THE CONTROL OF NECTAR AND POLLEN FORAGING IN *BOMBUS TERRESTRIS* (L.)

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SUMMARY

The authors present their first results about strategy and foraging control in *Bombus terrestris* (L.).

Observations of the behavioural sequences of the foragers allowed to understand the rules of nectar and pollen collection. When a forager returns to the nest with a nectar load, the decision to continue to collect nectar is dependant of the success of previous nectar's foraging trips, suggesting the existence of a learning process. Surprisingly, concerning the pollen, the decision to continue or not to collect it appears to be a stochastic process. This asymmetry between nectar and pollen collection strategy can be related to ecological constraints.

The authors propose the hypothesis that honey pots play a role in foraging activity control. The experimental filling of the honey pots reduces the level of foraging activity for both nectar and pollen. On the contrary, to empty the pots has no influence on the foragers. It could indicate that the two kinds of foraging are both regulated by the sole honey pot level.

INTRODUCTION

The majority of the studies about bumblebees foraging are focused on individual behavior (Shelly *et al.*, 1991). The few works dedicated to the social aspect of foraging concern the rhythm of activity (Free, 1955; Shelly *et al.*, 1991; Baal & Surholt, 1993). However, all the individual behaviors must cooperate to be adapted to the needs of the colony and to the resources availability. The foraging activity must be coordinated.

The importance of integration mechanisms is increased by the existence of two behavioral types of workers: foragers and nest-workers (Brian, 1952; Free, 1955; Pouvreau, 1989). This specialization imposes that foragers receive information about the needs of the colony. This can only occur during the short time they spend in the nest to unload the nectar and the pollen.

For bumblebees, two kinds of resources are collected: the nectar as source of sugar and water, and the pollen as source of amino-acids and lipids. In *Bombus terrestris* (L.), both are stored in pots inside the nests. Usually, the authors state that the foragers are more or less specialized on one kind of collect, according to their size. However, the same authors recognize that this distinction is more a trend than a real polymorphism (Brian, 1952; Free, 1955; Pouvreau, 1989).

The aims of this work were on one hand to study how pollen and nectar were collected by foragers, and on the other hand to explore the informational process which controls the foraging. We hypothesize that the amount of nectar inside the honey pots could play a role in the process.

MATERIAL AND METHODS

The nests studied were kept in our laboratory in semi-natural conditions. The colony was nested into a glass hive in a rearing room. The foragers could leave freely the nest by a tube connected to the outside and collect on the flowers in the gardens around the university campus.
Each day, the new emerged workers were labeled with a number to be identified.

A first batch of observations was obtained in April 1997. The foraging activity was recorded from 7 to 21h (GMT+2). The behavioral sequences (leaving the nest and coming back with pollen or nectar load) of foragers were recorded. For more detailed about those observations, see Verhaeghe *et al.* (1999).

A second batch of observations was performed from May to July 1999. During this period, experiments where honey pots were filled with syrup or emptied were done. The foraging activity before and after manipulation was recorded by the count of nectar and pollen loads brought back by the foragers. In this way, the role of honey pots as regulator of foraging was checked.

RESULTS

a. Pollen and nectar collection

The foragers could not be divided into pollen-gatherer or nectar-gatherer. All of them collect nectar and pollen regardless of their size or activity. Moreover all pollen foragers were also loaded with nectar. In the following text, "nectar foraging" means foraging for nectar alone, and "pollen foraging" means foraging for nectar and pollen.
The Fig. 1a shows how the probability to switch from pollen to nectar foraging evolves for a forager when it begins to collect pollen. The curve appears to be a negative exponential. That means that the switching probability is constant, trip after trip. However, the probability to change from nectar to pollen foraging (Fig. 1b.) is constant only for the first 6 trips. Then, the probability to continue nectar foraging increases and the curve differs significantly from the negative exponential (Kolmogorov-Smirnov, $P<0,01$).

Foraging for nectar or for pollen are two different strategies. When the pollen foraging appears to be stochastic, the nectar foraging shows an amplification process.

b. Role of honey pots in foraging activity control

Three manipulations of the honey pots were realized: filling all the pots with a sugar syrup, filling half of the pots and removing all the honey from all the pots. The results are presented in Fig. 2.

When the honey pots are full of syrup, the foraging activity decreases greatly (66% less than the control days). The difference is significant (χ^2; $P<0,001$). This is also true when only half of the honey pots are filled (χ^2; $P<0,001$), but the drop is less important (44% less). Surprisingly, when the honey pots are emptied, no increase of the foraging activity was observed (χ^2; $P>0,05$).

In any cases, there was never any significant difference in the ratio of nectar loads to pollen loads (χ^2; $P>0,05$).

It exists a negative feedback linked to the status of the honey pots. A pot full of nectar is a signal "STOP" for the foragers. The same signal regulates both the nectar- and pollen foraging for nectar and pollen.

DISCUSSION

Our results confirms that there is no division of labor between the "nectar foragers" and the "pollen foragers". All the foragers collect both resources. However, the rules for the collection of pollen and nectar are different. When a forager collect pollen, it can continue or switch to nectar collecting each time it leaves the nest. This choice is made under a constant probability. For the nectar collection, the choice (to switch or not) is influenced by the previous foraging trips and this is probably due to some learning process.

This behavioral asymmetry may reflect differences in the resources availability. Both pollen and nectar are necessary for the colony, but pollen is more spread and renewable than nectar in the field (Zimmerman, 1982). A stochastic strategy is then the better way to collect it.

Inversely, the nectar presents an aggregative distribution and is rare (Zimmerman, 1981). The best strategy is then to exploit a patch of flowers producing nectar till exhaustion.

The control of the foraging activity is probably complex, but a first feedback is identified: a filled honey pot acts as a "STOP" signal for foragers.

This signal is common for nectar and pollen collection. This is logical. If the pollen is stochastically collected, a foraging control based on it would not be efficient. However, our results differ from those of Free (1955). But he was working on other species and this can explain the difference. Also, some environmental factors as the richness of the meadow and the resources availability can influence the results. This must be studied in future.

There is still a lot of work to do in order to understand how the foraging is controlled in bumblebees. The feedback discovered here is probably a signal among others. For example, we still don't know what are the signals stimulating the foragers and how they are perceived.

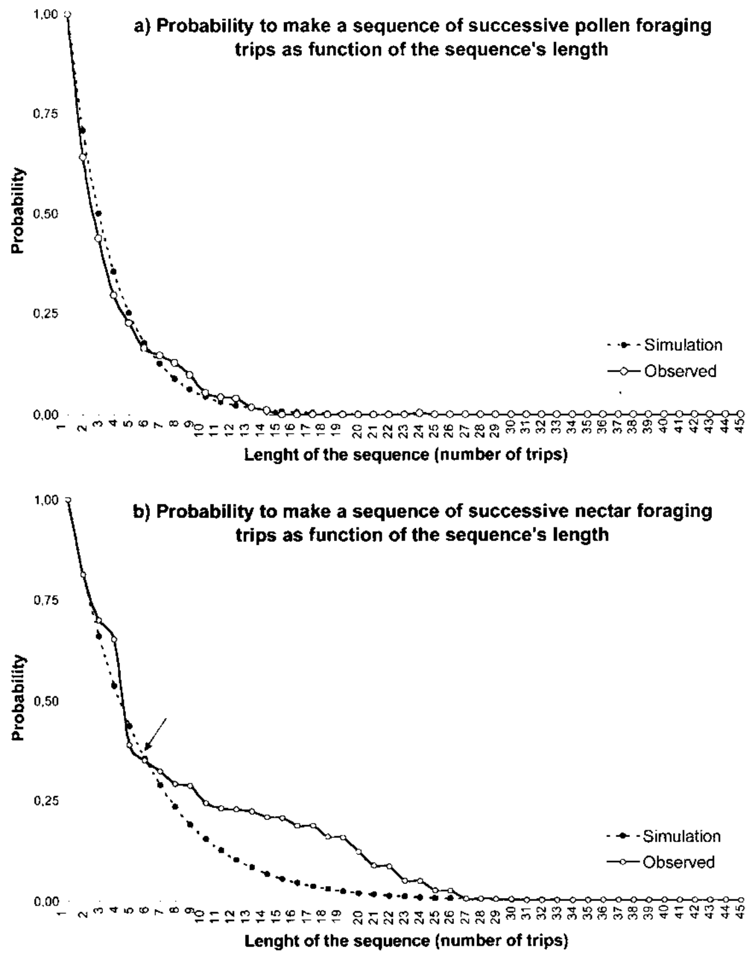

Fig. 1. *a) Probability of executing a sequence of pollen collection as function of the sequence's length. The simulation is done by the equation: $Y = 10^{-0.15x}$; where Y is the probability of the sequence and x its length.*
b) Probability of executing a sequence of nectar collection as function of its length. The simulation is done by the equation: $Y = 10^{-0.09x}$. The arrow shows where the observed and the simulated curves differs significantly.

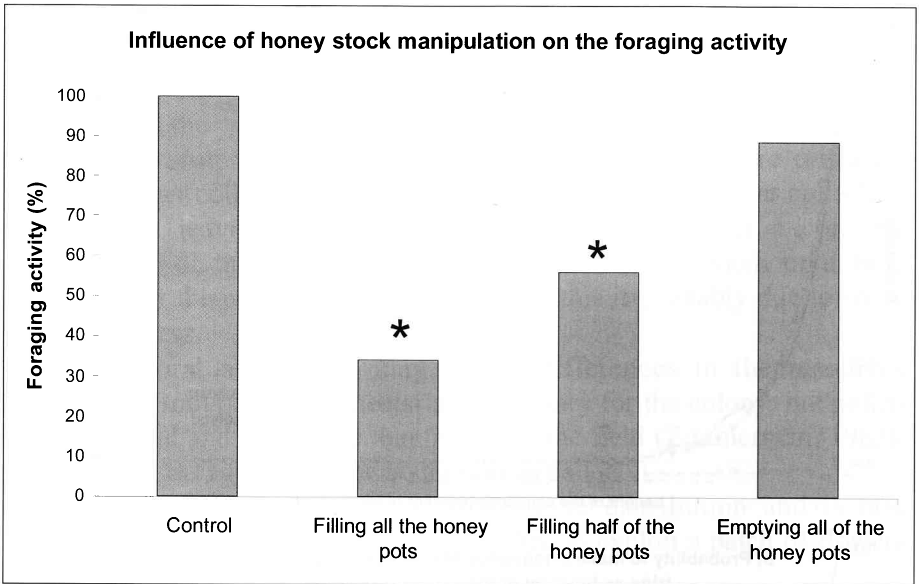

*Fig. 2. Influence of nectar store modification on the global foraging activity. The * indicates that the results is statistically significant from the control.*

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