieuwe foerageerster bleek enorm beïnvloed te worden door de voedselvoorraad in het nest en door de informatie die ervaren foerageersters meebrachten uit het veld. De invloed van deze factoren op de eerste keus van nieuwe foerageersters lijkt voordelig voor de kolonie, aangezien de kolonie zo extra werkkraft krijgt voor taken die het meeste nodig zijn of waarmee het meeste te halen valt. Ook bleek in deze studie dat de eerste keus van een foerageerster van groot belang is voor haar verder foerageercarrière, aangezien de meeste specialisten ditzelfde materiaal bleven verzamelen gedurende het experiment.

Om meer te leren over de latere keuzes in een foerageercarrière hebben we het voorkomen en de flexibiliteit van individuele foerageertaakspecialisatie bij de angellose bij *P. tobagoensis* beschreven in hoofdstuk 3. Door zich te specialiseren kunnen individuen hun foerageersnelheid verbeteren door te zoeken naar materialen waarvan het individu weet hoe en waar het verzameld moet worden. Wij vonden inderdaad dat de meeste individuen zich specialiseerden op één foerageertaak, zolang dit materiaal verkrijgbaar was. Gespecialiseerde individuen verzamelden meer en grotere ladingen dan bijen die regelmatig wisselden van foerageertaak. Wanneer we het voedselmateriaal verwijderden waarop de individuen waren gespecialiseerd, dan wisselde de helft van de specialisten van foerageertaak, ondanks de toename van het aantal onsuccesvolle vluchten na de wissel. Er waren maar enkele individuen die pas weer begonnen te verzamelen wanneer hun oorspronkelijke materiaalvoorkeur weer beschikbaar was. Dus ondanks het feit dat de meeste individuen zich specialiseerden, konden deze bijen van foerageertaak wisselen wanneer hun oorspronkelijk keus niet meer beschikbaar was.

Omdat de foerageerprestaties van gespecialiseerde bijen hoger bleken te zijn dan die van bijen die regelmatig wisselden tussen foerageertaken hebben we in hoofdstuk 4 gekeken naar de invloed van ervaring op foerageerprestatie bij *P. tobagoensis*. De duur van het manipuleren van de bron en de tijd die nodig was om de voedselbron te vinden nam significant af met de ervaring. Het hoogste prestatieniveau werd al bereikt op de eerste foerageerdag, aangezien



dit prestatieniveau weer afnam na een nacht niet foerageren. Dit specifieke prestatiepatroon maakt het wellicht eenvoudiger om van foerageertaak te wisselen op een nieuwe foerageerdag.

Wanneer we deze drie studies combineren, zien we dat de foerageertaak-specialisatie bij *P. tobagoensis* behoorlijk flexibel is. Ondanks dat individuen zich meestal specialiseren op een bepaalde foerageertaak, wisselen ze makkelijk tussen verschillende foerageertaken. Foerageertaakspecialisatie zorgt voor efficiëntere individuen, maar het kan de kolonieflexibiliteit dwarsbomen. Kleinere kolonies hebben simpelweg de mankracht niet om flexibel te zijn met gespecialiseerde individuen en het wisselen van taak kan een belangrijk mechanisme zijn om flexibiliteit op kolonieniveau te bewerkstelligen. Deze hypothese lijkt te worden onderbouwd door het feit dat werkstertaakspecialisatie beter ontwikkeld is bij soorten die zich reproduceren door zwermen en dus grote kolonies hebben dan soorten die zich reproduceren door middel van individuen die opnieuw een kolonie starten.

### **Foerageerarbeidsverdeling**

Om de betekenis van het wisselen tussen foerageertaken voor de flexibiliteit van het koloniefouerageren te onderzoeken hebben we de herverdeling van foerageerarbeid, als gevolg van veranderingen in kolonievoorraden of voedselaanwezigheid in het veld, bestudeerd (hoofdstuk 5, 6 en 7). De noodzaak van foerageerarbeid voor een bepaalde taak wordt bepaald door het verschil in vraag en aanbod voor deze arbeid. Door de arbeid voor een bepaalde taak aan te passen aan de noodzaak kan een kolonie reageren op de steeds veranderende omgeving. Wanneer we in onze experimenten een nieuwe foerageertaak introduceerden voor *P. tobagoensis* kolonies vonden we dat de meeste arbeidskracht toebedeeld aan deze nieuwe taak, voortkwam uit de inzet van nieuwe foerageersters (hoofdstuk 5). Dit lijkt een economische oplossing voor deze niet stressvolle situatie, aangezien het verzamelen van andere voedselbronnen gewoon door kan gaan en het aantal van taak wisselende individuen wordt geminimaliseerd.

Veranderingen in arbeidskracht gericht op een bepaalde foerageertaak kunnen ook veroorzaakt worden door veranderingen in individuele foerageerprestaties. Dit vonden we bij de angelloze bij *M. beecheii*, waar individuen het aantal vluchten per uur opschroefden wanneer ze geconfronteerd werden met een toename in voedselaanwezigheid in het veld (Hoofdstuk 6). Een toename in individuele prestaties heeft zijn prijs, aangezien hoge activiteit en het vervoeren van zware lasten de overlevingskansen verlagen. Ondanks deze kosten is het aanpassen van individuele prestaties een belangrijk mechanisme om kolonieactiviteit aan te passen aan de hoge voedselaanwezigheid in het veld.



Wanneer we stuifmeelvoorraden weghaalden uit *P. tobagoensis* kolonies, bleek de inzet van nieuwe foerageersters een belangrijke rol te spelen in het herverdelen van foerageerarbeid naar het verzamelen van stuifmeel. Dit komt overeen met reacties van honingbijen op stressvolle situaties als het verwijderen van stuifmeelvoorraden of het verhitten van het nest. Het is wel opvallend dat in deze studie geen duidelijke aanwijzingen zijn gevonden voor een toename in individuele foerageerprestatie aangezien dit mechanisme wel een belangrijke rol speelde in aanpassingen aan stuifmeelstress bij andere sociale bijen, zoals honingbijen en hommels. Dit verschil zou veroorzaakt kunnen worden door de manier waarop angelloze bijen hun broedcellen bevoorraden vergeleken met de manier waarop honingbijen en hommels dit doen.

De experimenten die beschreven worden in dit proefschrift, over de herverdeling van foerageerarbeid in een steeds veranderende omgeving, geven aan dat foerageertaakwisselingen voorkomen en ook bijdragen aan arbeidherverdeling in *P. tobagoensis*. Dit mechanisme is echter niet zo belangrijk als werd verwacht aan de hand van de resultaten van hoofdstuk 3. Foerageersters lijken alleen ontvankelijk voor informatie over andere foerageertaken als hun eigen efficiency afneemt. Wanneer foerageersucces nog hoog is, zijn bijen minder geneigd om te wisselen van taak, ondanks de toenemende vraag voor een andere foerageertaak. Foerageerkrachtverdeling tijdens stresssituaties en bij het ontstaan van nieuwe taken lijkt dus vooral het resultaat van het inzetten van nieuwe foerageersters.

Het inzetten van nieuwe foerageersters is een economische oplossing voor veranderingen in foerageerarbeid gericht op een bepaalde taak. Door taakwisselingen te voorkomen kan de verzameling van de andere voedselbronnen gewoon doorgaan en hoeven succesvolle individuen geen tijd en energie te spenderen aan het leren van andere locaties en verzamelmethoden. In honingbijen kolonies kunnen inderdaad grote hoeveelheden niet-actieve individuen gevonden worden die ingezet kunnen worden in periodes van hoge nood. Hommels, daarentegen, met kolonies die uit veel minder individuen bestaan (ongeveer 150 individuen), kunnen zich geen inactieve groepen veroorloven. Wanneer er grote vraag is naar extra foerageerarbeid, komen de ingezette nieuwe foerageersters bij hommels uit de groep van actieve werksters in het nest. De toename in foerageerarbeid gaat in dat geval ten kosten van arbeid bedoeld voor werk in de kolonie. Wanneer de vraag naar extra foerageerarbeid weer afneemt, nemen deze individuen weer taken in het nest op zich. Het heen en weer wisselen tussen foerageertaken en taken in het nest is bij honingbijen en angelloze bijen nooit waargenomen, en de veel striktere werkstertaakverdeling bij deze hoogsociale bijengroepen maakt dit ook onwaarschijnlijk. Ondanks het feit dat groepen inactieve bijen ook gevonden kunnen worden in angelloze



bijen kolonies, kan de oorsprong van de nieuw ingezette foerageersters niet achterhaald worden uit de gegevens van onze studie. Het kan zelfs mogelijk zijn dat de extra arbeidskrachten voor een bepaalde foerageertaak afkomstig zijn van het natuurlijk verloop van werkster naar foerageerster. De toename in arbeidskracht voor een bepaalde foerageertaak ontstaat in dat geval doordat de verdeling van deze nieuwe foerageersters over de verschillende taken verandert. Deze hypothese lijkt te worden onderbouwd door de resultaten van hoofdstuk 3, waar de verdeling van nieuwe bijen over de foerageertaken sterk wordt beïnvloed door veranderingen in voedselvoorraden en informatie van ervaren bijen. Maar het extreem hoge aantal nieuwe foerageersters dat gevonden werd in hoofdstuk 7 lijkt deze hypothese juist weer tegen te spreken. Hier kunnen de nieuwe foerageersters haast niet alleen afkomstig zijn van het natuurlijk verloop van werkster naar foerageerster. Dit lijkt er op te wijzen dat kolonies groot genoeg zijn om reservetroepen te kunnen hebben. Het vermogen van *P. tobagoensis* kolonies om grote groepen nieuwe bijen in te kunnen zetten, maakt het voor deze kolonies mogelijk om snel en economisch te kunnen reageren op veranderingen in hun omgeving.

## Conclusie

De resultaten uit dit proefschrift laten zien dat het aanpassen van het foerageergedrag van angelloze bijen kolonies zowel het aanpassen van het totaal aantal foerageersters in een taak, als het aanpassen van individuele foerageerprestaties kan behelzen. Het belang van elk van de mechanismen om foerageeractiviteit aan te passen lijkt sterk af te hangen van de situatie waarin de kolonie zich bevindt. Toename in individuele foerageerprestatie lijkt vooral voor te komen in situaties waarin veel voedsel aanwezig is in het veld. Een toename in foerageerprestatie verlaagt de levensduur, maar wanneer er extra veel voedsel te vinden is dicht bij het nest, kan de toename in influx de extra kosten waard zijn. Wisselen tussen foerageertaken wordt vooral gezien wanneer het individuele foerageersucces afneemt. De kosten van het wisselen van taak zijn lager wanneer het succes in de originele taak laag is. Het inzetten van nieuwe werkkrachten komt vooral voor in gevallen van stress of wanneer nieuwe foerageertaken ontstaan. Door nieuwe bijen in te zetten, kan het verzamelen van de andere materialen gewoon doorgaan. Dit voorkomt afname van de voorraden van deze materialen, wat weer een aanpassing in foerageerkrachtverdeling zou vereisen.

Deze studie draagt bij aan de identificatie van mechanismen die bij angelloze bijen voorkomen om de foerageeractiviteit van de kolonie aan te passen aan verschillende omstandigheden en maakt de complexiteit van de



organisatie van foerageeractiviteiten duidelijk. Er blijven echter nog vragen onbeantwoord.

Vergelijking tussen en binnen de verschillende sociale bijengroepen zouden bij kunnen dragen aan onze kennis over de invloed van specifieke karakteristieken, zoals broedbevoorradingssystemen en koloniegrootte, op de mechanismen die gebruikt worden om foerageerarbeidsverdeling aan te passen. Ondanks het feit dat er vele studies zijn gedaan naar het voorkomen van deze mechanismen bij honingbijen, is er maar één die expliciet kijkt naar hoe deze mechanismen naast elkaar voorkomen. Ook zijn alle studies die tot nu toe gedaan zijn aan foerageerarbeidsverdeling bij sociale bijen gedaan in het veld, waar vele andere factoren, buiten diegene die onderzocht werden, van invloed kunnen zijn. Dit maakt vergelijkingen tussen de verschillende sociale bijengroepen, op grond van deze publicaties, erg moeilijk.

De groep van angelloze bijen zelf bestaat uit meer dan 400 soorten. Deze soorten leven allen in complexe kolonies met ingewikkeld sociaal gedrag. De verschillende soorten kunnen echter behoorlijk verschillen in koloniegrootte, foerageerstrategieën, koloniekarakteristieken en communicatiemechanismen. Het zou interessant zijn om te kijken of en hoe deze soorten verschillen in foerageerarbeidsverdeling en of deze verschillen verband houden met andere interspecifieke verschillen.





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## Curriculum vitae

De auteur van dit proefschrift werd op 14 maart 1975 geboren in Vlaardingen. Op 2 -jarige leeftijd verhuisde zij naar Werkendam vanwaar zij haar VWO-diploma haalde op CSG Oude Hoven te Gorinchem in 1994. Zij vervolgde haar opleiding aan de Faculteit Biologie van de Universiteit Utrecht. In de specialisatiefase van deze studie werkte ze aan een onderzoek aan egelverkeersslachtoffers in samenwerking met de Vereniging voor Zoogdierkunde en Zoogdierbescherming en Britain's University of Surrey, Roehampton. Voor haar tweede stage, dit keer bij de afdeling Gedragsbiologie, vertrok zij, voor een onderzoek aan het sympatrisch voorkomen van verschillende hommelse soorten in tropische gebieden, naar Costa Rica.

Na het afstuderen in 1999 werd zij in 2001 aangesteld als Junior Docent bij de afdeling Gedragsbiologie. Hier hield zij zich vooral bezig met het coördineren van de internationale MSc cursus "Tropical Bees and Beekeeping in Tropical Climates" en het begeleiden van studenten uit de specialisatiefase van de Faculteit Biologie. Ook gaf zij college en organiseerde zij practica voor de cursus "Ethologie" van de Faculteit Biologie. In deze periode werd het onderzoek voor dit proefschrift verricht. Nadat haar aanstelling als Junior Docent in maart 2005 afliep, kreeg zij een beurs van de Universiteit Utrecht om het gedane onderzoek te beschrijven in dit proefschrift.

In oktober 2005 kreeg zij een aanstelling als onderzoeker bij Alterra, Centrum Landschap, Wad en Zee van de Universiteit Wageningen op Texel.





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