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MUTUAL BENEFIT FOR REPRODUCING AND NON-REPRODUCING FEMALES IN NESTS OF THE CARPENTER BEE *Xylocopa pubescens* Spinola

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SUMMARY

Since recently emerged adults of *X. pubescens* seem to depend on food and protection given by their mother, the species can be considered as being obligately social. After this initial phase, young females can choose between starting a solitary nest themselves, or staying in the maternal nest. Inside social nests, however, there is a distinct separation between reproducing and non-reproducing females. The advantages of this form of sociality for both egg layers and non-egg layers will be discussed. The severe competition for nesting sites is considered to be the most important factor inducing sociality.

Bénéfice mutuel pour des femelles reproductrices et non-reproductrices dans les nids de l'abeille de bois *Xylocopa pubescens* Spinola

RÉSUMÉ

Puisque les jeunes adultes de *X. pubescens* dépendent de la nourriture et de la protection offertes par la mère, l'espèce peut être classée comme obligatoirement sociale. Après cette première phase, les femelles peuvent choisir entre commencer un nouveau nid solitaire elles-mêmes, ou rester dans le nid maternel. Dans les nids sociaux, il y a pourtant une séparation évidente entre les femelles pondeuses et les femelles non-pondeuses. Les avantages de ce système (eu-)sociale pour ces deux groupes de femelles, notamment en fonction de la compétition pour les nids disponibles dans l'habitat, seront discutés.

INTRODUCTION

Carpenter bees make their nests in all kinds of wood in which they are able to dig a tunnel-system. This system may be linear and small, or it may have been extended to a complicated branched nest.

Since *Xylocopa pubescens* may live solitarily or share a nest with conspecifics, this species is very suitable for studying the factors leading to sociality. Earlier studies have revealed that about three overlapping

generations may be raised during the active season in spring and summer. The nests may then become inhabited by matrifilial colonies, in which the original foundress and/or one or more of her daughters will continue to reproduce (Ben Mordechai et al. 1978; Gerling et al. 1981).

Among others, Van der Blom & Velthuis (1988) have provided data concerning several factors that influence sociality. These data will be discussed and extended in this paper. The significance of the social system for reproducing and the non-reproducing individuals will be investigated.

MATERIAL AND METHODS

The study was performed in Israel, at the Hatzeva Field Centre in the Rift Valley, about 30 km South of the Dead Sea. It covered the period between half April and the end of August, the major part of the reproductive season of the bees. The population under study had become established in a shady place where suitable nest material (boards of soft timber and hollow *Arundo donax* canes) was provided by several investigators during subsequent years of research. Individually tagged females from 21 nests were observed daily during the activity periods; developments and behaviour inside the nests were observed by means of X-radiography. While using this method of observation, individuals could be recognized since they were, together with the paint mark, labeled with a tiny piece of lead. Further details can be found in Van der Blom & Velthuis (1988) (= B & V, '88).

RESULTS AND DISCUSSION

Figure 1 shows a model in which an attempt is made to outline factors relating to sociality. The first and very important character of the desert habitat is the scarcity of suitable wood for making nests. This causes strong competition for nesting sites (Ben Mordechai et al. 1978; Velthuis, 1987; data on usurpation of unguarded nests in our situation are given below). It is not only *X. pubescens* which depends on this resource; other carpenter bees (*X. sulcatipes*) and several species of wasps use the same substrate for nesting. Females of these species, which do not have a nest themselves, search for opportunities to start nesting. If they find an empty or unguarded tunnel, they enter, break down any cells present, clean it, and start to make new cells themselves (B &V, '88).

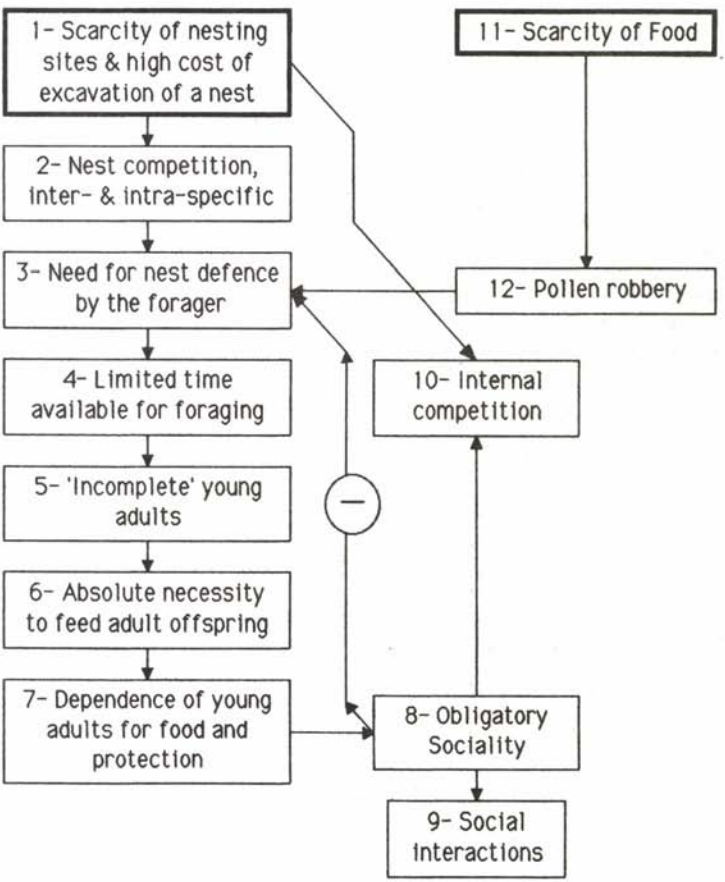
This competition is based not only on the scarcity of suitable substrate, but also on the value of an already constructed burrow, because we observed that bees fight for existing nests even when plenty of timber of the right quality (provided by the investigators) was available (B & V, '88).

Guarding the nest against intruders is important for females if they are not to lose their nest (B & V, '88)(3). As a consequence, they have to limit their absence from the nest, and thus reduce to a minimum the time spent foraging (4).

Velthuis & Gerling (1983) and Van der Blom & Velthuis (1988) showed that tenerals (during the first days of their adult life) eat at least as much pollen as they did throughout the larval stage. Also, they receive considerable quantities of nectar from the forager through trophallaxis (Gerling et al.

Fig. 1. — Factors relating to sociality.

Fig. 1. — Facteurs mis en relation avec la socialité. 1- Rareté des lieux de nidification; 2- Compétition pour les nids; 3- Nécessité de défendre le nid, inter- & intra-spécifique; 4-Limitation du temps disponible pour fourrager; 5- Jeunes adultes 'incomplets'; 6- Nécessité absolue de nourrir les descendants adultes; 7- Dépendance des jeunes adultes pour la nourriture et la protection; 8- Socialité obligatoire; 9- Interactions sociales; 10- Compétition interne; 11- Pénurie de nourriture; 12- Pillage de pollen.



1981,1983; B & V, '88). This food appears to be very important for the tenerals; they need it to become active and sexually mature (B & V, '88). Different from the truly solitary bees, *X. pubescens* thus postpones part of the provisioning from the larval stage until the young adult stage. In fact, because nest defence takes precedence at the time cells are being provisioned, the young adults are not fully developed upon emergence (5), and need additional feeding (6).

The young bees are thus absolutely dependent on their mother for protection and food (7), so the social phase has become an obligatory phenomenon (8).

Inside the nest, the bees engage in many social interactions (9), such as trophallaxis (both 'forced' and as a form of 'voluntary' feeding of nest mates) and allogrooming, the significance of which is only poorly understood (B & V, '88).

Cohabitation in one nest provides advantages but also creates problems for all individuals involved. For egg layers, which are also the exclusive foragers, nest mates can be seen as helpers against intruders that might take over the nest: Solitary nests were taken over frequently (16 times, which reflects about 64% of the cases of solitary breeding), whereas no nests were taken over once there were other adult and mature females present in addition to the forager (on average, this multi-female situation occurred about 45% of the time in the 21 nests under study).

Instead of taking over the nest for reproduction, intruders may steal food from nests of their own species, or of a different species of carpenter bees (12). Some individuals specialize in this foraging strategy (Velthuis, 1987). Such pollen robbery never occurred when a nest was guarded, but it happened frequently in solitary nests (B & V, '88).

However, in small nests there is only room for one individual to make cells and to lay eggs (B & V, '88). Since these nests are so valuable, it is only to be expected that within a nest there is competition for this dominant position (10). In 17 cases (12 different nests) we investigated which individuals proceeded to reproduce after a new generation had matured inside the same nest:

- 11 times this was the mother in presence of her daughter(s);
- 2 times a daughter immediately took over the reproduction after the mother died;
- 4 times a daughter took over in the presence of her mother. In total 33 females were born in these nests of which 6 (=18.2%) reproduced in the parental nest during the same season (if the observations would have been continued during the next season, this percentage might very well have become larger, since probably many females hibernate in their parental nest and start to lay eggs in spring).

In two of the four cases in which the mother was still present when a daughter took over, we noted that the mothers were not yet at the end of their reproductive capacities. After some time these mothers left (or were forced to leave) and started to excavate a new nest at a different place, in which they also made cells. In both cases, the mother landed on the original nest several times after the separation, but received the same agonistic treatment from the daughter as a strange intruder. In the other two cases, the mother stayed in the nest beside her daughter (and acted as a guard) for quite a long period.

Nest sharing by unrelated individuals was not observed during this research, except in one case, where an intruder left one pupa undamaged after

usurping the nest. The pupa emerged and remained inside the nest, as regular offspring in a normal situation, and acted as a guard lateron. This has also been observed by Velthuis & Gerling (1983), but the thusfar, frequency of such observations appears to bee too low to consider this a regular phenomenon in this species.

Considering the observed phenomena, *Xylocopa pubescens* can be classified as eusocial (c.f. Michener, 1985):
- there is a necessary overlap of generations;
- inside the nests there is a strict reproductive dominance and, consequently, a division of labour;
- non-reproductives actively engage in nest defence, which can be seen as a form of indirect brood-care.

I conclude that for non-reproducing females it appears to be a very attractive alternative to remain safely in the parental nest, and to wait for an opportunity to become an egg layer. Since the maintenance of the nest is very much in their own individual interest, it is only logical that they help to defend it. However, the option of staying in the maternal nest is only available to a small portion of the females. The majority will be forced out by their mother or their sisters. It is also obvious that egg layers do not only profit from the services of their nest mates (guards), but at the same time they have to compete with them for the dominant status.

Thus, eusociality in this species mainly seems to be rooted in mutualistic nest sharing. Observations on competition between a mother and her daughters (the daughters taking over from their mother) are hard to understand in terms of kin-selection theories. However, more observations are needed in order to be able to tackle this problem. The fact that nest sharing by unrelated individuals only seems to occur so seldom (as explained above) may indicate the importance of kin selection to the behaviour of this carpenter bee.

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