When to bee social: interactions among environmental constraints, incentives, guarding, and relatedness in a facultatively social carpenter bee

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In the facultatively social carpenter bee, *Xylocopa pubescens*, foundresses usually establish nests solitarily. However, nests may become social if a second foundress (referred to as alpha) successfully usurps the nest, with the original foundress (referred to as beta) remaining as a guard. Reproductive skew theory predicts that beta foundresses should remain as helpers only if alpha usurpers allow them a share of reproduction. Because alpha females destroy much of beta's brood and beta females do not lay eggs after takeovers, studies have concluded that usurpers offer no staying incentives or concessions in return for helping behavior. This conclusion is paradoxical, and we suggest that by refraining from destroying all of beta's brood, alpha females do indeed offer concessions to beta females. We constructed a model to examine the conditions under which social nesting is favored by both alpha and beta females. Female preference for social versus solitary nesting is proportional to expected fitness in either setting and is affected by current environmental conditions, the value of guarding behavior in protecting brood from pollen robbery, the size of the concession offered by alpha, and the degree of genetic relatedness between the foundresses. Our model shows that at a minimum, establishing sociality after unrelated usurpations always requires a concession, whereas in related usurpations, a concession is not always required. Generally, agreement between alpha and beta is difficult because alpha requires a much higher premium in pollen robbery protection than beta in order for sociality to be advantageous. Alpha females prefer social nesting only under the most severe environmental conditions because usually they gain less by the presence of a guard than by replacing beta brood with their own. In contrast, beta females always strongly prefer social nesting because the chances of successful renesting elsewhere are low and rarely outweigh the advantages of guarding their own brood that survive usurpation. Effects of relatedness between foundresses on preference for social nesting are nonintuitive: first, alpha's preference increases with relatedness, whereas beta's preference declines, and second, unrelated beta females prefer sociality more strongly than related ones. This is because replacement of beta's offspring with related alpha offspring partially compensates her for the loss of her own brood, even should she leave the nest. *Key words:* carpenter bees, colony founding, relatedness, sociality, *Xylocopa pubescens*. [*Behav Ecol* 14:417–424 (2003)]

I n facultatively social bees, some nests remain solitary, while others become social. Facultative sociality offers special opportunities for investigating the extrinsic (e.g., environmental) and intrinsic (e.g., genetic) factors that structure opportunities for social interactions among nest mates and thus ultimately influence the expression of helping behavior (Wcislo, 1997). In many, if not all, facultatively social bees, ecological factors such as competition for nesting sites and predation seem to promote social nesting, although genetic differences may also underlie social variation (Packer, 1990; Plateaux-Quénu and Packer, 1998; Schwarz et al., 1997, 1998; Soucy, 2002).

In xylocopine carpenter bees, sociality arises when a nest foundress loses dominance to a usurper, or when multiple nest foundresses establish dominance relationships leading to division of labor (Michener, 1974, 1988; Stark et al., 1990). In allodapine bees, societies form among whatever adult females are found within a nest, and therefore colonies vary widely, from solitary to semisocial or eusocial (Michener, 1974). The most detailed studies of facultative sociality in bees have focused on the large carpenter bee *Xylocopa pubescens*. In spring, single *X. pubescens* foundresses establish solitary nests and raise their brood alone (Gerling et al., 1989). Nests become social if a second foundress successfully usurps the nest with the original foundress remaining in the nest as a nonreproductive guard (if she leaves, the nest remains solitary). Nest usurpation is likely a response to difficult environmental conditions, since both nesting substrate and pollen availability seem to be limiting for many *Xylocopa* populations (Gerling et al., 1983, 1989).

Recently, Hogendoorn and Velthuis (1999) reviewed patterns of task allocation and reproductive skew in *X. pubescens*. As they pointed out, when social colonies are established after usurpation, the usurper lays all subsequent eggs. The defeated female acts as a guard but never resumes oviposition (except in rare cases where she regains her position as dominant). Yet reproductive skew theory suggests that in return for a subordinate's cooperation, the dominant should allow her some portion of future group reproduction (Reeve and Ratnieks, 1993). Because this does not happen, Hogendoorn and Velthuis (1999) suggested that neither peace nor staying incentives are offered in *X. pubescens* nest usurpations. This conclusion is paradoxical: why should defeated foundresses remain in the nest as nonreproductive guards, especially in cases where they are unrelated to the usurper?

We suggest that defeated foundresses do receive a staying incentive: a concession in the form of brood not killed by the

usurper at the time of nest takeover. We also suggest that carpenter bee nests should become social only when both usurper and defeated foundress can expect higher fitness in the social setting. We constructed a model to investigate how environmental constraints on pollen and nest site availability, relatedness between foundresses, the benefits of pollen guarding, and the magnitude of concessions interact to determine female fitness and the establishment of social nests.

Summary of *Xylocopa pubescens* social behavior

This summary and the analyses to follow are based on extensive detailed fieldwork and behavioral observations carried out by Hogendoorn and colleagues (Hogendoorn, 1991, 1996; Hogendoorn and Leys, 1993; Hogendoorn and Velthuis, 1993, 1995, 1999). Solitary foundresses establish nests in spring and provision each egg with all the pollen that a larva will consume before pupating. Pollen provisions are also supplied for newly emerged adult brood. In spring, there is relatively little competition for either nest sites or pollen, so environmental constraints appear to be mild (Gerling et al., 1989). As summer approaches, pollen availability declines and nest densities increase, sharpening competition among adult females for both these resources; as a result, rates of nest usurpation increase. Nest usurpations involve violent, noisy fights between resident and usurper females (Velthuis and Gerling, 1983). If a usurper is successful, she becomes the new dominant egg-layer in the nest, while the defeated foundress may either leave to found a new nest elsewhere or remain in the nest as a nonreproductive guard.

A usurper may be related to the resident, but usually she is an unrelated stranger. In *X. pubescens*, females can distinguish nest mates (which are mostly kin) from non-nest mates (mostly non-kin) (Hogendoorn, 1996); in effect then, foundresses can distinguish kin from non-kin. All usurpers destroy some of the defeated female's developing brood, but related usurpers apparently preferentially destroy young larvae whose brood cells contain pollen, whereas unrelated usurpers destroy brood randomly and also destroy more brood (Hogendoorn, 1996). Related usurpers are most often nest mates of the resident and so know which brood cells contain pollen, which may explain the differences in brood destruction patterns. Presumably non-nest mates destroy more brood cells in order to find their pollen contents (Hogendoorn, 1996).

Defeated foundresses that remain in the nest, as well as newly emerged adult daughters, exhibit guarding behavior. Guarding has two benefits for a colony. First, the presence of an adult bee is an effective defense against pollen robbery by conspecifics and *X. sulcatipes* foragers (Hogendoorn and Velthuis, 1993). Pollen robbery increases as the season progresses, and a robbed nest loses both pollen and the vulnerable brood within the robbed cells. Second, the presence of a guard allows the dominant bee to take more extended foraging trips. There is little evidence that the presence of a guard enhances brood protection from predators or parasites (Hogendoorn and Leys, 1993; Hogendoorn and Velthuis, 1993), so protection from pollen robbery is the main advantage of guarding.

The model

We refer to the nest usurper and new dominant of the nest as the alpha female and the subordinate female whose nest is usurped as the beta female. A solitary nest is one occupied by a single foundress, whereas a social nest is occupied by both bees.

First, we consider the possible outcomes of a usurpation event. If the usurper loses the fight, then the resident female retains ownership of the nest, which remains solitary. When the usurper is victorious, various outcomes may ensue. Alpha may kill all of beta's brood or spare some fraction of them; the spared brood can be considered as a concession offered by alpha to beta for staying in the nest. Beta also has two possible options after a usurpation event: she can stay in the nest as a guard or leave and attempt to nest elsewhere. If alpha and beta are unrelated, then complete brood destruction by alpha reduces beta's fitness to zero, so beta should guard only when enough of her brood is spared. If alpha and beta are related, then beta may experience some inclusive fitness benefits by enhancing alpha's brood productivity, even if her own direct fitness is reduced to zero by destruction of her brood. Thus beta's decision to stay or leave should depend on whether she expects greater inclusive fitness by staying and guarding related brood (including her own if spared) or by leaving and renesting elsewhere. Alpha should allow beta to remain in the nest only if the benefits of having a guard outweigh the costs of giving her a concession because beta's surviving brood will consume pollen that would otherwise be consumed by alpha's brood.

For both alpha and beta, the expected costs and benefits of social versus solitary nesting are influenced by environmental constraints, which increase throughout the summer as supplies of nest sites and pollen diminish and as rising summer temperatures limit foraging time. For simplicity, we assume that variables that change from spring to summer do so linearly.

Variables used in the model

Variables used in the model, as well as their numerical values, are summarized in Table 1.

The average number of eggs laid per female (N) declines through the season. Because young and old brood are differentially affected by brood destruction (see below), we estimated the numbers of young brood with pollen in their cells versus older brood that have consumed their pollen provisions. Larvae consume their pollen by the age of 9 days, and brood emerge as teneral adults at 28 days, so for solitary (sol) nests before takeover we estimate the number of eggs and larvae as $9/28(N_{sol})$ and the number of prepupae and pupae as $19/28(N_{sol})$.

When alpha usurps a nest, she destroys all or a proportion of beta's brood, represented by D. A related value is C, which represents the concession given by alpha to beta, in terms of the number of beta's brood that survive the takeover. Thus,

$$C = (1 - D)N_{sol}.$$

The consequences of a concession for both alpha and beta may be related to the age of the brood spared because pollen unconsumed by young beta brood at the time of takeover can be reallocated to alpha's brood. In some calculations it is necessary to distinguish between young (C_y) and old (C_o) brood because the former still have pollen in their cells (see below).

The survival advantage (or disadvantage) of brood from social nests has two components. The first component is the premium in brood survival that can be attributed to the protection of a guard against pollen robbery, whether an intermittent guard in solitary nests or a permanent guard in social (soc) nests. The quantities $(1 - G_{soc})$ and $(1 - G_{sol})$ represent the proportions of cells lost due to pollen robbery in social and solitary nests, respectively. Thus the premium in brood survival due to pollen-robbery protection in social nests is the ratio

$$G = G_{soc}/G_{sol}.$$

Hogendoorn and Velthuis (1993) observed that the number of brood cells lost due to pollen robbery in solitary nests

Table 1

Model variables and their empirical estimates where applicable

Variable	Definition	Spring	Summer
		Season	
C	Number of brood spared		
D	Proportion of beta's brood destroyed		0.365 unrelated, 0.319 related
D_y	Proportion of eggs and larvae		0.537 unrelated, 0.561 related
D_o	Proportion of prepupae and pupae		0.236 unrelated, 0.139 related
$(1 - G_{soc})$	Brood mortality rate due to pollen robbery in social nests	0.980	0.992
$(1 - G_{sol})$	Brood mortality rate due to pollen robbery in solitary nests	0.957	0.801
G	G_{soc}/G_{sol}	1.02	1.24
N	Number of eggs laid		
N_{sol}	In solitary nests	5.192	2.456
N_{soc}	In social nests	4.107	2.944
m	Number of alpha brood lost as a result of concession		
Q	Preference for sociality		
q_T	Proportion of pollen remaining in brood cell		
R	Relative relatedness of a foundress to the other's brood, compared to her own brood		
S_{soc}	Brood survival rate in social nests	0.747	0.849
S_{sol}	Brood survival rate in solitary nests	0.880	0.787
S	S_{soc}/S_{sol}	0.85	1.08
W_A	Expected fitness of alpha after usurpation		
W_{Asol}	In solitary nests		
W_{Asoc}	In social nests		
W_B	Expected fitness of beta after usurpation		
Y	Probability of beta successfully renesting elsewhere	0.40	0.14

Sources: Hogendoorn, 1996; Hogendoorn and Velthuis, 1993.

varied from about 4% in spring to 20% in summer, whereas the rate in social nests dropped slightly from about 2% in spring to < 1% in summer.

The second component of brood survival is that unaffected by the presence of a guard; guards provide no protection against subsequent nest usurpers, bird damage to nests, infection by parasites, and other causes (Hogendoorn and Velthuis, 1993). The quantities $(1 - S_{soc})$ and $(1 - S_{sol})$ represent the brood mortality due to such causes in social and solitary nests, respectively. The survival advantage or disadvantage of brood in social nests is the ratio

$$S = S_{soc}/S_{sol}.$$

When alpha does not destroy all of beta's brood, she incurs a cost that depends on the age composition of the brood. We call this cost m. The first component of m is the number of eggs that alpha could have provisioned with pollen reallocated from destroyed beta larvae with unconsumed pollen. The variable q_T is the fraction of pollen left in brood cells of average age T, and the quantity ($q_T C_y$) represents the cost to alpha of sparing young brood with pollen. Hogendoorn (1996) found that related usurpers preferentially destroy young brood: in these takeovers by related usurpers, the average age of beta's brood was 6.0 days ($n = 80$; recalculated from Hogendoorn, 1996), but the average age of the destroyed brood was only 5.1 days. In this case, $T = 5.1$ days and $qT = 50\%$. Unrelated usurpers destroy brood randomly (Hogendoorn, 1996), so we assume that the age of the destroyed brood is $T = 6.0$ days, and therefore $q_T = 29\%$. The second component of m is the cost to alpha of feeding beta's spared brood after they emerge as adults. Young adults remain in the nest for at least 8 days, during which they consume an amount of pollen about equal to that consumed as larvae (Van Der Blom and Velthuis, 1988), so adult offspring of beta will eventually consume pollen that otherwise would be consumed by alpha's adult brood (Hogen-

doorn, 1996). Therefore, the total number of brood lost by alpha because of a concession of size C is approximately

$$m = (q_T C_y) + \frac{1}{2}(C_o + C_y) = (q_T C_y) + \frac{1}{2}C.$$

One option for a usurped beta is to leave the nest and start a new one elsewhere. The probability that she will do so successfully (Y) is between 14 and 40% (Hogendoorn and Leys, 1993). Because nesting constraints increase from spring to summer, we use the maximum value as the probability of renesting in spring and the minimum value as the probability of renesting in summer and assume a linear decrease from spring to summer.

Fitness calculations

Female fitness after usurpations is the sum of personal fitness and inclusive fitness through the usurping bee. The direct component of fitness is the same in unrelated and related usurpations, while the inclusive fitness component is relevant only in related usurpations (it becomes zero in unrelated usurpations). For both alpha and beta, the inclusive fitness benefits of nesting socially must outweigh the inclusive fitness benefits of nesting solitarily, and the expected fitness value of their own brood must be weighed against the expected fitness value of the other foundress's brood. Relative relatedness (R) is the degree of relatedness of one foundress to the other's brood relative to her own brood. From alpha's point of view, the relative value of beta's brood is

$$R_A = r_{AB}/r_{AA}.$$

Likewise, from beta's point of view, the relative value of alpha's brood is

$$R_B = r_{BA}/r_{BB}.$$

When alpha and beta are symmetrically related to each other's brood, then R is simply the degree of relatedness between
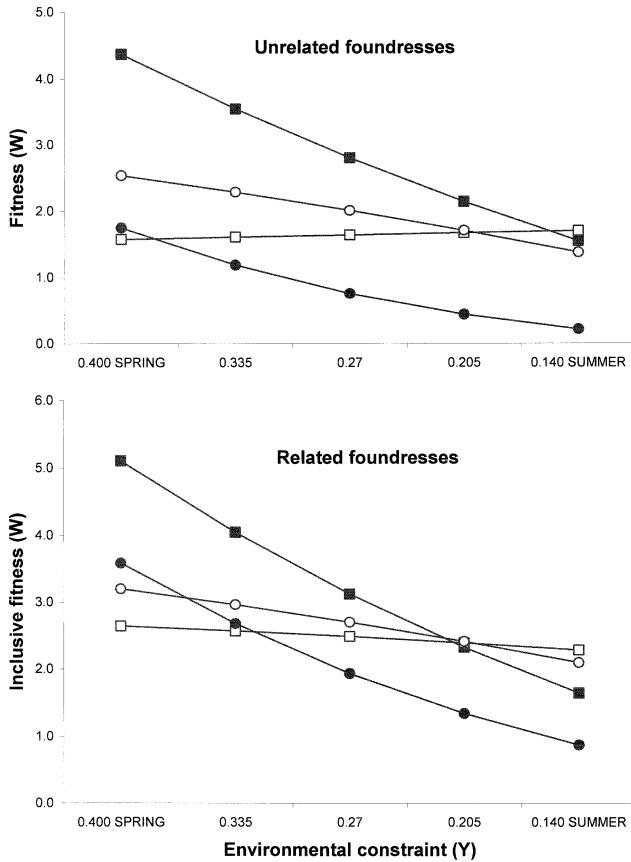
Figure 1
Fitness comparison for alpha (squares) and beta (circles) females. Solitary nests are represented by filled symbols and social nests by open symbols. The increasing harshness of environmental constraints from spring to summer is indicated in terms of Y, the probability that beta can successfully establish a new nest after nest usurpation. Top: unrelated usurpations; bottom: related usurpations ($R = 0.42$).

foundresses (for instance, a full sister's brood are worth three-quarters of a foundress's own brood). However, if relatedness between foundresses and brood is not symmetrical (for instance, if alpha is beta's daughter), or if beta is not the mother of all her brood (she may be their sister or even a previous usurper), then R must be calculated as above.

We define the fitness of each foundress under both solitary and social conditions. If beta leaves the nest, forcing alpha to nest alone, then the fitness (W) of alpha is

$$W_{Asol} = (S_{sol} G_{sol} N_{sol}) + R_A(S_{so} G_{sol} Y N_{sol}),$$

and the fitness of beta is

$$W_{Bsol} = (S_{sol} G_{sol} Y N_{sol}) + R_B(S_{sol} G_{sol} N_{sol}).$$

If beta remains in the nest, then the fitness of alpha is

$$W_{Asoc} = S_{soc} G_{soc}(N_{soc} - m) + R_A(S_{soc} G_{soc} C),$$

and the fitness of beta is

$$W_{Bsoc} = (S_{soc} G_{soc} C) + R_B[S_{soc} G_{soc}(N_{soc} - m)].$$

The magnitude of a female's preference for social versus solitary nesting should be proportional to the expected fitness in either setting, i.e.,
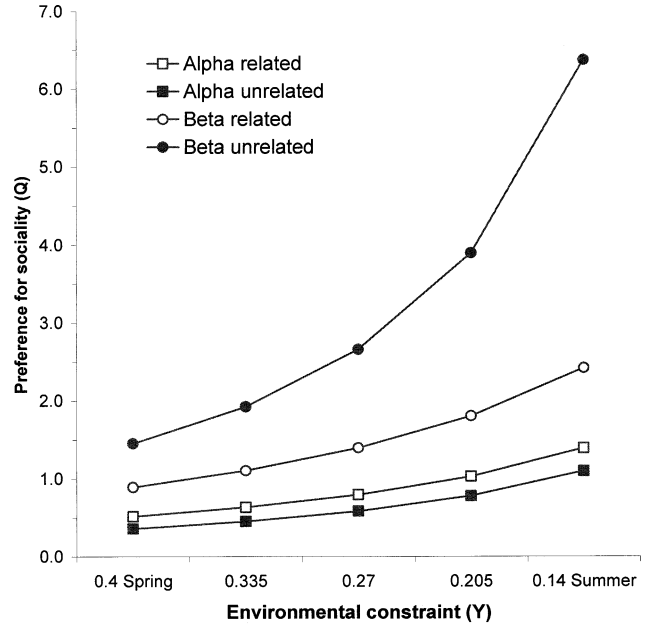
$$Q = W_{soc}/W_{sol}.$$

Figure 2
Change in preference for social nesting over the season after unrelated and related usurpations.

When $Q > 1$, a female prefers social nesting and when $Q < 1$, she prefers solitary nesting. For the alpha female

$$Q_A = W_{Asoc}/W_{Asol} = SG[(N_{soc} - m) + (R_A C)]/[N_{sol}(1 + R_A Y)],$$

whereas for the beta female

$$Q_B = W_{Bsoc}/W_{Bsol} = SG[C + R_B(N_{soc} - m)]/[N_{sol}(Y + R_B)].$$

RESULTS

Factors affecting bees' preference for sociality

In the *Xylocopa pubescens* population observed by Hogendoorn and colleagues, the reproductive success of both solitary and social bees declined from spring to summer as environmental constraints increased (Table 1). As a result, the fitness of alpha and beta females (as calculated by our model) declines, in both social and solitary settings. This means that the relative benefits of solitary and social nesting options are season dependent.

According to our model, the magnitude of bees' preference for social versus solitary nesting should be proportional to their expected fitness in either setting (Figures 1 and 2). Except under the most severe environmental conditions, alpha females almost always prefer to nest solitarily after usurping a nest. This is true whether or not they are related to beta and reflects the fact that they gain less by the presence of a guard than by killing more beta brood and replacing them with their own. Beta females strongly prefer social nesting because the chances of successfully establishing a new nest elsewhere are very low and rarely outweigh the advantages of guarding their brood that survive usurpation. Interestingly, the magnitude of beta's preference for social nesting is greater when she is unrelated to alpha than when she is related. This nonintuitive result occurs not so much because sociality is a better option for related beta females, but because solitary nesting is not as poor an option as it is for unrelated ones. In a related usurpation, alpha replaces beta's killed offspring with brood that are related to beta, providing some compensation for the loss of her own brood and raising
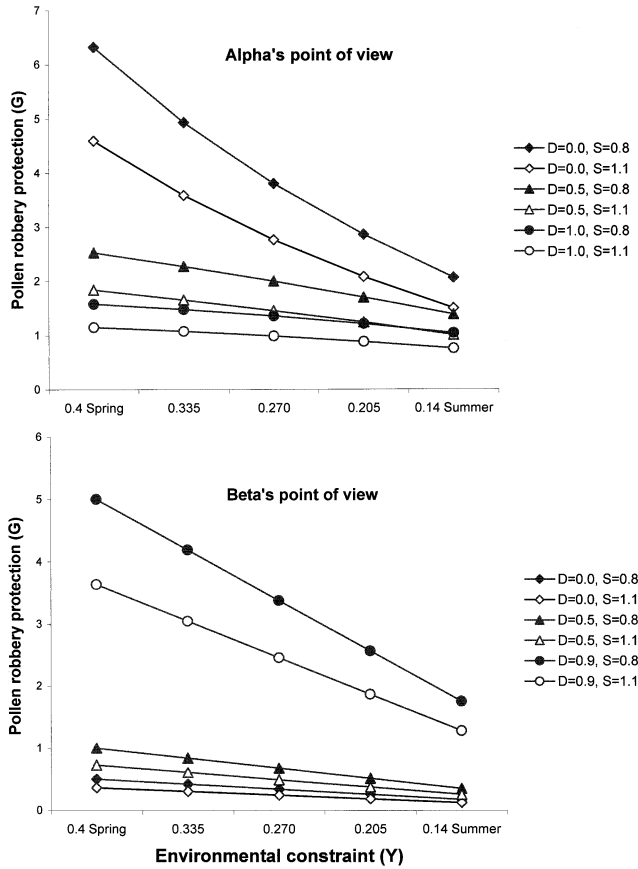
Figure 3
The minimum degree of pollen-robbery protection (G) required for foundresses to prefer social to solitary nesting as environmental constraints increase. Comparisons are for different levels of beta brood destruction (D) and minimum and maximum observed levels of brood survival in social nests (S). (A) From alpha's point of view; (B) from beta's point of view.

Figure 4
Effect of relatedness (R) on preference for social nesting in alpha (squares) and beta (circles) foundresses, based on average empirical estimates (Table 1). Degree of relatedness is indicated by increasing symbol size, starting with $R = 0.25, 0.50, 0.75,$ and 1.0 (alpha only).

Effects of relatedness between foundresses

The effect of relatedness (R) on preference for sociality (Q) is illustrated in Figure 4 (which is based on average empirical values from Table 1). Alpha's preference increases with R, whereas beta's preference declines. From alpha's point of view, the cost of a concession is offset by the fact that she is related to beta's offspring, so alpha gains more by allowing some of beta's offspring to survive than she would gain by killing them all and replacing them with fewer, younger brood. For beta, even if she does not remain in the nest, the destruction of her brood by alpha is partially offset by the fact that they will be replaced by related brood. This increases W_{Bsol}, which decreases her preference for sociality because $Q_B = W_{\text{Bsoc}}/W_{\text{Bsol}}$.

The above calculations are based on the assumption that relatedness between the two foundresses is symmetrical (both foundresses have the same degree of relatedness to each other's brood). However, in matrifilial relationships, relatedness is not symmetrical (Reeve, 1995). When beta is alpha's mother, then beta's offspring are worth twice as much to beta as are alpha's offspring ($R_B = 0.5$), but from alpha's point of view, beta's offspring and her own are worth the same ($R_A = 1$, assuming beta has mated only once and assuming a 1:1 sex ratio among her brood). Figure 4 indicates that alpha's preference for social nesting in matrifilial relationships ($R_A = 1$) is only slightly higher than her preference for social nesting with full sisters ($R_A = 0.75$) but considerably higher than her preference for half sisters ($R_A = 0.5$) or for the average level of relatedness observed among foundresses in the field ($R_A = 0.42$; Hogendoorn and Velthuis, 1999).

Conditions for agreement between alpha and beta

In *X. pubescens*, social nests have about a 20% advantage in brood survival due to guarding (i.e., $G = 1.2$, Table 1), so under the constraint that $G < 2.0$, we investigated the levels of brood destruction at which solitary and social nesting are equally valuable for both alpha and beta (i.e., $Q_A = 1$ and $Q_B = 1$). For alpha, this represents the minimum level of brood destruction that she must carry out during supersedure, and for beta this represents the maximum level of brood destruction which she can tolerate. Several important patterns are revealed by the analysis in Figure 5. First, under severe environmental conditions, alpha's minimum D decreases and

beta's inclusive fitness even if she leaves (compare the solitary fitness of beta in Figure 1). No such compensation occurs in an unrelated usurpation.

Figures 1 and 2 suggest that alpha and beta often disagree about whether beta should remain in the nest as a guard. Under what conditions will they agree? The factors most susceptible to behavioral manipulation are the proportion of beta brood killed (D), which is controlled by alpha, and the premium in brood survival in social nests due to pollen robbery protection by beta (G). Another important element, but one less obviously influenced by either bee's behavior, is the premium in brood survival not influenced by guarding (S). Our model suggests that alpha females should kill as many beta brood as possible, so for alpha we calculate the minimum value of D that makes social nesting preferable (at $Q_A = 1$). Beta females should prefer to have as few brood killed as possible, so for beta we calculate the maximum value of D that still permits social nesting ($Q_B = 1$). In both cases, the acceptable level of brood destruction (D) depends on whether social nests have higher brood survival, implying possible tradeoffs between D and G or S (Figure 3). For instance, the premium in pollen robbery protection (G) required to make social nesting preferable is lower when brood survival is higher (Figure 3). Moreover, G decreases as environmental constraints increase (Figure 3).
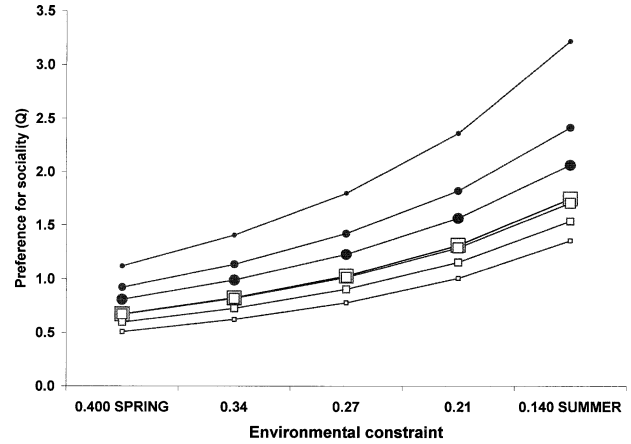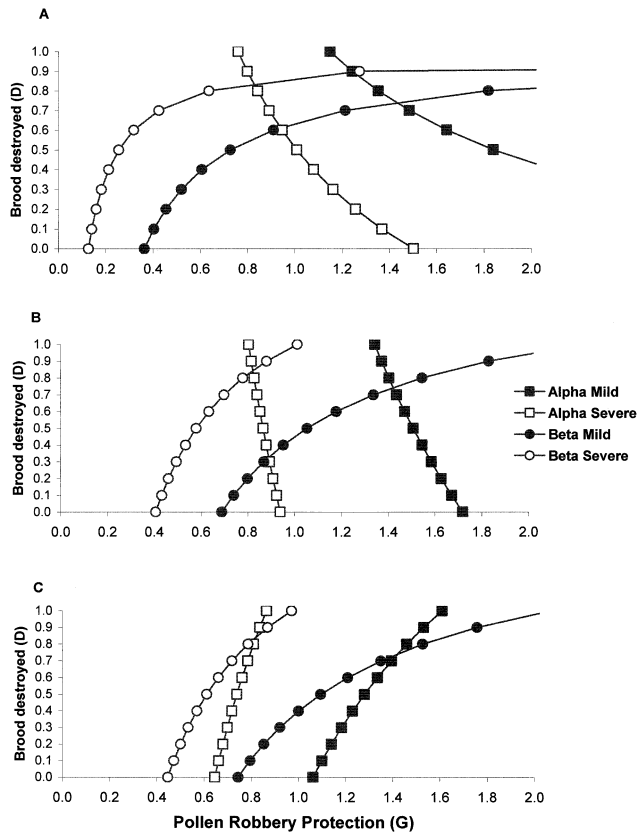
Figure 5
Levels of brood destruction (D) tolerated in social nests for realistic levels of pollen robbery protection (G, about 1.0–1.2) and assuming $S = 1.1$ in order to show the lower limit of G. For alpha, D represents the minimum acceptable value, while for beta, D represents the maximum value. Mild conditions refer to spring when the probability that beta can nest elsewhere is high ($Y = 0.40$); severe conditions refer to summer ($Y = 0.14$). (A) Unrelated usurpations; (B) symmetrically related usurpations ($R = 0.42$); (C) matrifilial usurpations.

beta's maximum D increases, indicating that concessions should be larger and sociality should be more likely under harsher conditions. Second, alpha requires a much higher premium in pollen robbery protection (G) than beta in order for sociality to be advantageous. Third, in return for a given level of G, alpha can offer a greater concession in related than unrelated usurpations, whereas unrelated betas require higher levels of concession than related betas. At a minimum, establishing sociality in unrelated usurpations always requires a concession (i.e., $C > 0$), whereas in related usurpations, a concession is not always required. Fourth, agreement between alpha and beta (indicated on Figure 5 as regions below the line for beta and above the line for alpha) is unlikely during mild conditions for realistic values of pollen robbery protection (say, $G \leq 1.2$ to 1.4). Matrifilial associations are an exception to this pattern and are favored by both foundresses even under mild conditions (Figure 5C).

DISCUSSION

When Hogendoorn and Velthuis (1999) reviewed the evidence for reproductive skew in *X. pubescens* and other mass provisioning carpenter bees, they drew three important conclusions. First, increasing environmental constraint leads to higher reproductive skew in social nests. Second, the degree of skew is not clearly affected by the degree of

relatedness among the foundresses. Third, usurper females offer neither peace nor staying incentives to defeated foundresses, which the authors suggested was either a contradiction of optimal skew theory or showed that guarding behavior has been selected in the context of young subordinate females, weak environmental constraints, and low group benefits. Their first conclusion is in perfect agreement with our results, but the second and third are not. However, the contradiction is more apparent than real and hinges on the currency in which staying incentives are usually measured (Reeve and Keller, 2001).

Two behaviors observed in *X. pubescens* usurpations only make sense if alpha spare brood as a concession to beta: first, beta females sometimes remain as guards in nests usurped by unrelated bees, even though they can distinguish non-nest mates, and second, alpha females refrain from destroying all of beta's brood, although there is no risk involved in killing them. Therefore, we modified the definition of incentives to include the proportion of group "parental" investment obtained by the subordinate. In the case of *X. pubescens*, this extension is necessary because, although beta females may have laid their eggs in a solitary setting, they develop into brood that consume provisions that could otherwise be invested in alpha's offspring. More generally, this extension of the definition also fits better with parental investment theory (Trivers, 1972). Hogendoorn and Velthuis's (1999) analyses were based on a strict definition of incentives or concessions as that proportion of group reproduction obtained by the subordinate; technically, because beta lays no eggs after the group is established, she does not participate in group reproduction and cannot have received a concession from alpha.

If concessions are defined in terms of the proportion of colony investment in offspring that is obtained by the subordinate, then perhaps reproductive skew should also be defined this way. With the strict definition of reproductive skew as the distribution of reproduction among adults in the group, skew is certainly complete in social *X. pubescens* nests because the dominant bee lays all the eggs. However, if investment by the group were used for the calculation, then skew would still strongly favor alpha but would not be complete. This would accord with our conclusion that, for any given level of environmental constraint, the concession required by an unrelated beta is higher (i.e., skew is lower) than that required by a related beta (i.e., skew is higher). Extension of reproductive skew models to include investment is analogous to calculating optimal sex ratios in terms of investment sex ratios rather than numeric sex ratios (Trivers and Hare, 1976).

In *X. pubescens* nesting in the Negev Desert (Gerling et al., 1989), nesting success and the probability of renesting after usurpation both decline as environmental constraints increase throughout the breeding season. Insufficient information was available for us to directly consider factors such as nesting site and pollen availability or temperature limitations on foraging time (Gerling et al., 1983, 1989; Hogendoorn and Leys, 1993), but these effects are indirectly considered in the model insofar as they influence brood sizes (N) and the probability of successful renesting (Y). We also did not explicitly consider the effect of beta's age, although young beta females are less likely to remain in the nest than old beta females (Hogendoorn and Leys, 1993). In effect, we have averaged the ages of beta females by using an overall estimate of renesting success for different points in time during the breeding season. However, after usurpation young betas are more likely to successfully establish new nests than older females; in effect younger beta females experience a higher value of Y.

Both alpha and beta are predicted to increase their preference for social nesting from spring to summer, but beta's preference is always expected to be stronger. The two bees do not always agree because alphas prefer solitary nesting until quite late in the season when environmental constraints become severe, whereas betas usually prefer sociality. Agreement between theory and behavior is found in the observation that alpha females sometimes evict beta females from the nest after a takeover (Gerling et al., 1983, 1989; Hogendoorn and Leys, 1993; Van Der Blom and Velthuis, 1988). It seems likely that one reason for disagreement between alpha and beta is that alpha has just successfully usurped a nest, whereas beta is faced with the prospect of having to establish or usurp a new one.

In related usurpations, both alpha and beta prefer solitary nesting under mild constraint in spring, then beta switches to a preference for sociality quite early in the season, and alpha switches in mid-summer. Thus agreement between alpha and beta for sociality occurs earlier in the season at lower levels of constraint when they are related, so related usurpations should be observed earlier and more often than unrelated usurpations. Opportunities for related usurpations do not occur until later in the season, when the earliest brood have reached adulthood, and yet usurpations by nest mates appear to be more common than unrelated usurpations (Hogendoorn and Leys, 1993). Perhaps this is because in matrifilial usurpations alpha and beta are often likely to agree that sociality is preferable to solitary nesting (Figure 5). This would also explain the empirical observation that matrifilial usurpations are less likely to result in the departure of the beta female (Hogendoorn and Leys, 1993).

In these analyses we mainly considered situations in which guards obtain the average concession and provide average pollen robbery protection. We considered how large a concession is required for sociality when G (the guarding advantage) has realistic values. Observed values of G range from 1 to 1.2. Under mild conditions, the minimum level of G required by alpha is almost always higher than can be provided by beta, which is why alpha strongly prefers to nest solitarily in spring. Under harsh conditions, however, alpha can benefit from guarding by beta. From beta's point of view, the situation is different. First of all, if she receives no concession in an unrelated usurpation, no amount of guarding can compensate; the minimum concession required is at least 10% of her brood (Figure 4). Only under the harshest conditions and when the usurper is closely related should beta ever tolerate the complete destruction of her brood because then she can still raise her inclusive fitness by protecting alpha's brood from pollen robbers.

A somewhat counterintuitive result is that the degree of relatedness between alpha and beta has opposite effects on their preference for social nesting: for alpha, the effect is positive, whereas for beta the effect is negative. How does this happen? After symmetrically related usurpations, the inclusive fitness of either bee is higher when relatedness is higher, in either the social or the solitary situation. However, for alpha, the increment in social fitness is greater than the increment in solitary fitness, whereas the opposite is true for beta. In other words, renesting solitarily is relatively more attractive for beta if her original nest is usurped by a closely related nest mate (who is often a daughter) than if it is usurped by an unrelated stranger because beta is assured some fitness through her related nest mate, even if the remainder of her brood are destroyed. On the other hand, the fitness cost to alpha of a concession to beta is less in related than in unrelated usurpations because she is related to beta's brood and does not lose as much by sparing them. From alpha's point of view, there is little difference between matrifilial and full-sister

nests, which perhaps is one reason that nest mate discrimination has evolved in this bee (indirectly allowing discrimination of kin vs. non-kin) but direct kin discrimination has not (Hogendoorn, 1996; Hogendoorn and Leys, 1993). A point that would have to be clarified empirically is whether a beta's decision to leave or stay in a usurped nest is more affected by her preference for sociality (which is inversely correlated with relatedness to the usurper) or by whether or not she and alpha are in agreement.

Conclusions

Our analyses suggest that in *X. pubescens*, and probably in other socially variable species such as *X. sulcatipes* (Stark, 1992), subordinate females prefer sociality more than do dominants. This is in fascinating contrast with eusocial colony organization in other insects, such as halictine bees in which queens actively coerce and maintain worker engagement in activities such as foraging (Michener, 1974), hinting that queens have higher preferences for sociality than do workers. The major difference between xylocopine sociality and that of other bees is not in division of reproduction but in division of risk. In social nests of *Xylocopa*, the dominant monopolizes oviposition, but she also takes on the high risks of foraging for her own and her subordinate's offspring. This is very different from eusocial societies in which workers not only lay few or no eggs, but also carry out risky colony activities. A possible consequence of such a division of risk is that a defeated foundress might regain her nest if the usurper dies. Hogendoorn and Leys (1993) calculated the probability of this happening as only about 6%, after an average of 25 days spent as a guard. Given seasonal declines in brood sizes and increasing probability of usurpation, re-inheriting the nest is less likely as an explanation for sociality than the fitness payoffs suggested in our model.

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