

Review article

Task allocation and reproductive skew in social mass provisioning carpenter bees in relation to age and size

Dedicated to the late Professor S. F. Sakagami

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Summary

The mass provisioning carpenter bees comprise two tribes, the Xylocopini and the Ceratinini. Although social nesting occurs in both tribes, no morphological castes have evolved and females are totipotent, which makes the tribe as a whole highly suitable to test predictions of reproductive skew models. We review current information for the two tribes with respect to reproductive competition and reproductive skew and then investigate whether the observed skew fits with predictions from optimal skew theory. Social nests of *Xylocopa* species include a non-foraging guard and a foraging egg layer who completely dominates reproduction. Reproductive dominance is settled by aggression, and the probability of winning this fight is influenced by both age and size. In *Ceratina* species, task allocation is also very clear: one female guards the nest, while the other female(s) forage(s). Although the guard is usually the first to produce an egg, her eggs are frequently replaced by those of the forager, and skew is incomplete.

Using comparisons between species and genera the impact of ecological constraints on solitary nesting, relative group productivity and relatedness on reproductive partitioning between dominants and subordinates are investigated in a qualitative way. In support of the optimal skew model, strong constraints on solitary nesting coincided with strong skew. However, the predicted effects of relatedness and group productivity on skew were not found. Furthermore, no support was found for the predictions of the optimal skew model that high skew coincides with frequent aggressive testing and risky task performance by subordinates.

Key words: Reproductive competition, *Xylocopa*, *Ceratina*, oophagy.

Introduction

One of the key features that differentiate animal societies is the way reproduction is apportioned among group members. Allocation of reproduction by group members is measured as reproductive skew, which varies between zero, when all reproduction is shared equally, and one, when a single individual completely dominates reproduction (Reeve and Keller, 1995, Pamilo and Crozier, 1996). Recent models of the evolution of reproductive skew (Vehrencamp, 1983; Reeve, 1991; Reeve and Ratnieks, 1993; Keller and Reeve, 1994; Reeve and Keller, 1995) address the conditions under which reproduction becomes either monopolized or shared. This so called “optimal skew” (Reeve et al., 1998) or “concession” (Clutton-Brock, 1998) model assumes that dominants can completely control both whether, and how much the subordinate reproduces in the group. The optimal skew model makes use of four parameters to specify the amount of reproductive sharing to be expected: (1) the expected reproductive success of the subordinate should it leave the group and remain alone; (2) the benefit in reproductive output of the group should the subordinate remain in the nest; (3) the relative asymmetry in physical dominance (or fighting ability) between potential breeders, and (4) the genetic relatedness between potential breeders. Following the model, high skew is expected under high constraints for solitary nesting, high relative group productivity, high relatedness and large differences in fighting ability.

The degree of reproductive skew has been predicted to influence key societal attributes such as the frequency and intensity of dominance interaction in a group and the willingness of subordinates to perform risky or energetically costly tasks (Reeve and Ratnieks, 1993; Keller and Reeve, 1994). Under high skew, a high payoff is expected to the sub-

ordinate for aggressively testing the quality of the dominant. If the subordinate has a very low expected personal reproduction, in the social condition as well as in the solitary situation, it should be particularly willing to perform costly tasks that increase group output. Her only hope is to increase her indirect fitness as much as she can.

In this paper, we review the current information about reproductive skew and task allocation for representatives of two tribes of mass provisioning carpenter bees (tribes Xylocopini and Ceratinini, within the subfamily of the Xylocopinae). It will be investigated whether the observed differences between the two tribes and between species within tribes are consistent with predictions deriving from reproductive skew theory. Furthermore, we will discuss whether the basic assumption of the optimal skew model, that the dominant has complete control over reproduction, is likely to apply to the mass provisioning carpenter bees.

Mass provisioning carpenter bees are a very suitable group for testing reproductive skew theory, because colonies are small and frequently consist of only two females, all females are totipotent and there is within-species variation in size, age and relatedness of nestmates. In addition, many species occur in a relatively broad range of climatic conditions, and therefore ecological constraints to solitary nesting, a key parameter of skew models, are likely to vary between and within species.

Recently, more detailed information has become available about task allocation and social organisation of the multivoltine ceratinine bee *Ceratinidia okinawana* (Maeta and Sakagami, 1995; Sakagami and Maeta, 1995) and of two multivoltine xylocopine species: *Xylocopa sulcatipes* and *X. pubescens* (van der Blom and Velthuis, 1989; Stark et al., 1990; Stark, 1992 a, b; Hogendoorn and Leys, 1993; Hogendoorn and Velthuis, 1993, 1995; Hogendoorn, 1996). This information does not only permit detailed comparisons of the social organisation in the two mass provisioning tribes, Ceratinini and Xylocopini, as was performed by Maeta and Sakagami (1995), but also allows comparison of the two groups with respect to reproductive skew. If the concession model applies to these societies, differences in skew between the two groups should be a consequence of differences in the parameter values that pertain to skew.

In the following, we will review social organisation and reproductive skew in Ceratinini and Xylocopini for those species that have been studied in sufficient detail. Using a comparative approach at different levels (i.e., by comparison of nests within species, species within tribes, and between tribes), we will then address whether the observed patterns are consistent with the following predictions derived from skew theory (Reeve and Ratnieks, 1993; Keller and Reeve, 1994; Reeve and Keller, 1995): (1) The proportion of reproduction by the subordinate is lower when constraints on solitary breeding are high; (2) The proportion of reproduction by the subordinate decreases with increasing group productivity relative to solitary productivity; (3) The proportion of reproduction by the subordinate decreases with increasing relatedness between a subordinate and the dominant; (4) High skew coincides with performance of costly tasks by

subordinates; (5) High skew coincides with high levels of aggressive testing of the dominant by subordinates.

General biology

The subfamily Xylocopinae contains four tribes: the Xylocopini, Manueliini, Allodapini and Ceratinini (Daly et al., 1987; Sakagami and Michener, 1987). In all species of Ceratinini and Xylocopini that have been studied, generations overlap in a sense that the mother is still present in the nest when the first adult offspring eclose. Carpenter bees of the speciose genus *Xylocopa* are largely restricted to tropical and subtropical areas (Hurd and Moure, 1963), while the distribution of ceratinine bees overlaps with that of *Xylocopa*, but ceratinine bees are also found in more temperate regions (Michener, 1979).

Reviews exist of the nesting and social behaviour of Xylocopini (Gerling et al., 1989) Allodapini (Schwarz et al., 1997; Schwarz et al., 1998), and Ceratinini (Sakagami and Maeta, 1995). Furthermore Michener (1990) compared social behaviour within the subfamily, while Sakagami and Laroca (1971), and Sakagami and Maeta (1995) compared nesting behaviour and sociality of Xylocopini and Ceratinini. We will therefore limit ourselves to the attributes pertaining to reproductive skew.

Nest structure

All ceratinine and several xylocopine species construct linear nests that consist of a single tunnel either by using pre-existing cavities, or by digging into dead stems and branches of plants and trees. Other xylocopine species make branched nests that contain several, usually relatively short, tunnels or galleries in dead branches and tree trunks (Sakagami and Laroca, 1971; Michener 1990). Brood is reared in individual cells and each cell is provisioned with a "bee bread" that is kneaded out of pollen and nectar on top of which an exceptionally large egg (Iwata and Sakagami, 1966) is laid ("mass provisioning"). The structure of the nest (linear, with one tunnel or branched) bears upon the social organisation (Velthuis, 1987; Sakagami and Maeta, 1995), since in linear nests only one brood cell can be provisioned at a time, whereas in branched nests cells can be provisioned simultaneously in more than one gallery.

Cooperative nesting

Reports of communal nesting in the two tribes are relatively rare, and are restricted to *Xylocopa* species that have branched nests. In three such species, Camillo and Garófalo (1989) observed long periods when more than one pollen foraging female with activated ovaries (i.e., ovaries that contained large oocytes) remained in the nest. Communal nesting has further been suggested by Watmough (1974), Sakagami and Laroca (1971), Gerling et al. (1983), Steen (pers. comm.), on the basis of equal ovary size of the two females and the presence of multiple galleries containing cells under construction.

Social nesting has been described for several species (Gerling et al., 1989; Michener, 1990). Sakagami and Maeta (1987, 1989, 1995) differentiate four types of sociality in xylocopine nests: Social organisation can arise between sisters or less related females of the same generation either through remaining in the nest (“semisocial”) or through joining (“quasisocial”), or between females of different generations. In the latter type of nests, either the older or the younger female is the main egg layer, and such groups have been called respectively “eusocial” or “reversed eusocial” (Sakagami and Maeta, 1989, 1995). For the remainder of this paper, we will adopt this terminology to indicate social nesting between females of different ages and relatedness. Below, we briefly review differences between the tribes with respect to reproductive competition, skew in relation to age and size, performance of risky tasks and aggression.

Reproductive competition and egg replacement

In both tribes, competition over reproductive opportunities has been observed in multi-female nests. However, the form of the competition differs between tribes.

1. *Xylocopa*. In social *Xylocopa* nests, task differentiation occurs during a period of intense competition for egg laying. Reproductive competition has been studied in some detail for *X. sulcatipes* (Stark et al., 1990) and *X. pubescens* (Hogendoorn and Velthuis, 1995; Hogendoorn, 1996), which have been studied in the Negev desert in Israel. Interactions between individually marked bees inside the nest were monitored using an X-ray technique described by Gerling et al. (1983), and by using perspex topped observation nests (Hogendoorn and Velthuis, 1995).

Competition over reproduction occurs between female nestmates after winter, between nest-owners and intruding conspecifics and between nestmates (mother and daughter, sisters, cousins, or unrelated nestmates; Hogendoorn and Leys, 1993). Such bouts are apparent from the frequent occurrence of noisy fights within the nest, during which biting of antennae, legs and wings, and attempts to sting have been observed (Velthuis and Gerling, 1983). Combatants both have active ovaries, and both bring pollen back to the nest (Velthuis, unpubl. data; Hogendoorn, unpubl. data). During periods of stable social nesting, when only one female forages for pollen, fighting between nestmates is rare (Hogendoorn, 1996; Hogendoorn and Velthuis, 1995; Stark et al., 1990). In such stable social nests the pollen forager is the sole egg layer.

During competitive bouts, brood cells are opened, and the brood is destroyed (Stark et al., 1990; Hogendoorn, 1996). Usurping non-nestmates usually destroy all brood cells present, whereas superseding nestmates generally open only one or two newly made cells. If the brood cell contains an egg the contesting female will devour it, reshape the pollen mass, lay her own egg upon the pollen mass and close the cell (Stark et al., 1990; Stark, 1992a; Hogendoorn, 1996). In some cases, the cell is then again opened by the other female, and the egg

is replaced once more (*X. pubescens*: Hogendoorn, pers. obs; *X. sulcatipes*: Stark et al., 1990). In some nests of the latter species, egg replacement occurred in several consecutively built cells, but a stable reproductive division of labour was usually established after the first three brood cells had been completed.

2. *Ceratina*. Task allocation and reproductive competition has been studied for *C. flavipes*, *C. japonica* and *C. okinawana* by Sakagami and Maeta (1985, 1987, 1989, 1995) and Maeta and Sakagami (1995). The social nests used in these studies were established by inducing two females to nest together in an observation nest, which was then placed in an isolated flight cage containing ample food resources.

In these social nests, interactions of an aggressive nature were extremely rare, and overt fighting was never observed. Opening of brood cells and egg replacement, however, occurs more frequently than in *Xylocopa*, and has been observed in all three species throughout the reproductive period (Sakagami and Maeta, 1987, 1995; Maeta and Sakagami, 1995). In many instances, eggs were replaced several times before the next cell was provisioned. Egg replacement did not only occur during the construction of the first few cells, but continued throughout the brood rearing period. This on-going egg replacement differs from *Xylocopa* egg replacement, because in the latter species reproductive dominance is settled after a brief period of competition (Maeta and Sakagami, 1995).

The egg replacement observed in both tribes is interesting, when one takes into account the “giant” egg size of all mass provisioning carpenter bees (Iwata and Sakagami, 1966; Michener, 1973). In these species eggs are as a rule slightly longer than the abdomen. It is likely that such large eggs strongly limit the egg laying rate (Rosenheim, 1996). If that is the case, one female will be the last to oviposit in a cell because the other female is not physically able to produce another egg in a short period of time, and egg replacement itself may be the only way in which competition for reproductive opportunity is expressed.

Task allocation and reproductive skew

1. *Xylocopa*. Sociality, involving a non egg laying guard bee and a dominant egg laying forager has been demonstrated in eight species of large carpenter bees (Gerling et al., 1989). In all of these species, the foraging female completely dominates reproduction. In nests of species that contained more than two females, the additional females remained inactive (Gerling and Hermann, 1978; Gerling et al., 1989; Hogendoorn and Velthuis, 1993, 1995; Stark, 1992a).

Guarding females were either young females that had eclosed in the nest or old, formerly reproductive females that had lost the fight over dominance (Gerling and Hermann, 1971; Stark, 1992a; Hogendoorn and Leys, 1993; Hogendoorn and Velthuis, 1995). In *X. pubescens*, one of the young females (usually the first that had eclosed), guarded the nest for an average of ten days before attempting to take over dominance. Of such young guards, 50% gained dominance

in the maternal nest (Hogendoorn and Velthuis, 1995). If a young female succeeded in gaining dominance, the defeated formerly reproductive female frequently remained guarding for the rest of her life, or until the nest was usurped. Whether or not a superseded female remained guarding correlated with her reproductive age, not with her relatedness to the nestmate that took over dominance (Hogendoorn and Leys, 1993).

Old guard bees remain in the nest entrance and will not produce any brood in the nest. Some direct fitness benefits are obtained by the guard if she protects her own brood still present in the nest, but more direct benefits can only be gained if the guard succeeds in re-establishing dominance. In *X. pubescens*, only 5 out of 88 old guards regained dominance and these produced very few cells (Hogendoorn and Leys, 1993).

2. *Ceratina*. In *Ceratina*, the female that starts to knead a pollen loaf and oviposit once enough pollen had been collected is referred to as the “queen” by Sakagami and Maeta (1995). This is usually the largest female in the nest, who also functions as a guard, while the other female performs nearly all of the foraging trips, and is referred to as the “worker”. However, since egg replacement is a common phenomenon, the first female that laid an egg is not necessarily the one that dominated reproduction (e.g., Sakagami and Maeta 1985, 1987, 1989, 1995). By extending observations during the night, to account for egg replacement Sakagami and Maeta (1995) were able to quantify the reproductive success of the guard and the forager. We summarized their data in Figure 1.

In all semisocial nests of *C. japonica* and *C. flavipes*, the forager appears to produce more surviving eggs than the guard (statistical treatment not possible due to low sample sizes). However, the guarding female produced at least one surviving egg in all cases (average of 2 for *C. japonica*, and 1.5 for *C. flavipes*). In eusocial nests of *C. japonica* ($n = 2$)

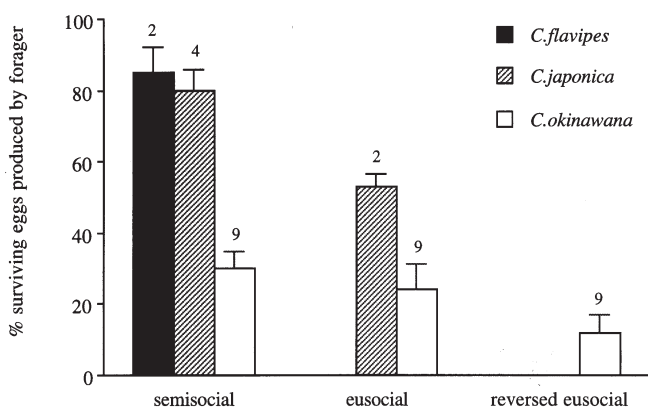


Figure 1. Average percentage of surviving eggs (\pm SE) that were produced by the forager in different types of social nests of *C. flavipes* (closed bars), *C. japonica* (hatched bars) and *C. okinawana* (open bars). The number of nests studied are given above each bar. For *C. okinawana*, the difference between reversed eusocial and semisocial nests was significant (data from Maeta and Sakagami, 1995: Table 1 and 2)

the reproductive output of the guarding mother was approximately similar to that of the foraging daughter. In all nesting types of *C. okinawana* the guarding female produced significantly more surviving eggs than the forager (semisocial nests: $p = 0.013$; eusocial nests (mother guards): $p = 0.02$ reversed eusocial nests (mother forages): $p = 0.008$, Wilcoxon’s matched pairs signed ranks tests). Eggs produced by the forager survived in all semisocial nests, in seven of the nine eusocial nests and in five out of nine reversed eusocial nests. In these three respective nesting types foragers produced 3.4, 1.8 and 0.9 eggs on average. The percentage of eggs produced by the foraging female was significantly lower in reversed eusocial than in semisocial nests (Fig. 1).

The proportion of surviving eggs laid by the forager is significantly different between these *Ceratina* species, even when only semisocial nests are included (data from Maeta and Sakagami, 1995: Kruskal-Wallis test, $H = 10.3$, $p = 0.006$). When further exploring these differences, it becomes clear that in the univoltine *C. flavipes* and *C. japonica* proportion of surviving offspring produced by the forager differed significantly from 0.5 in favour of the forager (t-test: $t = 4.96$, $p = 0.002$; $n = 6$, using arcsine transformed data for the two species combined), while in the more social, multivoltine species *C. okinawana* skew was towards the guard (t-test: $t = 2.95$, $p = 0.007$, $n = 26$, using arcsine transformed data). In addition, reproductive skew is considerably less in the *Ceratina* than in *Xylocopa* species studied here.

Size and age of dominant and subordinate females

In many primitively social organisations, body size is an important factor in obtaining dominance. While there are indications that female size affects dominance in both tribes, there is also evidence that age differences are important. In *Xylocopa*, females that had been reproductively active for a long period of time remained in the nest as a guard after defeat whereas younger females would leave, to search for a new nest (Hogendoorn and Leys, 1993; Hogendoorn, pers. obs.). In *C. okinawana*, both the percentage of eggs laid by the forager and the percentage of the forager’s eggs that escaped oophagy were significantly lower for reversed eusocial nests (percentage of eggs laid by forager: $31.7 \pm 3.2\%$ in 9 semisocial, and $18.8 \pm 5.7\%$ in 9 reversed eusocial nests, $t = 2.06$, $P = 0.05$; percentage of forager laid eggs that escaped oophagy: $60.4 \pm 8.4\%$ in semisocial and $28.1 \pm 11.5\%$ in reversed eusocial nests, $t = 2.59$, $P = 0.02$; all tests were done using arcsine transformed data from Sakagami and Maeta, 1995). These observations suggest that age differences can reduce the intensity of competition in both xylocopine and ceratinine bees.

The importance of age in winning the competition is further analysed below for *X. pubescens*. The wing length was recorded for individually marked females that were involved in dominance contests (for methods: see Hogendoorn and Leys, 1993). In such contests females could be either of the same cohort (sisters or resident females and intruders) or of a different generation (e.g., mother and daughter, aunt and

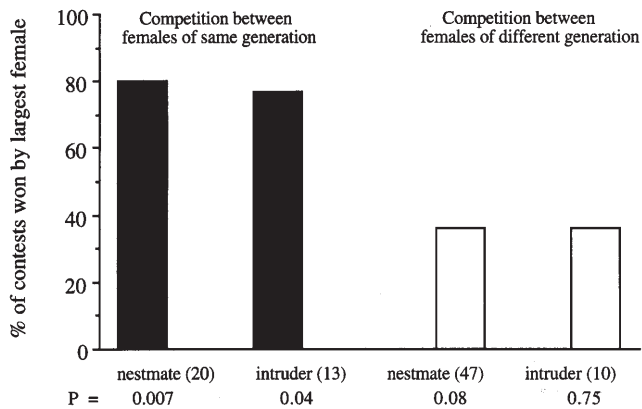


Figure 2. Percentage of fights over dominance won by the largest female of *Xylocopa pubescens*, when females involved were of similar (closed bars) and of different (open bars) cohorts (sample sizes are given between brackets). The significance of the size differences between the winning and losing females was tested using a Wilcoxon's matched pairs signed ranks test. P-values (below the x-axis) show that winners were significantly larger than losers if females were of the same cohort, but this was not found for competitors of different cohorts

niece, or a young intruder and an old resident female). The largest female won approximately 80% of the contests when females were of the same age, and less than 50% of the contests when females differed in age (Fig. 2). Thus size seems to be decisive in winning the contest for same generation females, but not for females from different generations.

Age differences are likely to have a stabilizing effect on social organisation in both *Xylocopa* and *Ceratina*. Old, less vigorous females have a relatively low reproductive value, because of their low probability of maintaining dominance and of gaining dominance elsewhere after defeat. By abandoning dominance in favour of a more vigorous daughter, old females may gain both direct fitness benefits, because their own brood that is still present in the nest gains protection, and indirect benefits, because of the increase of their daughters' reproductive rate due to guarding (Hogendoorn and Leys, 1993).

Skew, task allocation and aggression

For both tribes, the information about size, reproductive skew and task allocation is summarized in Table 1. In *C. flavipes*, *C. japonica* and *Xylocopa* the foraging female has the highest reproductive output. However, the foraging females in nests of these *Ceratina* species were generally the smaller of two females, and therefore their high reproductive output is puzzling and unexpected. An explanation for this finding could be that the results are confounded by the optimal circumstances under which skew was investigated. The absence of predators, and the presence of ample food resources close to the nest makes foraging energetically cheap, leaving the forager with abundant energy to produce eggs. Under natural, more unfavourable circumstances, foraging may limit egg production, in which case a smaller proportion of the eggs produced by the larger guarding female would be replaced by the forager.

To summarize, the most obvious differences between the two tribes in relation to task allocation and reproductive skew are: (1) Aggression determines dominance in *Xylocopa*, and fighting does not occur in *Ceratina* in any context; (2) In stable social nests of *Xylocopa*, the reproductive skew is complete, whereas skew was less than unity for all *Ceratina* species studied; (3) In *Ceratina okinawana*, the small subordinate female forages, whereas in *Xylocopa*, the only activity performed by the subordinate guard is being present in the nest-entrance.

Does observed skew fit the predictions?

We will now attempt to interpret the skew in both tribes, as well as the differences between the two tribes in the context of the reproductive skew model developed by Reeve and Ratnieks (1993). Reproductive skew models use four parameters to specify both the conditions under which to expect cooperative breeding and the extent of reproductive skew:

k: the expected output of the group if the subordinate stays (relative to the output of an unjoined breeder)

Table 1. Direct reproductive success (in % of all surviving eggs produced by either the guard or the foraging female) and task allocation between the large and the small female (semisocial nests) and the old and the young female (eusocial and reversed eusocial nests). In natural eusocial nests of *Ceratina*, the dominant was as a rule the largest of the two females (Sakagami and Maeta, 1989). References: *X. pubescens*: Van der Blom and Velthuis, 1989; Hogendoorn and Velthuis, 1993; *X. sulcatipes*: Gerling et al. 1973, Stark, 1992a; *Ceratina* spp.: Maeta and Sakagami 1995. For some nesting types, no data are available (N.A.)

	Semisocial		Eusocial		Reversed eusocial	
	guard	forager	guard	forager	guard	forager
<i>X. pubescens</i>	0% (small)	100%	0% (young)	100%	0% (old)	100%
<i>X. sulcatipes</i>	0% (small)	100%	0% (young)	100%	0% (old)	100%
<i>C. flavipes</i>	14% (large)	83%	N.A.	N.A.	N.A.	N.A.
<i>C. japonica</i>	20% (large)	80%	50% (old)	50%	N.A.	N.A.
<i>C. okinawana</i>	70% (large)	33%	77% (old)	23%	89% (young)	11%

- x : the expected reproductive success of the subordinate should it leave and attempt to rear brood alone (relative to the output of an unjoined established female)
- r_{sd} : the relatedness of the subordinate to the dominant's brood (relative to the relatedness of the subordinate to her own brood)
- f : the probability that a subordinate wins a severely damaging fight without being seriously injured herself

Under specific sets of parameter values it is expected that the dominant will yield some reproduction to subordinates as inducements to remain in the society (staying incentives) or to cooperate peacefully (peace incentives). The impact of each of the parameters on skew has been explored in detail by Reeve and Ratnieks (1993), summarized by Keller and Reeve (1994), and elaborated for cases of asymmetrical relatedness (matrifilial societies) by Reeve and Keller (1995).

It is unlikely that peace incentives are present in the subject species of *Xylocopa* and *Ceratina*: In *Xylocopa* skew is maximal and therefore neither peace nor staying incentives are given; in *Ceratina* fighting has never been observed. Therefore, we will ignore predictions about peace incentives and focus on predictions regarding staying incentives, aggressive testing and performance of risky tasks. These predictions are: (1) Staying incentives decrease with increasing constraints on solitary breeding; (2) Staying incentives decrease with increasing group productivity; (3) Staying incentives decrease with increasing relatedness between a subordinate and the dominant; (4) High skew coincides with performance of costly tasks by subordinates; (5) High skew coincides with high levels of aggressive testing.

Parameter estimates

On the basis of the existing literature, the value of the parameters can be estimated for situations involving guarding females in *Xylocopa pubescens* and in a comparative way for *C. okinawana* and *C. japonica*. The parameter estimates are summarized in Table 2 for *Xylocopa pubescens*, and are discussed below.

k : In *Xylocopa pubescens*, social nests did not have a higher reproductive output than solitary nests during spring, but during summer months the guard increased the output of the dominant female by approximately 30% (Hogendoorn and Velthuis, 1993), which yields a value for k of 1 during spring and 1.3 during summer. For *X. sulcatipes*, estimates of k varied between 1.3 to 3.5 over two consecutive years (Stark, 1992a), but the cause of this variation is not clear (Bourke, 1997).

For both *C. japonica* (Sakagami and Maeta, 1985) and *C. okinawana* (Sakagami and Maeta, 1989), social nests found in the field produced twice as much brood as solitary nests. All failed nests were excluded from analysis in these studies. If solitary nests have a higher likelihood of complete nest failure, as has been found for other carpenter bees (Stark, 1992a; Bull and Schwarz, 1996), relative reproductive output of social nests might be even higher. Therefore k is larger than 2.0.

Table 2. Estimated parameter values used by the optimal skew model for *Xylocopa pubescens*. Data are from Hogendoorn and Velthuis, 1993 (k), Hogendoorn and Leys, 1993 (x), and Hogendoorn, 1996 (r). For some periods, no data were available (N.A.)

	Old females		Young females
	spring	summer	
Group benefits (k)	1.0	1.3	1.3
Probability of finding a nest (x)	N.A.	> 0.01	0.15 – 0.4
Relative relatedness of the subordinate to dominant's brood (r_{sd})	N.A.	0.42	0.70
$r(k-1)$	0	0.13	0.21

x : The chances for subordinates of successfully founding a nest are difficult to measure and are likely to vary with age, as indicated above. A rough estimate by Hogendoorn and Leys (1993) for *X. pubescens* showed that the probability of successfully founding or usurping a nest elsewhere was between 0.16 and 0.40 for all females and between 0.10 and 0.29 for defeated females. However, the latter estimate is probably too high for two reasons: (1) The estimate is based only on those defeated females that left, while most of the older formerly reproductive females remained in the nest after defeat (Hogendoorn and Leys, 1993); (2) Only 4 out of the 8 formerly reproductive females that managed to found or usurp a new nest (Hogendoorn and Leys, 1993) successfully produced any brood. Taking this into account, we roughly estimate x to be smaller than 0.1 for all defeated reproductive females. Ecological constraints on solitary nesting are reportedly weak or moderate for *C. japonica* (Sakagami and Maeta, 1985) and may be moderate for *C. okinawana* during summer (Sakagami and Maeta, 1989). However, no information is available on the success of subordinate females that left the nest.

r : Relatedness between subordinate and dominant in natural nests has been estimated using genealogies (*Xylocopa*) assuming that females only mate once (sex ratios did not differ from equality, Hogendoorn, 1996). Experiments did not provide any evidence for kin recognition in *Xylocopa pubescens* with respect to either acceptance of eclosing brood, competition over dominance, duration of the guarding period (Hogendoorn and Leys, 1993) or brood destruction during nestmate take-overs (Hogendoorn, 1996). The average relatedness of the subordinate to the brood of the dominant relative to the subordinate's relatedness to her own brood (r_{sd}) was 0.42 ± 0.03 ($n = 82$; calculated from data presented in Hogendoorn, 1996) for old females and 0.70 for young guards.

In *Ceratina* newly founded nests were always solitary, and because neither joining nor usurpation seemed to occur, cooperative breeders are generally related. Relatedness has been inferred from differences in wing- and mandibular wear and ovarian condition, assuming nest-

mates to be either mother and daughters (eusocial or reversed eusocial) or sisters (semisocial; e.g., Sakagami and Maeta, 1989). Natural two female nests of *C. japonica* contained females of equal age only (sisters, Sakagami and Maeta, 1985). Of 53 natural two female nests of *C. okinawana*, 70% was eusocial, and 15% was semisocial (Sakagami and Maeta, 1989). In the other nests (15%) no differences were found in ovarian conditions of the females. Maeta and Sakagami showed experimentally that neither the frequency of oophagy nor the skew differed between kin and non kin colonies, and thus there is no evidence for kin recognition.

The correlates of skew

1. *Xylocopa*. In *Xylocopa*, no staying incentives are given, and therefore the impact of parameter values on the size of the staying incentive cannot be investigated. However it is possible to analyse whether both overwintered females and newly eclosed young females are expected to leave after defeat, whereas old females are expected to remain in the nest without staying incentives.

During spring, the presence of a guard does not increase the reproductive output of the dominant, and therefore $(k - 1)$ equals 0. Such conditions [$x > (k - 1)$] are referred to as weak ecological constraints to solitary nesting, no matter how small the actual probability of successfully founding a nest is. Under these conditions, females are expected to fight over dominance, and to leave if defeated. These expectations are met in *X. pubescens*: Hibernated females disperse from the nest after winter, either following a fight or not (Van der Blom and Velthuis, 1989, Hogendoorn and Velthuis, 1993). For the situation in summer, a distinction between old formerly reproductive and young defeated females needs to be made. For old females, benefits of solitary nest founding are small compared to the indirect fitness benefits of remaining in the nest, $x < r(k - 1)$ (Table 2). Under these circumstances, the females are expected to remain after defeat, and a staying incentive is not required.

For young females constraints on solitary nesting vary with size (see above) and the estimated range is considerable. Constraints may be called moderate, as $r(k - 1) < x < k - 1$, for the major part of the range of x (if x is between 0.21 and 0.3). Under moderate skew, the dominant female is expected to yield a staying incentive. Following Reeve and Ratnieks (1993) the expected size of this staying incentive (p_s) is $p_s = (x - r[k - 1])/k(1 - r)$. Substitution of values from Table 2 gives a range for the expected staying incentive between 0, for $x < 0.21$ [i.e., $x < r(k - 1)$], and 0.23 for $x = 0.3$ (i.e., $x = k - 1$). However, a staying incentive is never given by the dominant. This may either be in contradiction with expectations from optimal skew theory, or the behaviour of young females may have been selected under weak environmental constraints ($x > k - 1$) and low group benefits. Under such lenient conditions the subordinate is not expected to accept a staying incentive: she may either fight or leave the nest (Reeve and Ratnieks, 1993). The latter possibility does not seem unlikely, since the species has a broad distribution in

less arid regions, and does not seem to be optimally adapted to the harsh arid environment (Velthuis, 1987).

2. *Ceratina*. In none of the *Ceratina* species studied, was skew maximal. Because no fighting was observed under any circumstances, it seems unlikely that peace incentives are given. Within the context of the optimal skew model, the incomplete skew therefore must be a consequence of staying incentives being yielded by the dominant to the subordinate. Although for most species hardly any of the parameters in the skew model have been quantified, it is possible to explore the effect of some of the parameters on skew in a qualitative and comparative way. Below, we will discuss what trends occur.

(1) *Do staying incentives decrease with increased constraints for nest founding?*

Constraints on solitary breeding have not been quantified for any of the *Ceratina* species although Sakagami and Maeta (1995) mention that there is generally ample nesting material available. According to skew theory, staying incentives are expected under a combination of high success of solitary nest founding and high group benefits, and therefore our preliminary conclusion is that the observed skew of less than unity fits the model. This conclusion however needs to be substantiated by an accurate measurement of the probability for subordinates to found a nest.

(2) *Do staying incentives decrease with increasing group productivity?*

For the three nesting types of *C. okinawana* studied in observation nests, no correlation was found between the reproductive output and the percentage of eggs laid by the subordinate forager (semisocial nests: $r^2 = 0.21$, $F = 1.87$, $p = 0.21$, $n = 9$; eusocial nests: $r^2 = 0.21$, $F = 0.67$, $p = 0.44$, $n = 9$; reversed eusocial nests: $r^2 = 0.03$, $F = 0.18$, $p = 0.68$, $n = 9$; our analysis, using data from Sakagami and Maeta, 1995). Therefore, unlike predicted by skew theory, staying incentives did not decrease with increasing group productivity. At another level, comparison between reversed eusocial nests in *Xylocopa* and *Ceratina* does indicate decreased skew with increased group productivity, since group productivity was relatively higher in *Ceratina* ($k = 2$) than in *Xylocopa* ($k = 1.3$), while skew was less in *Ceratina*. However, such gross comparisons may not be valid due to large differences in environmental circumstances.

(3) *Do staying incentives decrease with increasing relatedness?*

For *C. japonica*, skew was higher in semisocial than in matrilineal nests (Fig. 1; $t = 3.5$, $p = 0.02$). However, as has been mentioned before, this result should be treated with care as it may be an artefact of the experimental set up and sample sizes are small. Skew is similar for semisocial nests and eusocial nests of *C. okinawana* (Fig. 1; $t = 1.3$, $p = 0.19$) but higher in reversed eusocial nests than in semi-social nests (Fig. 1; $t = 2.89$, $p = 0.01$), while the supposed relatedness between the subordinate foraging female (mother) and the grand offspring she helps rearing is lower in reversed eusocial than in semisocial nests. This result was not predicted by the skew model. To interpret this result we have to invoke differences in quality (i.e., constraints on solitary nesting) be-

tween old and young females, similar to those in *Xylocopa pubescens*. That such differences in quality may exist for eusocial nests of *C. okinawana* is indicated by the larger size differences found between subordinate and dominant females in natural eusocial nests compared to semisocial nests (Sakagami and Maeta, 1989).

Of the five predictions mentioned above, the last two focus on the consequences of skew for performance of risky and energetically costly tasks, and for aggressive testing. These predictions can be investigated in a comparative way for both tribes.

(4) *Does high skew and low probability of dominance reversal coincide with performance of costly tasks by the subordinate?*

In the following, we assume that foraging is a more risky and energetically costly task than guarding in both tribes. In *Xylocopa*, role reversals between the young guard and the dominant are frequent (50% of young guards gain dominance, Hogendoorn and Velthuis, 1995), and the young female does not forage, as was expected. However, role reversals are extremely rare between the old guard and the dominant, skew is maximal, and yet the subordinate does not forage. How is this explained? Firstly, for old females, the average relatedness between the old guard and the brood of the dominant is relatively low (0.21; Hogendoorn and Leys, 1993). Therefore, incentives to forage may be absent. Secondly, for old and young females alike, if there is any chance a guard could gain (or regain) dominance, she would have the highest probability of doing so by remaining relatively inactive, thereby minimising senescence.

In *Ceratina*, skew is considerably less than in *Xylocopa*, and therefore the subordinate is expected not to specialize in risky tasks. In contrast to this expectation, subordinate females performed $87 \pm 3\%$ of all foraging flights observed in *C. okinawana* ($n = 27$ nests; data from Sakagami and Maeta, 1995). In addition, there was no correlation between skew (measured as the percentage of surviving eggs laid by the forager) and the proportion of foraging flights performed by the subordinate female ($r^2 = 0.002$, $p = 0.834$, $n = 27$; data from Sakagami and Maeta, 1995 and Maeta and Sakagami, 1995). Thus, the predictions of reproductive skew theory with respect to the effects of skew on task performance are not supported by the available data from either of the two tribes.

(5) *Does high skew coincide with high levels of aggressive testing by the subordinate?*

Xylocopa exhibits high skew, and therefore on-going aggressive testing by the subordinate is expected. However, overt aggression was only observed during phases of competition over dominance. During the periods of stable social nesting, hardly any aggressive interactions were seen, although the frequent pushing and pulling during passing (Velthuis and Gerling, 1983; Hogendoorn and Velthuis, 1995) may be interpreted as on-going testing of one another's strength. In *Ceratina*, no aggressive interactions have been observed in any of the species at any time of colony development. The least we can therefore say is that aggressive testing in *Ceratina* is not related to skew. Comparison of the two tribes yields high levels of aggression in association with

complete skew, and an absence of aggressive interactions with lower levels of skew. This result may be seen as supporting the prediction, but other possible explanations are discussed below.

Discussion

Both the comparisons within species and between tribes of mass provisioning carpenter bees only partly conform with predictions from the optimal skew theory. Specifically, the predictions relating to the effect of ecological constraints on skew were generally supported: higher skew was found for species and nests that suffered higher constraints on solitary breeding. Within species comparisons for *Ceratina*, did not provide support for the prediction that skew increases with increased group productivity. In addition, no support was found for the effects of relatedness on skew, or of the effect of skew on performance of risky tasks. Although these results are firm for *Xylocopa* species, a provision should be made when comparing these results to those obtained for *Ceratina*, partly because sample sizes were small for two of the three species, and partly because the nests were kept under artificial circumstances which could affect skew. In particular, ample food supply combined with small travel distances in the cages could explain the high frequency of egg replacement (see above). The complete absence of opportunities to nest elsewhere, however, should result in maximal skew. Because maximal skew was not observed, the size of the staying incentive does not seem to be the result of active decision making by the dominant.

No clear effects of relatedness on skew have been found. For comparisons between nests within populations, the effect of relatedness on skew critically depends on the ability to recognise kinship, because individuals are able to act upon relatedness only if they are able to recognize levels of relatedness. No indications that females are able to recognize kinship have been found for either *Xylocopa pubescens* (Hogendoorn and Leys, 1993; Hogendoorn, 1996) or for *Ceratina okinawana* (Maeta and Sakagami, 1995). In the absence of kin recognition abilities, individuals may use other cues, such as age, size and wear, as a rule of thumb for estimating relatedness. If such cues are not used, the average degree of relatedness of nestmates in the population may be important in shaping skew in a population, but within the population, a correlation between skew and relatedness will not be found. The effect of relatedness on skew can then only be investigated by comparisons between populations or species. Although for *Ceratina okinawana* higher skew was found in eusocial than in semisocial nests, this is unlikely to be the result of differences in relatedness of the subordinate to the brood they help rearing (r_{sd}): In reversed eusocial nests, skew was highest of all while r_{sd} was smallest. We therefore argue that skew was the result of differences between the two females in competitive ability and potential to found nests elsewhere. For *Xylocopa pubescens* competitive ability, possibilities to found nests elsewhere and likelihood to remain in the nest as a subordinate guard vary with age and with size (Hogendoorn and Leys, 1993, and results presented above).

If differences between females in these aspects are large, e.g., in eusocial and reversed eusocial nests, one might expect strong skew. If qualitative differences are smaller, as might be expected for semisocial nests, less skew is expected.

In a more general context, Reeve and Keller (1995) found a tendency for lower skew in semisocial nests and higher skew in matrifilial associations, and concluded that differences are largely due to differences in relatedness between the co-operating individuals. Although Reeve and Keller (1995) mention that their results may have been confounded by differences in competitive ability between individuals of different generations, they did not attempt to disentangle the effects of relatedness from the effects of competitive ability. Generally, individuals of the same generation are likely to differ less in quality than females of different generations, for several reasons: (1) Same generation females have been influenced by the same ecological factors during the juvenile period, (2) They suffer simultaneously from ageing, and (3) For sibs, parental care and maternal effects are more or less similar. Therefore, on the basis of competitive ability alone, one would expect higher skew in matrifilial than in semisocial associations. The unexpectedly high skew in reversed eusocial *Ceratina* nests, as well as the age dependent guarding in *Xylocopa* underline the importance of differences in nest founding and competitive ability.

Reeve and Ratnieks (1993) predict that high skew may lead to subordinates performing the more risky and energetically costly tasks. This is likely to be true for social systems in which role reversals are rare, or precluded by adult morphology (e.g., in highly eusocial situations). If role reversals are more frequent, direct reproduction by the subordinate could provide an incentive to forage, in which case risky task performance could coincide with low skew. One might call this kind of incentive a "work incentive". Such a work incentive will be affected by ecological constraints and relatedness in the same way as a staying incentive. The above argument would explain the coincidence of high skew with guarding behaviour by old females in *Xylocopa*, and low skew with foraging by subordinates in *Ceratina* (Sakagami and Maeta, 1995).

Two of the most important assumptions of the optimal skew model are that dominant individuals completely control the reproduction of the subordinates without suffering a cost, and that subordinate individuals are less likely to leave or to challenge the dominant when they are allowed some direct reproduction (Emlen, 1995; Clutton-Brock, 1998). For the carpenter bees discussed above, it is unrealistic to assume that egg replacement does not include a cost to the dominant. Eggs are very large in all mass provisioning carpenter bees (as long or longer than the abdomen (Iwata and Sakagami, 1966)), and therefore investment in the egg is considerable. If such an egg is eaten by the subordinate, the investment into the egg by the dominant is lost. In addition, and possibly more important, it is unlikely that the dominant female of *Ceratina* makes a reproductive concession to her subordinate in return for help. Although the direct fitness benefits of the subordinate probably provide an incentive to remain in the nest and to forage, the continuous opening of one another's

brood cells does not take the appearance of a dominant yielding this incentive voluntarily. Rather, the frequent egg replacement indicates on-going competition, or "tug-of-war" between nestmates. Thus, it seems that instead of yielding a staying incentive, the dominant has been selected to tolerate a certain amount of direct reproduction by the forager. The model that should be applied may therefore not be the optimal skew model (Reeve and Ratnieks, 1993), but rather some type of incomplete control model (Reeve et al., 1998). If this tug of war over reproduction is decided by overt aggression in *Xylocopa* and by highest egg production rate in *Ceratina*, then the higher levels of aggression in *Xylocopa* than in *Ceratina* would not be directly related to levels of skew.

Many authors have presented results that were not in contradiction with expectations under optimal skew (e.g., Bourke and Heinze, 1994; McRae, 1996; Bourke et al., 1997; Jamieson, 1997), but these studies did not involve critical testing of alternative hypotheses (Clutton-Brock, 1998; Reeve et al. 1998). The above exercise shows that although skew in mass provisioning carpenter bees concurs with the optimal skew model on some points (i.e. effects of ecological constraints to solitary nesting), the existence of a concessive dominant was not supported by the evidence. To come to firmer conclusions with respect to the selective factors involved in the evolution of reproductive skew a more elaborate and critical testing of the alternative models needs to be done. Such testing should preferably include a combination of experimental research to study the impact of parameter values on skew and on decision making by dominants and subordinates, and of comparative analyses of parameter values and skew in closely related species to investigate evolutionary pathways (Keller and Reeve, 1994).

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