Effect of food availability on individual foraging specialisation in the stingless bee *Plebeia tobagoensis* (Hymenoptera, Meliponini)[1]

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Abstract – This study reports on the occurrence and dynamics of foraging task specialisation in the stingless bee *Plebeia tobagoensis*. We test the hypothesis that in a stable environment foraging task specialisation is preferred, but that individuals readily switch to other foraging tasks when changes in food availability occur. The study was performed in a greenhouse, where food availability could be controlled. When all food sources were available, most individuals (71%) specialised on the collection of one food commodity. When this commodity was removed 50% of the specialists switched foraging tasks. When comparing foraging performance of flexible and specialised foragers we found that specialised bees performed better. However, most specialised foragers do make a costly switch to other foraging tasks when a change in food availability occurs. It seems likely that this high individual flexibility is adaptive for relatively small social bee colonies, living in a dynamic environment.

task specialisation / foraging performance / food availability / stingless bees / *Plebeia*

1. 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 and 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 reacting to these changes by flexibly recruiting new foragers, changes in colony foraging behaviour can also result from changes in individual foraging behaviour (Fewell and 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 bumble bees 30–40% of the foragers are 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 and 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 and Tóth, 1998; O'Donnell, 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 and 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 influences foraging performance of individuals.

2. MATERIALS AND METHODS

2.1. Bee colonies and experimental conditions

The stingless bee *Plebeia tobagoensis* is common on Tobago, West Indies. Melo and 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 ºC (natural temperature range: 23–31 ºC).

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.

2.2. 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).

2.3. 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).

2.4. Behavioural observations

2.4.1. Observations on foraging behaviour

Incoming individuals and the materials collected were identified by the use of a video camera (Sony CCD-TVR228) 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 and 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.

2.4.2. 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 forced 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 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.

3. RESULTS

3.1. 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 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 eighteen 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
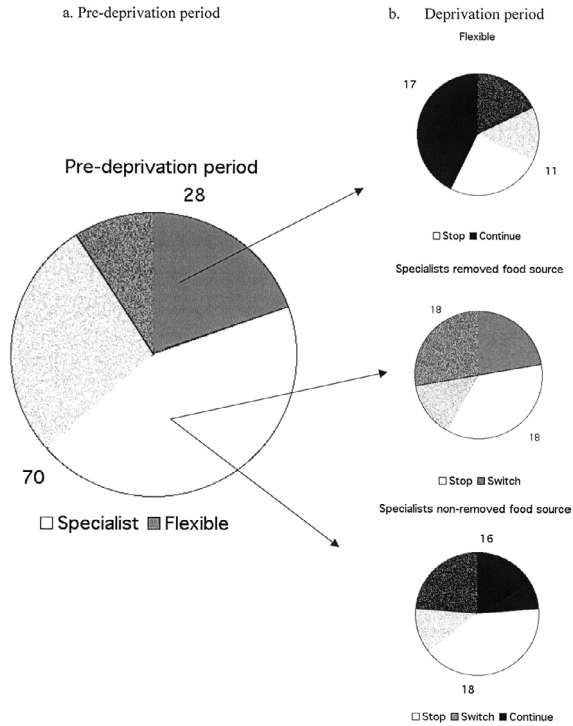
Figure 1. (a) Proportion of specialised compared to flexible foragers when all food sources were available in the greenhouse compartment (pre-deprivation period). Specialised bees collected the same material on more than 80% of their flights. Sample size numbers are indicated in the graph. (b) Proportion 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 pattern in the figures.

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

3.2. Individual foraging performance of specialised and flexible foragers
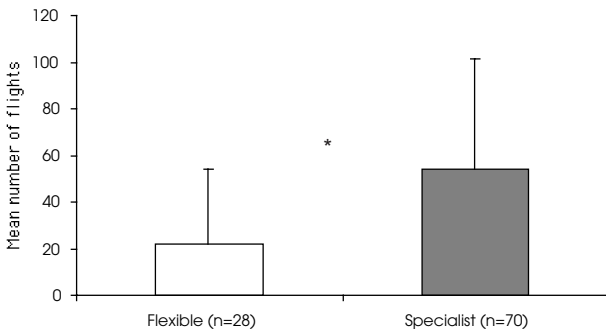
3.2.1. Pre-deprivation period

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.
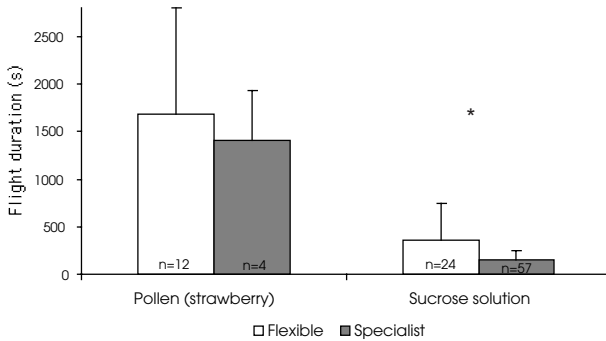
Figure 2. Mean duration of foraging flights in seconds on artificial flowers for sugar solution collection and on strawberry for pollen collection of specialised and flexible forager in the pre-deprivation period. The mean duration + SE and sample sizes are given in each bar. Results were tested using the Mann-Whitney-U test. Asterisk indicates significant difference ($P < 0.05$).
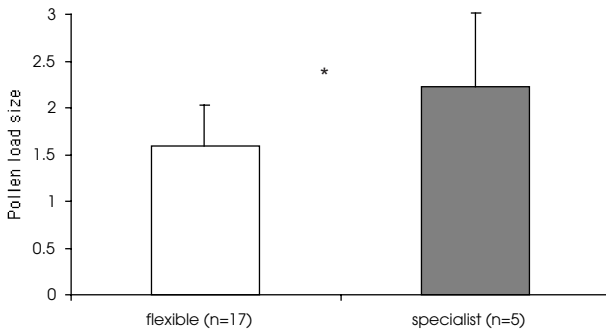
Figure 3. Mean pollen load size of specialised and flexible foragers in the pre-deprivation period. Load size categories were estimated from video recordings. The mean pollen load sizes + SE are given in each bar; sample sizes are indicated on the x-axis. Results were tested using the Mann-Whitney-U test. Asterisk indicates significant difference ($P < 0.05$).

Figure 4. Mean number of flights of specialised and flexible foragers in the pre-deprivation period. The mean number of flights + SE is 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 ($P < 0.05$).

There was no significant difference 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).

The total number of flights during the pre-deprivation period was greater in specialists than in flexible foragers (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).

3.2.2. Deprivation period

Specialists that switched foraging task because of the removal of their preferred food commodity in the deprivation period performed
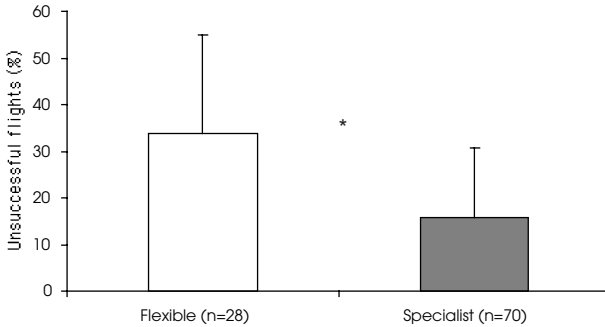
Figure 5. Mean percentage of unsuccessful flights for specialised and flexible foragers in the pre-deprivation period. Flights were indicated as unsuccessful when no visible load was present when entering the hive. The mean number of flights + SE are given in each bar; sample sizes are indicated on the x-axis. Results were tested using the Mann-Whitney-U test. Asterisk indicates significant difference ($P < 0.05$).
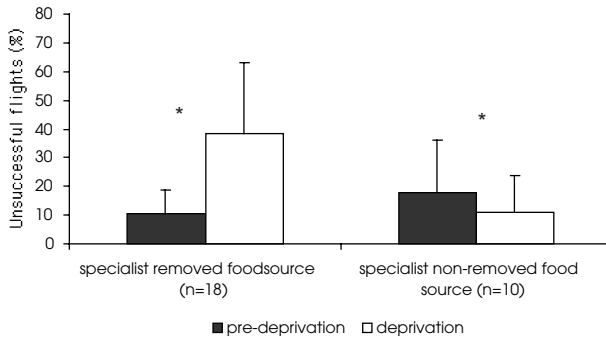
Figure 6. Mean percentage of unsuccessful flights in the pre-deprivation and deprivation period, both for specialised sucrose solution foragers that could continue foraging on sucrose solution in the deprivation period and for specialised individuals that switched to another food source in the deprivation 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 ($P < 0.05$).

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 less 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).

4. DISCUSSION

4.1. 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 and Wilson,

1978). 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 and 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, like 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 and 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* (+/– 1200 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 +/– 250 individuals, pers. comm. 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)).

4.2. 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 and Weidenmuller, 2002; Thomson and Chittka, 2001; Robinson and Page, 1989; Fewell and Page, 1993; Fewell and Bertram, 2002; Ranger and 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 and Bertram, 2002) and in the polygynous or polyandrous stingless bee *Partamona bilineata* (Ranger and 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 and 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 and 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.

4.3. Foraging performance of specialised and flexible foragers

Our results support the hypothesis that task specialisation increases individual foraging performance (Oster and 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 forced 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 and 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 and 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 and 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 commodities of the first learned motor pattern for the second learned task, where it is interfering with foraging performance (Chittka and 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.

5. 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.

Résumé – Action de la disponibilité en nourriture sur la spécialisation individuelle lors du butinage chez l'abeille sans aiguillon *Plebeia tobagoensis* (Hymenoptera, Meliponini). La spécialisation individuelle du comportement de butinage chez les abeilles sociales est censée augmenter la performance du butinage, augmentant ainsi la valeur adaptative (« fitness ») de la colonie. Mais dans un environnement dynamique les colonies doivent être capables de répondre à des changements à court terme de la disponibilité en nourriture. Il en résulte que des changements coûteux dans le comportement individuel de butinage peuvent être nécessaires à la flexibilité de la colonie. Nous avons testé l'hypo- thèse selon laquelle la spécialisation lors du butinage est préférée dans un environnement stable mais avec des changements individuels vers d'autres tâches de butinage lorsque surviennent des changements dans la disponibilité en nourriture. Cette étude, qui porte sur l'abeille sans aiguillon *Plebeia tobagoensis*, a été réalisée dans un compartiment de serre, dans lequel la disponibilité en nourriture était contrôlée. Quand toutes les matières premières (nectar, pollen, résine, eau) étaient présentes dans le compartiment, la plu- part des individus (71 %) n'en récoltaient qu'une seule (Fig. 1a). Quand on retirait cette matière pre- mière au cours de la période de privation, 50 % des anciennes butineuses spécialisées passaient à un autre type de nourriture (Fig. 1b). En comparant les performances de butinage des individus flexibles et des spécialisés, nous avons trouvé que les abeilles spécialisées effectuaient des vols plus nombreux (Fig. 4) et plus courts (Fig. 2) et récoltaient des pelo- tes de pollen plus lourdes (Fig. 3) par rapport aux butineuses flexibles. Après un changement imposé de tâche de butinage le nombre de vols sans succès des anciennes spécialistes a augmenté considérable- ment (Fig. 6). Pourtant la plupart des butineuses spécialisées font bien le choix coûteux de changer de type de nourriture lorsque survient une modification dans la disponibilité en nourriture. Cette flexibilité élevée est vraisemblablement une faculté adaptative pour des colonies d'abeilles sociales de taille relati- vement petite vivant des conditions de butinage variables.

Plebeia / abeille sans aiguillon / spécialisation du travail / performance de butinage / disponibilité en nourriture

Zusammenfassung – Rolle der Verfügbarkeit von Nahrungsquellen in der individuellen Spe- zialisierung von Sammlerinnen der stachellosen Biene *Plebeia tobagoensis* (Hymenoptera, Meli- ponini). Die individuelle Spezialisierung im Sammelverhalten wird als Grund für die hohe Effi- zienz im Nahrungssuchverhalten sozialer Bienen angeführt und sollte eine gesteigerte Koloniefitness mit sich bringen. In einer dynamisch sich verändern- den Umwelt müssen Kolonien jedoch in der Lage sein, rasch auf kurzfristige Wechsel in der Verfüg- barkeit des Nahrungsangebots zu reagieren. Für die notwendige Flexibilität auf Kolonieebene könnte damit ein kostenungünstiger Wechsel im individuell spezialisierten Sammelverhalten verbunden sein. In dieser Studie testen wir die Hypothese, dass in einer stabilen Umweltsituation eine Spezialisierung im Sammelverhalten bevorzugt sein sollte, dass Arbeiterinnen aber ihr Suchverhalten wechseln soll- ten, wenn Veränderungen im Nahrungsangebot eintreten. Wir führten die Untersuchungen an der stachellosen Biene *Plebeia tobagoensis* durch. Kolonien wurden im Gewächshaus unter kontrol- liertem Futterangebot gehalten. Wenn mehrere Nahrungstypen angeboten wurden, sammelten die

meisten Bienen (71 %) einen jeweils einzigen Nahrungstyp (Abb. 1a). Nach Entfernung dieses Nahrungstyps wechselten in der anschliessenden Entzugsperiode 50 % der spezialisierten Sammlerinnen auf eine andere Nahrungsquelle (Abb. 1b). Im Vergleich der Sammelleistungen zwischen spezialisierten und flexiblen Sammlerinnen zeigten die spezialisierten Bienen eine höhere Anzahl an Sammelflügen (Abb. 4), sowie eine kürzere Flugdauer (Abb. 2) und höhere Pollenladungen (Abb. 3). Nach einem erzwungenen Wechsel im Sammelverhalten erwies sich die Zahl an erfolglosen Sammelflügen bei zuvor spezialisierten Sammlerinnen als stark erhöht (Abb. 6). Die meisten der spezialisierten Sammlerinnen wechselten jedoch die Futterquelle, nachdem sich die Nahrungsverfügbarkeit geändert hatte. Diese hohe Flexibilität scheint damit adaptativ zu sein für relativ kleine Kolonien sozialer Bienen, die mit einem sich stetig ändernden Nahrungsangebot konfrontiert sind.

Verhaltensspezialisierung / Sammelleistung / Nahrungsangebot / stachellose Bienen / *Plebeia*

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