# The superseded female's dilemma: ultimate and proximate factors that influence guarding behaviour of the carpenter bee *Xylocopa pubescens*

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**Abstract.** Both solitary and primitively social nests of the facultatively social carpenter bee *Xylocopa pubescens* can be found throughout most of the breeding season. In social nests there is reproductive division of labour between a dominant forager and a guarding female. Two types of guarding females can be discerned: the young pre-reproductive guards, and older, formerly reproductive guards. The latter type of guard is found when, after a take-over of reproductive dominance either by a nestmate (mostly a daughter) or an intruder, the defeated female stays in the nest instead of leaving to try and found or usurp another nest. She is then manipulated into the role of a guard. The dominant female profits from the presence of the guard since she protects the nest against pollen robbery by conspecifics (Hogendoorn and Velthuis 1993). We have studied why superseded females might "prefer" to remain as a guard, rather than try their luck somewhere else. The hypotheses investigated pertain to (1) the difficulty for the defeated female of finding a new nest and of restarting reproductive activities due to (a) ecological constraints (nest and pollen shortage) and (b) the effect of age and wear on the defeated female; (2) the effects of guarding in terms of inclusive fitness. We found that superseded females remained as guards significantly more often when a nestmate (not necessarily close kin) took over reproductive dominance than when an intruder did so. Other factors associated with the decision of the defeated female to stay or leave were her age and the number of her own young still present after the supersedure. The probability of finding or constructing a new nest was lower for old than for young females. After finding a nest, old females produced less brood than young foundresses. As a result of these two factors old superseded females gained, in terms of inclusive fitness, by staying as guards, whereas young females profited from leaving the nest. We interpret these results as an indication that guarding behaviour has evolved due to kin selection. However, kin discrimination apparently did not occur. Therefore we conclude that in this species kin selection is not, in the proximate frame of reference, based on kin recognition and preference for helping kin.

**Key words:** *Xylocopa* – Supersedure – Guarding – Kin selection – Kin recognition

## Introduction

The factors involved in the evolution and ontogeny of sociality in Hymenoptera have been a recurring matter of debate to ethologists, particularly since Hamilton (1964) formulated the theory of kin selection (e.g. West Eberhard 1975; Andersson 1984; Brockmann 1984; Alexander et al. 1991; Gadagkar 1991). By now, it has become widely accepted that at the ultimate level sociality is favoured at least in part by kin selection.

In addition it is clear that at the level of the individual, various proximate factors may influence the individual's decision to start helping instead of breeding solitarily. These proximate factors, which are not mutually exclusive, include: (1) lowered possibility of reproducing solitarily due to ecological conditions (Emlen 1982) or to manipulation (Alexander 1974), both of which may increase (a) the indirect fitness pay-off from helping a nestmate compared with the direct fitness pay-off from breeding and (b) the direct benefits obtained through helping, for example due to increased survival by being allowed to stay at the sheltered nest or den in return for help (cf. Emlen 1984), or to the production of some offspring while helping, a possibility which helpers would not have if they started nesting solitarily (e.g. Noonan 1981; Lin and Michener 1972); (2) possible future benefits arising from performing helping behaviour, due to learning (e.g. Rowley and Russell 1990) or to inheritance of the nest or of the reproductive dominance in the nest (West Eberhard 1975); (3) the high inclusive fitness pay-off from preferentially helping close kin (which as a proximate factor requires kin discrimination).

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Although various authors have presented logically correct deductions concerning the different causes of helping behaviour, others still fail to make the appropriate distinction between proximate and ultimate explanations. For example, the evidence that, in the Florida scrub jay, habitat constraints influence the individual young jay's decision to stay as a helper at the nest instead of starting a new nest (Woolfenden and Fitzpatrick 1978) has been interpreted as a disproof of the role of kin selection in the evolution of helping behaviour in this species (Koenig and Pitelka 1981). *Mutatis mutandis*, several authors consider the kin recognition abilities of highly eusocial insects as support for the hypothesis that kin selection is at the basis of sociality (e.g. Breed 1981; Getz et al. 1982). However, on the one hand, in many cases kin recognition may well be a side-effect of nestmate recognition (Carlin 1989; Grafen 1990), and on the other hand, nepotistic behaviour of workers within the colony may have evolved after, and in response to, their functional sterility.

Investigations of the factors influencing the occurrence of sociality in facultatively social species may provide an insight into the factors of importance in the evolution of obligate sociality. Therefore, unravelling the ultimate and proximate reasons for the occurrence of helping behaviour is of special interest in primitively social Hymenoptera species, which in an evolutionary sense may be "at the brink of sociality" (Velthuis and Gerling 1983).

In this context, many species belonging to the subfamily of the Xylocopinae are interesting subjects for study for two very different reasons. Firstly, the Xylocopinae are considered to be, phylogenetically, the sister group of the Apidae (Winston and Michener 1977; Sakagami and Michener 1987), which contains all the highly eusocial bee species. Secondly, because many species belonging to the Xylocopinae nest socially during part of the reproductive cycle (Michener 1990), we can compare the circumstances under which social and solitary nesting is favourable.

In this paper we examine the possible reasons for the helping behaviour of females of the primitively social carpenter bee *Xylocopa pubescens* Spinola. An attempt is made to distinguish proximate reasons that affect the motivation to help from reasons that may have played a role in the evolution of the helping behaviour.

Solitary and social nests of *X. pubescens* can be found simultaneously during most of the breeding season, which usually lasts from the beginning of March until the end of October. Nests are founded solitarily, and brood is produced continuously as long as space is available in the nest, and as long as there are no other limiting factors, such as pollen shortage or extreme temperatures (Velthuis 1987; Hogendoorn and Velthuis 1993).

Young males and females emerge continuously from the end of April on. These tenerals remain in the nest until they are at least 7 days old. They are fed nectar trophallactically by the mother, and they eat pollen from the cells under construction. From an average age of 6 days on, young females can be found sitting in the nest entrance. This behaviour has been interpreted as guarding behaviour (Velthuis and Gerling 1983; van der Blom and Velthuis 1988). It is presumed to be a consequence of competition between young for the nectar brought in by the mother upon her return from a foraging flight (Velthuis and Gerling 1983). At an average age of 16 days (Hogendoorn, in prep.) the young females may leave the nest in order to try to found or usurp a nest elsewhere, or they may try to take over reproductive dominance in the maternal nest. A nest may thus contain between 1 and 8 adult females at a time.

Normally, during attempts to take over reproductive dominance, either by a nestmate or by an intruding female, fighting is observed. If the take-over is successful, the defeated female may leave, or she may stay in the nest as a guard. After such a take-over, the new reproductive dominant may destroy all or part of the brood. In addition, she may evict the other adults and the teneral bees present in the nest. The question that arises is what determines whether the former reproductive will nevertheless stay as a guard or will depart. Is it the new dominant that decides this, is it the defeated female, or both?

The presence of a guard leads on average to an increase in the reproductive output of the reproductively dominant female (Hogendoorn and Velthuis 1993). However, the guarding female may also constitute a threat to the position of the reproductive dominant, especially if she is still young and vigorous or if the relatedness between the defeated female and the new reproductive dominant is low, provided the females have the ability to discriminate kinship (e.g. Smith 1987). Under these circumstances, it might still be better for the new reproductive dominant to chase the defeated female from the nest instead of allowing her to stay as a guard. In other words, the choice between staying as a guard or leaving the nest is not necessarily made by the superseded female.

We can distinguish two general, but not mutually exclusive, explanations for the evolution of this guarding behaviour. Firstly, the probability that guards will regain reproductive dominance in their own nest may be higher than their chances of starting a new nest by founding or usurping one ("hopeful reproductive", West Eberhard 1975). Secondly, the average increase in inclusive fitness through guarding the nest of a related female may be higher than the average gain in direct fitness if the female leaves the nest. Both of these considerations depend on the chance that the defeated female will become successfully reproductive in another nest.

The chance of founding a new nest successfully is assumed to be affected by ecological constraints, of which the most important are shortage of pollen and of nesting materials (van der Blom and Velthuis 1988; Hogendoorn and Velthuis 1993). It is therefore hypothesized that during periods of severe competition for nesting sites or pollen selection should favour superseded females remaining as guards more frequently. In addition, the age of the defeated females and the accompanying wear of their wings and mandibles (Camillo and Garofalo 1989; van der Blom and Velthuis 1988) may influence the probability of re-nesting successfully. If this

is so, old females should remain as guards more frequently.

Kinship may have an effect in two different ways. Firstly, the relatedness with the new reproductive dominant may be important in the decision to stay or leave. In that case, one would expect the superseded female to stay more often when a nestmate takes over reproductive dominance than when an intruder does so. If kin recognition exists in this species a defeated female may further improve her inclusive fitness by taking into account the degree of relatedness with the nestmate that takes over reproductive dominance. Secondly, the brood and young of the defeated female, which may still be present in the nest after take-over, could affect the female's decision to stay as a guard. The guard may ultimately profit simply by protecting her own brood and young, one of which may in the future gain reproductive dominance in the nest. In that case, the superseded female is expected to stay more often if the nest contains her own brood or young than if it does not.

## Methods

The biology of *Xylocopa pubescens* was studied at the Hazeva Field Study Centre, in the Arava valley (Rift Valley), which is a part of the Negev desert in Israel, 30 km south of the Dead Sea (see also Gerling et al. 1981, 1983; Velthuis and Gerling 1983; Velthuis 1987; van der Blom and Velthuis 1988). This is an arid region, where the finding of suitable nesting materials and food is often difficult for the bees.

The bees readily started to nest in boards of balsawood, which the investigators placed once a year (in early spring) under a shaded arcade (70 m²). The females foraged in the gardens of the field study centre and in the surrounding desert. During 1988 (March to mid-August), 1989 (May to mid-August) and 1990 (March to mid-October), nest development was followed in a total of 96 nests.

The contents of the nests, and the role and presence of the individual females were monitored every other day by means of X-ray radioscopy (Gerling et al. 1981). To permit individual recognition, the bees were marked with thin, differently shaped pieces of lead, which were glued upon the thorax. The lead pieces were coated with quick-drying enamel paint of various colours to permit individual recognition in the field.

For marking, adult females were caught near their nests. During the summer of 1988 a technique was developed for marking young females directly after they had emerged from their pupal skin. They were taken from their cells as mature pupae, through windows cut in one side of the nesting boards. Each pupa was placed in a short stretch of Arundo cane. After casting their pupal skin outside the nests, the females were marked and put back into their original cells (and in occasional experiments, into cells in other nests) through the window. These young females emerged from their cells in the usual way, by gnawing away the cell closure, which was left intact when the window was cut.

During 1989 and 1990 nearly all females present in the nests were marked by means of this "window-incubator" method. This allowed us to distinguish unequivocally between nestmates and intruders taking over reproductive dominance. In addition, due to this marking technique it was possible to reliably estimate relatedness between the nestmates competing for reproductive dominance. Moreover, we could manipulate the relatedness within the nest to some extent by exchanging young females between nests.

Additional X-ray scans of nests were done regularly (a) to identify the females involved in a fight (the sounds produced by fighting females could be heard 20 m from the nests), and (b) to ascertain the role of individual females in the nest by checking which female laid an egg once enough pollen had been collected.

Here we will refer to females younger than 8 days as "young" (or teneral) females. Females younger than this age were never seen to leave the maternal nest unless they were pushed out, which often happened during a take-over. Formerly reproductive females were considered to be guards when they had stayed in their original nest for more than 1 week after their defeat. These females always positioned themselves near the nest entrance, except when they went on their daily nectar-foraging trip.

To test the hopeful-reproductive theory experimentally, the reproductive dominants of 24 guarded nests were caught, and the subsequent behaviour of the guards was monitored for 2 weeks.

A stepwise logistic regression analysis (using the NCSS statistical program; Hintze 1981) was performed to test which variables were significantly associated with staying and leaving by the defeated female. Only the data collected 1989 and 1990 were included in this analysis; the data from 1988 were excluded since the young females were often not marked before taking over reproductive dominance, and therefore the relatedness with the defeated female was not always known. The independent variables that were chosen to test the hypotheses emanating from the different theories concerning the reasons why the defeated females either stayed as guards or left the nest (i.e. the dependent variable), were as follows:

*Aggression.* We did not collect data about the length or the intensity of the fights. However, the fierceness of the superseding female may be reflected in its effects. Therefore we used the following three variables to test whether the aggressive behaviour of the dominant was correlated with staying or leaving by the superseded females: 1) The number of nestmates of the defeated female that had left the nest after a take-over. 2) The number of brood cells that was destroyed by the new reproductive dominant. 3) The sum of the number of cells destroyed and the number of nestmates that had disappeared. The third variable was chosen because it may directly reflect the level of aggression of the usurper.

*Environmental constraints.* Environmental constraints were represented by two parameters, one for the shortage of nesting materials, and one for the shortage of pollen. The severity of nest competition was estimated by subtracting the semi-monthly number of females that founded or usurped one of the nests under study from the number of females leaving these nests ("number of searchers"). This variable provides a relative measure of the severity of competition for nests, since only nest-searching females originating from the nests under study were included.

Pollen availability was estimated by calculating the semi-monthly average duration of pollen collecting trips of socially nesting females. The duration of flights of solitary nesting females was not taken into account since these females may shorten their absence from the nest in response to a high number of potential usurpers (Hogendoorn and Velthuis 1993). The duration and the number of pollen flights of females from ten or more nests (usually 18 nests were included) were monitored at least once a weak during morning hours (i.e. from half an hour before sunrise until 9 a.m. (cf. Hogendoorn and Velthuis 1993). For each semi-monthly period, the mean durations per female were averaged.

*Age.* The reproductive age (i.e. the number of days that the female had spent as reproductive dominant) and the number of eggs she had laid were taken as estimates of physiological age.

*Kinship.* The importance of kinship was tested by using three variables: (1) whether the new reproductive dominant was a nestmate (whether or not related) or an unrelated intruder; (2) the relatedness between the defeated female and the new reproductive dominant estimated on the basis of genealogy (the "objective $r$"); (3) the "subjective $r$": the relatedness which the defeated female could have expected on the basis of the age difference between herself and the new reproductive dominant nestmate at the time the latter

**Table 1.** Number of defeated females that stayed as guards or left the nest after take-over by a nestmate or by an intruder (data from 1988, 1989 and 1990; $n=174$ take-overs; in parentheses the data from 1989 and 1990, which were used in the logistic regression analysis)

|  |  | Stay as guard | Leave the nest |  |
|---|---|---|---|---|
| $n$ supersedures by: | Nestmates | 76 (60) | 28 (22) |  |
|  | Intruders | 12 (10) | 58 (40) | $\chi^2 = 52.37$*** |
| Average reproductive age |  |  |  |  |
| at take-over by: | Nestmates | 43.8 ($\pm$3.1) | 31.3 ($\pm$4.6) | $t=2.151$* |
|  | Intruders | 58.3 ($\pm$14.0) | 29.0 (3.4) | $t=3.037$** |

The average reproductive age (in days $\pm$ SE) of stayers and leavers is given at the bottom of the table. There was no significant difference in reproductive age between the females that were superseded by nestmates and by intruders (t-tests)

n.s.: $P>0.05$; *: $0.05 \geq P > 0.01$; **: $0.01 \geq P > 0.001$; ***: $P \leq 0.001$

emerged from her cell. Thus, if the defeated female was already reproducing at the time the new reproductive dominant emerged from her cell, we calculate the subjective $r$ as 0.5 (mother-daughter). If she was not reproductively active yet, the subjective $r$ is 0.75 (sister-sister). The subjective $r$ differs from the objective $r$ in the instances where the defeated female did not destroy all brood present at the time she became dominant, and also in the case where young females were exchanged between the nests by the investigators after marking.

*Presence of brood or young.* The influence of the presence of brood or young of the defeated female, still in the nest after take-over, was tested using four variables: the presence or absence of (1) brood and (2) young, and the actual number of (3) brood and of (4) young present.

The occurrence of kin discrimination was investigated by comparing the frequency of (1) acceptance by the reproductive dominant of daughters and of unrelated young females emerging in the nest ("foster-daughters") (we define acceptance as being allowed to stay in the nest for more than 3 days); (2) supersedure by daughters and by foster-daughters. Emergence of unrelated females occurred when an intruder left some brood of the defeated female after a take-over or when brood was experimentally exchanged between nests.

The statistical tests used are indicated in the text and in the table headings. Averages are given with their standard errors.

## Results

### Behavioural observations

The background data collected are summarized in Table 1. We observed the behaviour of the females during 61 take-overs. During all of these take-overs, fighting occurred. In six instances, the new reproductive dominant evicted the defeated female, and refused her entry to the nest during at least 1 h after the fight. This happened when an intruder took over reproductive dominance ($n=2$), and also when a nestmate took over ($n=4$). However, two defeated females (with reproductive ages of 50 and 70 days) were guarding in the nest entrance of their former nest later on the day of their "eviction" by a nestmate. Therefore, on the basis of these observations, we cannot decide whether defeated leavers were evicted from the nest, or whether they left by their own choice without being further attacked. The females that did not return after they had been evicted had only just started to reproduce: their average reproductive age was 5.8 days ($n=4$).

During the 1st week after the take-over, the defeated females that stayed as guards in the nest could usually be seen sitting in the nest entrance. They occasionally undertook pollen flights. We scanned the foraging behaviour of 12 guarding females within a week after their defeat, at different times of the day for various times. These 12 guards were observed to return to the nest 25 times without pollen, 20 times with approximately half a load of pollen, and 7 times with a full pollen load. However, they often did not discard their load at the pollen slant, because they were attacked by the new reproductive dominant as soon as they entered the central part of the nest ($n=15$ times). Subsequently, some of these females brushed off their pollen outside the nest ($n=8$), and some discarded their pollen load in the entrance tunnel ($n=7$), after which the reproductive dominant female transported it to the cell under construction. After approximately 1 week, the superseded female gradually ceased to collect pollen. From that time on, she could always be found sitting in the nest entrance except when she left the nest (once or twice a day), presumably to obtain nectar for her own use.

Out of 88 guards, 47 were observed until the end of their guarding period. These females had been guarding for $28.9 \pm 2.8$ days on average. Guards usually remained guarding until the end of their lives; by that time their wings were so worn that they could hardly fly, and they had great difficulty in returning to the nest. Some of these females ($n=9$) were found dead or exhausted near their nest.

Since guarding females were never seen searching for nests, it is postulated that they hardly ever do this. However, two females did manage to find a new nest after a short period (9 and 12 days respectively) of guarding, one by usurping a nest, the other by founding a new nest. It was not clear whether these guards were evicted from the nest at a later stage or whether they actually searched for nests in between their periods of guarding activity.

**Table 2.** Calculations to estimate the probability of finding a nest (*P*), based on the number of marked nest leavers found as reproductive dominants in other nests under study (A) and on the number of marked and unmarked females which started to breed in one of the nests under observation during late spring and summer of 1990, when all females leaving the nests had been marked (B)

A. (data from 1989 and 1990)

|  |  | Pre-reproductive females | Superseded females |
|---|---|---|---|
| *a.* | *n* marked females leaving the nest | 79 | 80 |
| *b.* | *n* marked foundresses | 13 | 8 |
| *c.* | $P_{min}$ ([*a/b*] · 100) | 16% | 10% |

B. (data from summer 1990)

|  |  | All females | Superseded females |
|---|---|---|---|
| *d.* | *n* marked leavers | 77 | 32 |
| *e.* | *n* marked foundresses | 10 | 3 |
| *f.* | *n* unmarked foundresses | 21 | unknown |
| *g.* | estim. proportion of population under study (*e*/[*e*+*f*]) | 0.32 | – |
| *h.* | estim. *n* marked foundresses in population (*e/g*) | 31 | 9.3 (3/0.32) |
| *i.* | $P_{max}$ [(*h/d*) · 100] | 40% | 29% |

## Is the guard a hopeful reproductive?

Only 5 out of 88 guards managed to regain reproductive dominance in their own nest in a total of 2405 observed guarding days. Thus the probability that an average guard will regain the dominant position was 5/2405 = 0.0021 per day. The reason for calculating this daily rate is that, although 41 guards were not observed until the end of their guarding period, they did not regain reproductive dominance during the time they were observed, and they should therefore be included in the calculations. Since guards guarded for 28.9 days on average, the probability that an average guard would regain reproductive dominance was 28.9 times 0.0021 = 6.1%. The five guards that did regain dominance did so after guarding for 24.6 ± 5.1 days.

The probability of regaining dominance at home should be compared with the probability of defeated females that left the nest becoming reproductive dominants again elsewhere. Since we were not able to follow the females that left the arcade, it was not possible to give a reliable estimate of the defeated females' chances of obtaining a nest elsewhere. Therefore, we give a minimum and a maximum estimate of the probability of re-nesting.

*Minimum estimate of the probability of obtaining a new nest after defeat.* This estimate is based on the number of marked defeated leavers that managed to become reproductively active in one of the nests under observation. Eight defeated females which had left the nest were found as reproductive dominants in other nests under study. These females founded or usurped a nest within 8 days of their departure. Therefore, to estimate the probability of regaining reproductive dominance after leaving, we did not take into account the six females that departed within 8 days prior to the end of the observation period. Thus, excluding the possibility that new

nesting materials could be found outside the arcade, we calculated the minimum probability of finding or usurping a nest to be 10% (8 out of 80) for old leavers, and 16% (13 out of 79) for young leavers (Table 2 A).

The eight defeated females that succeeded in gaining dominance elsewhere had an average reproductive age of 16.5 (±3.0) days. The defeated leavers that were not observed to regain the reproductive dominant status elsewhere had been reproductively active for 31.0 (±2.6, *n* = 72) days on average. Thus, defeated leavers that gained dominant status elsewhere were significantly younger than the females that failed to obtain a new nest (ANOVA, *F* = 3.491, 0.05 > *P* > 0.025).

*Maximum estimate of the probability of obtaining a new nest after defeat.* This estimate is based on a calculation of the number of nests available in the population as a whole. To quantify the percentage of nests in the population that were under observation, we compared the numbers of marked and unmarked females which usurped or founded a nest during late spring and summer of 1990 (Table 2 B). By this time, all females in the nests under study were marked. By extrapolation, the maximum probability of defeated leavers, obtaining a new nest was estimated to be 29% (40% for all leavers, including young females).

The probability that a guard would regain dominance in the original nest did not differ from the minimum estimate of the probability that she would become dominant elsewhere after leaving ($\chi^2$ = 1.45, *P* = 0.23). However, the maximum estimate of the probability of obtaining a new nest after defeat was significantly higher than the probability of regaining reproductive dominance at home ($\chi^2$ = 6.73, *P* = 0.01). Therefore we conclude that guards are in general not hopeful reproductives.

However, the significant age differences between (a) the defeated females that did and that did not find a new nest and (b) the females that stayed as guards and

**Table 3.** Status of 24 guard bees 2 weeks after the reproductive dominant had been removed from the nest

| | n | % |
|---|---|---|
| Reproductive dominant (r.d.) | 2 | 8.3% |
| Solitary and inactive | 3 | 12.5% |
| Guard (other female became r.d.) | 9 | 37.5% |
| Found dead | 8 ⎫ | |
| Disappeared | 2 ⎭ | 41.7% |



**Fig. 1.** The relative frequency of staying as a guard superseded females of different age classes. The observations were classified according to age, so that each age-class contained 33 observations. The *total number* of superseded females is given *above each column*; the *significance* of the difference between nests taken over by a nestmate (*white columns*) or by an intruder (*shaded columns*) within each age-class is indicated at the top of the figure ($\chi^2_{\text{test}}$; cf. Table 1)

that left the nest (Table 1) indicate that there is an age-dependent reduction in the possibility of re-nesting successfully elsewhere. Therefore, although young females have a higher probability of reproducing if they leave the nest, for old females the probability of regaining dominance if they stay as guards may be higher than the probability of taking over reproductive dominance elsewhere.

If a guarding female is indeed a hopeful reproductive, she must be likely to regain dominance if the reproductive dominant does not return from a foraging trip. We studied this experimentally by catching 24 reproductive dominants on foraging flights, and by monitoring the subsequent behaviour of the guards. These guards had been guarding for 39.1 ($\pm 5.17$) days on average.

After removal of the reproductive dominants, the behaviour of the guards changed conspicuously. After a few hours all guards could be found in the central part of the nest. After 2 days, 6 out of 24 former guards had started to collect pollen, but only two females managed to lay an egg later on. Of the other four females that started to collect pollen, two became guards again within 2 weeks, one was found dead and one had disappeared (and was presumably dead as well).

The six females that started to collect pollen had been guarding for 23.7±7.1 days on average, which was a significantly shorter time than that spent by the females that did not start to collect pollen (40.0±2.5 days; Mann-Whitney $U=80.5$, $P=0.05$). The status of the former guards 2 weeks after the removal of the reproductive dominants is listed in Table 3. These results suggest that the guard's ability to replace the reproductive dominant is age-dependent.

Summarizing, the probability of a guard's regaining dominance at home is lower than or equal to the probability that a defeated leaver will find a nest or will gain dominance elsewhere.

## The correlates of staying

Altogether 132 take-overs (Fig. 1) were used to analyse which factors contributed to the decision to remain as a guard or to leave the nest. The significance of association of each of the individual variables with staying as a guard or leaving the nest after take-over, which is the outcome of the first step in the logistic regression analysis, is presented in Table 4.
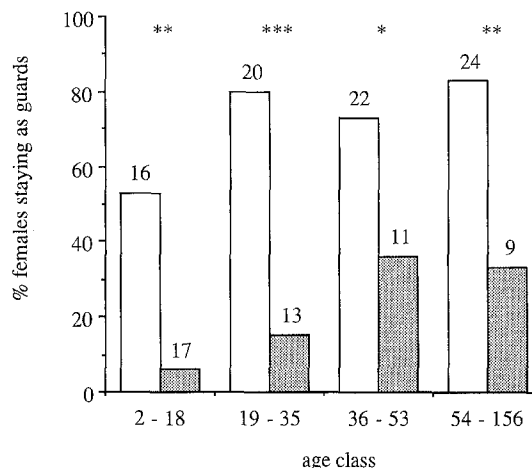
However, many of these variables covary. Some of these associations are obvious [for example a highly significant correlation between nestmateship and relatedness (Mann-Whitney $U$-test, $t=7.782$, $P<0.001$)], but others are less obvious [e.g. a negative association between the number of cells destroyed during the take-over and the reproductive age of the defeated female (Kendall's rank correlation, $t=-2.54$, $0.025>P>0.01$)]. Therefore, a step-wise logistic regression analysis seemed to be more appropriate.

This analysis revealed that only three variables were directly and significantly associated with the decision to stay or to leave (Table 5). This result allows us to make some statements about the reasons for the occurrence of helping behaviour, as described in the Introduction:

*Aggression.* Neither the number of nestmates removed by the new reproductive dominant at take-over, nor the number of cells destroyed, nor the sum of these two, was significantly associated with staying or leaving by the defeated female.

*Environmental constraints.* Surprisingly, neither the estimated number of searchers for nests nor the measure of pollen availability was correlated with staying or leaving. Therefore the defeated females' decision to stay as a guard is not made on the basis of pollen availability or nest availability.

*Age.* The reproductive age was significantly associated with staying or leaving. Upon looking more closely at the data, it becomes clear that after a take-over, young females that have only just started to reproduce in the nest leave the nest significantly more often than old females (Fig. 1).

**Table 4.** Significance of each individual variable selected to test hypotheses about the reasons why defeated females either stay as a guard or leave the nest, as calculated in the first step of the regression analysis

| Hypothesis | Variables | $\chi^2$ |
|---|---|---|
| *a*. Aggression | 1. *n* nestmates disappearing from the nest during take-over | 3.16 n.s. |
|  | 2. *n* cells destroyed at take-over | 2.88 n.s. |
|  | 3. sum of n cells destroyed and n nestmates disappeared | 2.83 n.s. |
| *b*. Environmental constraints | 1. *n* searchers for nests per semi-monthly period | 0.62 n.s. |
|  | 2. avg. duration of pollen flights per semi-monthly period | 0.01 n.s. |
| *c*. Age | 1. time the defeated female had spent as reproductive dominant | 15.64*** |
|  | 2. *n* eggs laid by the defeated female | 36.11*** |
| *d*. Kinship | 1. take-over was by a nestmate (versus by an intruder) | 38.41*** |
|  | 2. *r* between defeated female and the new reproductive dominant | 14.24*** |
|  | 3. *r* females might expect on the basis of nestmateship | 27.19*** |
| *e*. Presence of brood or young of the defeated female | 1. presence of brood after take-over | 12.21*** |
|  | 2. presence of young after take-over | 16.22*** |
|  | 3. *n* cells left after take-over | 16.20*** |
|  | 4. *n* young present after take-over | 18.23** |

All significant results were positively associated with staying as a guard. (avg: average; r: relatedness)

**Table 5.** Parameter estimation report of the logistic regression analysis of the variables significantly associated with the decision of 132 females to either leave the nest or stay as a guard

|  | $\beta$ estimate | SE | $P_{\beta=0}$ |
|---|---|---|---|
| Take-over by nestmate or intruder | 3.3928 | 0.7661 | >0.001 |
| *n* young present after take-over | 1.1015 | 0.3510 | 0.002 |
| Time spent as reproductive dominant | 0.0335 | 0.0138 | 0.015 |

The $\beta$-estimate is the logistic regression coefficient. All three variables were positively associated with staying as a guard.
On the basis of the logistic regression model 81% of the observations was classified in the correct category (i.e. staying or leaving)

**Table 6.** Relationships to superseding nestmates of defeated females that stayed to guard and that left the nest

| Relatedness | Stayers | Leavers |
|---|---|---|
| Unrelated nestmates ($r=0$) | 15 (25%) | 5 (23%) |
| Daughter of cousin ($r=0.19$) | 1 (2%) | 0 |
| Daughter ($r=0.5$) | 33 (55%) | 10 (45%) |
| Sister ($r=0.75$) | 11 (18%) | 7 (32%) |

Relatedness estimates were based on genealogies. No difference in relatedness between females that stayed and that left when a nestmate took over was found (Mann-Whitney *U*-test, $t=-0.953$, n.s.)

*Kinship.* The most important element in the decision to stay or leave appeared to be whether or not the new reproductive dominant was a nestmate of the defeated female. Females stayed guarding significantly more often if a nestmate took over reproductive dominance (Table 1; Fig. 1). However, neither actual nor the subjective relatedness was associated significantly with staying or leaving (cf. Table 6). Thus, previous social interactions are decisive in the matter of staying as a guard or leaving the nest, but the level of relatedness is of no consequence as a proximate factor.

*Presence of brood or young.* The number of young emerged females ($<8$ days) present in the nest after take-over seemed to influence the decision to stay or leave. The other variables (the number of cells present after take-over and whether or not brood or young were present) were not significantly correlated with the behaviour of the defeated females.

## Kin recognition

The finding that defeated females stayed to guard significantly more often for a nestmate than for an intruder (Table 1, Fig. 1) indicates that kinship has been an important factor in the evolution of guarding behaviour in *X. pubescens*. It would thus be adaptive for the potential guard to recognize the level of relatedness with the new reproductive dominant. There are, however, several reasons for believing that the females, in spite of their ability to distinguish nestmates from usurpers from outside, do not possess the ability to discriminate kin from non-kin:

1. Using the window-incubator method, we exchanged young females between nests. No difference was found in the rate of acceptance between the exchanged foster-daughters and the foster-daughters that naturally emerged in a nest of an unrelated female, which is what happens when a usurper does not destroy all the brood present at take-over (Table 7A). Therefore, we lumped these observations and compared them to the rate of acceptance of true daughters. No significant difference in the rate of acceptance of daughters and foster-daughters was found (Table 7B).

**Table 7.** Number of related and unrelated emerging females that were either accepted (i.e. allowed to stay in the nest for more than three days) or rejected by the reproductive dominant: A: the frequency of acceptance of experimentally swapped foster-daughters and of natural foster-daughters; B: The frequency of acceptance of daughters and foster-daughters

|  |  | Young female accepted | Young female rejected | $\chi^2$ |
|---|---|---|---|---|
| A. | Foster-daughters by swapping | 20 | 3 | |
|  | Natural foster-daughters | 25 | 3 | 0.79 n.s. |
| B. | Daughters | 124 | 8 | |
|  | Foster-daughters | 45 | 6 | 1.69 n.s. |

2. Out of 124 daughters produced, 38 took over reproductive dominance from their mothers. This frequency did not differ from that found for foster-daughters (19 out of 45; $\chi^2 = 2.16$, n.s.).

3. If kin recognition existed in this species, we would expect to find a correlation between the frequency of staying as a guard and the relatedness between the defeated female and the new dominant, in those cases where a nestmate took over. However, no such difference was found (Mann-Whitney $U$-test, $t = 0.935$, n.s.).

Since we have found no evidence for the existence of kin discrimination, we conclude that the level of relatedness in itself does not affect the choice of whether or not to perform guarding behaviour.

However, the finding that the decision to stay as a guard or to leave does depend on whether the new reproductive dominant is a nestmate of the defeated female may indicate that kinship played a role in the evolution of guarding behaviour. To ascertain this we need to discover whether the inclusive fitness gains that arise from guarding for a nestmate are higher than the expected direct fitness gains when the defeated female leaves the nest.

*Inclusive fitness benefits of guarding*

The average contribution made by the guard to the reproductive output of the dominant has been calculated as 0.07 cells per day (Hogendoorn and Velthuis 1993).

On the basis of this estimate, we have calculated the inclusive fitness benefits of staying as a guard as 0.475 (Table 8).

The benefits of leaving the nest (i.e. the costs of staying) depend on the probability of finding a new nest [10–29% (Table 2)] and the average amount of brood produced. The eight defeated females that managed to found a new nest within our study area produced a total of 12 young offspring (i.e. 1.5 on average). This means that the average direct fitness benefits accruing to leaving females are between 10% (minimum) and 29% (maximum) of 1.5 times the relatedness to their own brood (0.5), which is 0.08–0.22. The average inclusive fitness benefits of females that remained guarding were therefore higher than the estimated direct benefits of leaving the nest.

The probability that young females leaving the nest would find a new nest was between 16% (minimum) and 40% (maximum; Table 2), while the average lifetime reproductive output of all nesting females was 5.1 ($\pm$ 0.278, $n = 206$) emerging adults. Thus, the direct fitness benefits of leaving for young females are between 0.41 and 1.02.

## Discussion

We have shown that, by guarding for a nestmate, the old defeated females that decided to remain as guards gained more in terms of inclusive fitness than did females that left the nest to try and resume reproductive activities elsewhere. By contrast, young females gained more than old females from leaving the nest (provided that they were unable to gain reproductive dominance at home), than from staying as guards due to the fact that they (1) had a slight, though not significantly higher probability of finding or usurping a nest, and (2) subsequently remained egglayers for a longer period of time, thus producing more offspring.

Defeated females remained guarding more frequently after take-over by a nestmate than by an intruder, indicating that indirect fitness benefits are important in the decision to remain as a guard. However, taking into accoung supersedures by nestmates only, the frequency of guarding was not associated with the degree of relatedness between the defeated female and the new domi-

**Table 8.** Calculation of the indirect (A) and direct (B) fitness benefits of guarding. Averages are given $\pm$ SE

| A. | Indirect fitness benefits of guarding | | |
|---|---|---|---|
|  | a. | $n$ days of guarding | 28.9($\pm$2.8; $n=47$) |
|  | b. | additional cells due to guarding | 2.02 |
|  | c. | average relatedness of guard to brood | 0.208 ($\pm$0.034; $n=60$) |
|  | d. | average indirect fitness benefit of guarding ($b \cdot c$) | 0.421 |
| B. | Direct fitness benefits of guarding | | |
|  | e. | probability of regaining dominance as a guard | 6% |
|  | f. | average number of eggs produced by former guards | 1.8 ($\pm$0.23; $n=5$) |
|  | g. | relatedness with their own brood | 0.5 |
|  | h. | direct fitness benefits of guarding ($e \cdot f \cdot g$) | 0.054 |
| | Expected inclusive fitness benefits of guarding ($f + h$) | | 0.475 |

nant. Thus, similar to what was found for guarding females of *Lasioglossum zephyrum* (Buckle and Greenberg 1981), familiarity was important in decision-making, but the females did not take into account the actual level of relatedness. However, even though kin recognition does not occur in this species, the greater motivation of the superseded female to guard for nestmates could be the result of kin selection, since by helping a nestmate a guard bee would gain more inclusive fitness than be leaving the nest.

Estimates of fitness benefits due to a particular decision are always plagued by the problem of not being able to measure the fitness of the same individual if it had made the opposite decision. In some cases, this problem can be solved experimentally by manipulating individuals into a decision other than that they actually made themselves (e.g. Daan et al. 1990). In this case, the females could not be manipulated into guarding after they had decided to leave. We decided not to make guarding females leave, because the probability that we would be able to measure their reproductive success after they had left the nest was low (we discovered the whereabouts of only 8 out of 80 leaving females). Therefore we have chosen to compare the fitness benefits of various options for unmanipulated individuals.

The situation in which the bees were studied was a semi-natural one, and this affects our findings to some extent. The reproductive output of the nests under study was probably higher than under natural conditions, since we protected the nests from ant raids, which we believe is the most important threat under natural conditions. Although guards may often succeed in preventing individual ants from entering the nest, persistent ant visitors may enter through cracks in the sides of the nests or they may profit from moments when the nest is unguarded. The mortality of carpenter bee brood due to ants has been documented by Gerling et al. (1983) and Watmough (1974).

The density of the nests was rather high, as was nesting availability in early spring, due to the new boards provided by the investigators. However, we do not think that these two factors invalidate our results, since comparable high densities can be found under natural circumstances, as a result of the patchy distribution and sudden appearance of suitable nesting materials (e.g. dead trees; Malyshev 1931; Hurd 1958; Cruden 1966; Velthuis pers. comm.).

However, this high concentration of nests may well lead to a relative increase in the number of females attempting to find a nest in our study area, compared to the number searching for nests outside our view. We therefore suppose that the true probability to find a new nest was close to our minimum estimate of the probability of gaining dominance elsewhere. This idea is supported by the fact that we found only very few nests outside the arcade.

There are two caveats in the estimates of relatedness by genealogy. Firstly, due to the high concentration of nests and the scarcity of nesting substrate in the surroundings, the population studied may have reached some level of inbreeding. However, we expect that some exchange between local populations occurs. This is based on our observations of male territories in very small and remote oases, which we did not consider suitable for maintaining a population. The effects of inbreeding would not affect our conclusions in a qualitative way.

Secondly, the estimated relatedness between nestmates was based on the assumption that females mate once. Behavioural observations indicate that females do not mate frequently, since during the intensive and long-lasting observations of male mating territories by several authors (Ben Mordechai et al. 1978; Gerling et al. 1983; Leys pers. comm.), mating was never observed in this species. In addition, several authors have suggested that females of *Xylocopa* species that have a so-called "dispersed lek mating system" mate once only (Watmough 1974; Alcock 1980; Marshall and Alcock 1981). However, no evidence has been provided yet.

Twelve superseded females remained guarding for an unrelated intruder. This result is in contrast with the observations of van der Blom and Velthuis (1988), who state that whenever an intruder takes over reproductive dominance, defeated females are always forced out of the nest. Since we have observed four times that superseded females were evicted from the nests (two times by a nestmate and two times by an intruder), we agree that in some cases females may have been evicted instead of leaving by their own choice. The four females that were forced to leave the nest had been reproductively active for a very short time (5.8 days). If such females are evicted because they may try to regain the dominant position, the usurper needs a way of comparing her own strength to the strength of the defeated female. Such a comparison could be made during the fight. This may also be true for the other females that are present in the nest during a take-over. In that case the number of nestmates removed reflects the condition of the nestmates involved, rather than the level of aggression of the superseding female.

We have shown that those females that remained as guards hardly constituted a threat to the position of the reproductive dominant. Reproductive dominants profit from having such guards (Hogendoorn and Velthuis 1993), mainly because the nest is then protected against pollen robbery. Therefore, the best option for the new reproductive dominant could be not to expel the defeated female.

The observation that the guard returned to the central part of the nest when the reproductive dominant was removed indicates that her guarding behaviour and, probably more important, the cessation of her reproductive activities, are at least in part the result of manipulation by the reproductive dominant. The high percentage of guards that died after the removal of the reproductive dominant, and the low percentage of former guards that managed to lay an egg, suggest that many former guard bees are unfit for reproductive activities. A weak point in this experiment was that the guard bees used had been guarding for a comparatively long time. The significant difference in the time spent guarding by females that started to collect pollen and females that did not suggests that the result of the experiment was affected

by the age of the guards. Therefore, the possibility that younger defeated females remain to guard as hopeful reproductives remains open. Since the superseded females remain as guards more frequently when nestmates take over than when intruders take over, we conclude that if the probability of regaining reproductive dominance plays a role in the decision to stay, it is not the only factor of importance.

The environmental constraints considered did not affect the decision to remain as a guard. This is not surprising, as far as nest shortage is concerned: we have never seen defeated females searching for a nest and returning to their original nest after failing to find one. Therefore, the superseded female probably has no means of assessing nest availability before she takes the decision to stay or leave. However, the strategy of staying as a guard may be selected for during periods of nest shortage, and the evolution of this trait therefore does not require the individual females to have any knowledge of the severity of competition for nests.

In addition, we suppose that pollen is in short supply throughout the season, except, perhaps, during the blooming period of *Acacia* and *Tamarix* species in mid summer. However, during the hot summer months foraging time is limited to early morning hours, due to the high ambient temperatures (Gerling et al. 1983; Hogendoorn and Velthuis 1993). The continuous shortage of pollen and the presumed lack of knowledge about nest shortage could explain the lack of correlation between those environmental constraints and the defeated females' frequency of staying. However, although the degree of ecological constraint plays no important role in influencing the decision to remain as a guard, it has probably been an important factor in selection for guarding behaviour.

The finding that a superseded female stayed more often while her own young were present after take-over is difficult to interpret. We offer two possible explanations, neither of which could be tested. In the first place, staying on by a defeated female may be favoured due to the probability that, later on, one of her own daughters will become the egg layer. This, indeed happened in 4 out of the 12 cases in which the defeated females decided to stay with an intruder. However, these data are far too few to enable an analysis of the costs and benefits. In the second place, a defeated female may have a difficulty in recognizing intruders at a time when she has not yet learned to recognize her young nestmates. In that case, we would expect nests containing young to be taken over by intruders more frequently. This was indeed what happened: nests consisting of a mother and young offspring were usurped significantly more often than solitary nests. However, comparison of social nests containing young and without young did not yield the same result (unpublished data).

We suggest that the superseded females use the following rules of thumb in their decision to stay or leave:

1. If a nestmate takes over reproductive dominance, make the best of this bad situation by staying as a guard, unless you had only just become reproductive dominant yourself and your reproductive value is still high.

2. If an intruder takes over reproductive dominance, leave, unless you are very old and your chances of becoming reproductively active elsewhere are almost nil. If you stay, you may have the luck that the new dominant female meets with an accident (e.g. will be eaten by a bee eater, cf. Stark 1992), and you may then be able to regain reproductive dominance.

These simple rules are strikingly similar to the ones Rabenold (1985, 1990) suggested to explain the evolution and maintenance of helping behaviour in stripe-back wrens. He also found that at the proximate level, the decision to help was neither influenced by the degree of relatedness nor by ecological constraints.

The conclusions do not pertain directly to the route followed in the evolution of eusociality in Hymenoptera, where daughters (workers) usually give aid to their mother (the queen). Guarding by daughters has been observed in several species of *Xylocopa* (Gerling and Hermann 1978; Gerling 1983; Gerlin et al. 1983; Stark et al. 1990). In *X. pubescens*, young females may perform guard duties, but they usually guard for a limited period of time (approximately 10 days), prior to an attempt to take over reproductive dominance from their mother. For *X. sulcatipes*, Stark (1992) found that, in terms of inclusive fitness, guarding daughters gained over solitary females during one year but not during the other year of his analysis. However, it was not clear whether the daughters' motivation to guard was influenced by this potential gain or whether it was based on the probability of inheriting the nest. With regard to *X. pubescens*, the role of young guards in protecting the nest and its contents, as well as their reasons for guarding for some days prior to dispersal or take-over, are still under investigation.

Even though the conclusions do not bear upon the matrifilial division of labour found in eusocial species they demonstrate what factors may contribute to the evolution and maintenance of helping behaviour in primitively social bee societies. These undoubtedly preceded the more highly organized, specialized forms of social organization, and set the stage for their evolution.

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