Multiple-foundress associations in a temperate population of *Halictus ligatus* (Hymenoptera; Halictidae)

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Thirteen pleometrotic (multiple-foundress) nests of the primitively social sweat bee *Halictus ligatus* were excavated in the summer of 1984 at Victoria, near Toronto, southern Ontario. Subordinate foundresses were significantly smaller than both dominant females in pleometrotic nests and females that nested solitarily. Most subordinates were smaller than the workers that they helped to raise. These small females could have been surviving workers from the previous summer or the offspring of workers. It seems unlikely that they were malnourished reproductive brood individuals produced as a result of parental manipulation. In successful nests, the number of workers produced was positively correlated with the number of founding females such that productivity per foundress remained fairly constant. Pleometrotic nests also produced more reproductives than haplometrotic (single-foundress) ones. Subordinates may occasionally lay reproductive brood eggs. The increased productivity of multiple-foundress nests was not quite sufficient, by itself, to select for subordinate behaviour. The small subordinates had lower potential productivities in comparison to the larger females. This decreased reproductive potential, when combined with the increased productivity of pleometrotic nests, was sufficient to make subordinate behaviour selectively advantageous. When both factors are taken together, subordinate behaviour is selected for as long as the coefficient of relatedness between dominant and subordinate individuals is greater than 1/4. This indicates that high coefficients of relatedness are not necessary for pleometrosis to be selectively advantageous under the conditions found in this study. Dominant females may suffer increased reproductive competition from their numerous workers. This, plus the difficulty of ensuring association with siblings in spring, may be the reason why multiple-foundress associations were uncommon at this locality. The data presented here are compared with those from other studies of this species. The factors promoting pleometrosis in halictines are compared with those that result in multiple-foundress associations in temperate polistine wasps.

Treize nids pléométropiques (à plusieurs fondatrices) de l'abeille sociale primitive *Halictus ligatus* ont été déterrés au cours de l'été 1984 à Victoria, près de Toronto, dans le sud de l'Ontario. Les fondatrices subordonnées sont significativement plus petites que les femelles dominantes des nids à plusieurs fondatrices et plus petites aussi que les femelles solitaires. La plupart des subordonnées sont plus petites que les ouvrières qu'elles participent à élever. Il est possible que ces femelles plus petites soient des ouvrières survivantes de l'été précédent ou des descendantes des ouvrières. Il semble peu probable qu'il s'agisse d'individus mal nourris d'une ponte reproductrice produite à la suite de manipulations parentales. Dans les nids réussis, le nombre d'ouvrières produit est en corrélation positive avec le nombre de femelles fondatrices, de telle sorte que la productivité par femelle demeure relativement constante. Les nids pléométropiques produisent aussi plus d'abeilles reproductrices que les nids d'abeilles solitaires (à une seule fondatrice). Les femelles subordonnées peuvent quelquefois produire des oeufs qui donneront des individus reproducteurs. La productivité plus grande dans les nids pléométropiques n'est pas en soi un facteur suffisant pour expliquer que la sélection ait favorisé le comportement subordonné. Les petits individus subordonnés ont un potentiel de productivité plus faible que les femelles plus grosses. Cette diminution du potentiel reproducteur, combinée à l'augmentation de productivité dans les nids à plusieurs fondatrices, a suffi à rendre le comportement subordonné avantageux. Lorsque les deux facteurs sont combinés, la sélection favorise le comportement subordonné aussi longtemps que le coefficient de relation entre dominant et subordonné dépasse 1/4. Cela indique qu'il n'est pas nécessaire que les coefficients de relation soient élevés pour que la sélection favorise la pléométrose dans les conditions de cette étude. Les femelles dominantes peuvent avoir à subir la compétition reproductrice de leurs nombreuses ouvrières. Ce phénomène, combiné à la difficulté d'assurer le maintien de l'association avec les abeilles apparentées au printemps, peut expliquer pourquoi les associations à plusieurs fondatrices sont rares en cet endroit. Les résultats présentés ici ont été comparés à ceux d'autres études sur les abeilles de cette espèce. Les facteurs qui favorisent la pléométrose chez les halictinés sont comparés à ceux qui prévalent dans les associations à plusieurs fondatrices chez les guêpes polistinées des climats tempérés.

[Traduit par la revue]

Introduction

A eusocial colony can develop through one of two routes: as a result of the activities of a single foundress or from an association of more than one female in a semisocial society. Comparative studies of these single- (haplometrotic) and multiple- (pleometrotic) foundress associations are of importance for several reasons. Firstly, semisociality may have been an intermediate step in the evolution of eusociality (Michener 1974; West-Eberhard 1978; Brockmann 1984) and, therefore, studies of pleometrotic associations may throw light upon the route to sociality taken by a particular taxon. Secondly, coefficients of relatedness between one individual and the offspring of a sister are lower than those between parent and offspring. This reduction in r makes the conditions required for the evolution of semisociality more stringent under the kin selection hypothesis than those that lead to matrifilial associations. Thirdly, parental manipulation is less likely to result in the formation of associations between individuals of the same generation than is kin selection. Thus, studies of the factors that result in some females becoming subordinates in pleometrotic nests should help clarify some of the important issues associated with the origin of eusociality in Hymenoptera.

The selective advantages to both dominant and subordinate individuals and the mechanisms whereby pleometrotic associa-

tions arise have been well investigated in polistine wasps. Dominant females gain a clear advantage in that they do not have to run the risks of active foraging for nesting material and prey items; therefore, they suffer reduced mortality in comparison to subordinates (Pfennig and Klahn 1985).

The advantages accruing to subordinate individuals are less clear and several hypotheses have been put forward to explain this seemingly maladaptive trait: (*i*) improved early colony survival, (*ii*) increased colony productivity, (*iii*) less fertile or less able individuals join more fecund relatives, and (*iv*) direct contribution to the reproductive brood. In the absence of any direct reproductive production by subordinates, the associating females must be relatives for subordinate behaviour to be selectively advantageous by kin selection. There is good evidence that females in multiple-foundress polistine associations are sisters (Klahn 1979; Noonan 1981).

Comparisons of colony productivity and survival differences between haplometrotic and pleometrotic polistine nests indicate that subordinates derive inclusive fitness benefits from increased nest and brood survival rather than from gross productivity *per se* (Metcalf and Whitt 1977; Gamboa 1978; Gibo 1978; Gibo and Metcalf 1978; Noonan 1981; Strassmann 1981). Subordinates usually die before the period of reproductive production (Gamboa *et al.* 1978; Pfennig and Klahn 1985). Oviposition by subordinates is, therefore, likely to result in worker production. Nonetheless, eggs laid by subordinates are often eaten by the dominant female (Gamboa *et al.* 1978). Thus, subordinate individuals are unlikely to be "hopeful reproductives." There is some evidence that subordinates may be reproductively less competent than dominant individuals (Noonan 1981). However, Sullivan and Strassmann (1984) failed to find any evidence of this in a field study of *Polistes annularis*, Bendegem *et al.* (1981) found the subordinates to be more productive in a laboratory study of a small number of *P. fuscatus* nests, and Craig (1983) concluded that there were no data that unequivocally supported the subfertility hypothesis. In general, research on polistine wasps indicates that inclusive fitness benefits from improved colony survival provide the major selective advantage that results in subordinate behaviour in pleometrotic foundress associations.

As for the mechanisms whereby pleometrotic associations are formed, it is now well known that kin recognition mechanisms allow individual wasps to form associations with sisters (Gamboa *et al.* 1986). Mechanisms whereby dominance and subordinance are established are less clear. The suggestion that subordinates are malnourished individuals forced to become subordinate to their sisters by parental manipulation (West 1967; West-Eberhard 1969; Gibo 1974) has not been borne out by detailed investigations (Haggard and Gamboa 1980; Sullivan and Strassmann 1984). Dominance hierarchies are established as a result of differences in size (Gamboa and Dropkin 1979; Sullivan and Strassmann 1984) and ovarian development (Dropkin and Gamboa 1981; but see Röseler *et al.* 1980; Röseler *et al.* 1984).

Results of investigations into the social biology of *Halictus ligatus* in southern Ontario were analysed to investigate the selective advantages of pleometrosis in this social sweat bee. In particular, the mechanism whereby subordinates are produced, the manner in which dominance relationships are established, and the advantages of pleometrosis to dominant and subordinate individuals were investigated. The results are compared with published data on polistine wasps to see if the same selective processes could have led to multiple-foundress associations in both taxa.

Details of the social organisation of this population are presented elsewhere (Packer 1986) as are analyses of variation in nest architecture (Packer and Knerer 1986*b*). A detailed analysis of sex ratio and worker oviposition is in preparation.

Methods

The study site was visited several times each week from the beginning of the spring provisioning phase until the end of the emergence of the reproductive brood. Several visits were made before pollen foraging began, but bees were not marked at this time because many individuals would be leaving their natal nests to initiate new ones elsewhere and could not be associated with particular burrows with certainty.

Bees were marked with Testors PLA enamel paint, in the field, once pollen foraging had begun. Individually distinctive markings were made on the frons and (or) vertex of each individual. Yellow paint was used to mark the first bee associated with a particular nest, red for the second, and green for the third (no more than three individuals were marked in any one nest during the spring phase). At the time of marking, the head width of each female was measured with an eyepiece micrometer, accurate to 0.1 mm.

A nest was considered to be pleometrotic if several marked females were observed flying from it, or guarding at the entrance, for several days during the spring provisioning phase when only females that had overwintered were present. In some nests, only one individual female was marked at this time but another was seen guarding the nest while the marked bee was away foraging. These nests were also considered to be pleometrotic if both bees were observed regularly during the spring activity phase. Pleometrosis was detected in two nests only after excavation and subsequent dissection of occupants. In these cases, the only surviving spring female was not the individual that had been observed foraging earlier in spring.

The observations reported here are considered to represent pleometrosis and not usurpation because the marked foraging individuals were observed repeatedly returning to the same nest during the spring provisioning period. The two nests in which the unmarked queen had not been observed earlier in spring are the only ones in which usurpation and pleometrosis could have been confused. However, these nests had similarly high productivities to the other pleometrotic nests. If usurpation had occurred, such high productivity would not be expected. Additional evidence that intraspecific usurpation was not important in this population comes from results of observations of interactions at nest entrances between females of *H. ligatus* and *Lasioglossum leucozonium*. Several usurpation attempts were observed in which females of the latter species tried to take over *H. ligatus* nests (Packer and Knerer 1986*b*). Marked females of *H. ligatus* were much more numerous at the study site than were females of *L. leucozonium* (in a ratio exceeding 30:1); thus the fact that interspecific interactions were observed but intraspecific usurpation never detected indicates that the latter must have been comparatively rare. Additionally, no behaviours that would be indicative of intraspecific nest usurpation were observed during the course of the study.

In the following account, dominant individuals are defined as those females in multiple-foundress associations that remained in the nest during the spring foraging phase. These individuals became queens when the workers emerged. Subordinates did all of the foraging in pleometrotic nests and did not survive long after the period of worker emergence or died before that time. The term subordinate is synonymous with the word auxiliary as used by Knerer (1980). In halictine bees, workers are, by definition, not present in the early stages of nest founding: they are the offspring of the founding female(s).

Nest excavation techniques are described elsewhere (Packer and Knerer 1986*a*). Because the size distribution of subordinate individuals was bimodal (Fig. 1), nonparametric tests were used to compare the sizes of these with other bee classes. Except where otherwise stated, the following results refer to the population studied at Victoria, southern Ontario, in 1984, when 130 nests were excavated. For a more detailed description of the methods employed in this study, the accompanying paper (Packer 1986) should be consulted.
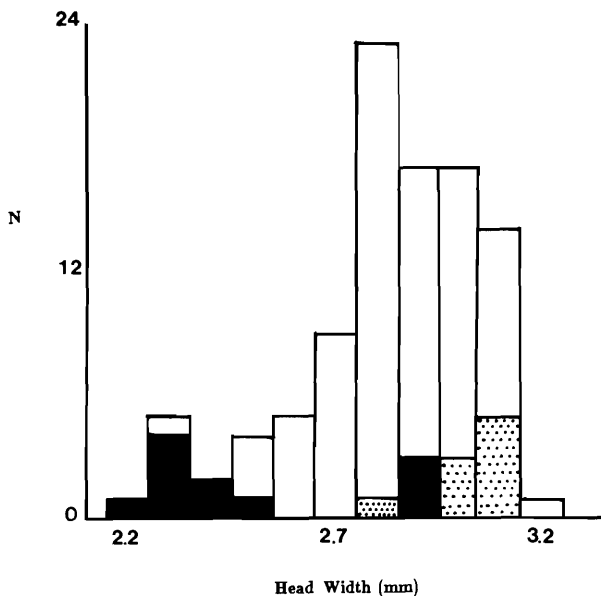
FIG. 1. Histogram showing the variation in size of dominant and subordinate females in pleometrotic nests and solitary nesting females at Victoria, southern Ontario in 1984. Open bars represent solitarily nesting foundresses, stippled bars indicate dominant individuals in pleometrotic associations, and shaded bars represent subordinate females.

Results and discussion

The prevalence of pleometrosis

The mean number of females in spring nests was 1.18; 77 nests were haplometrotic, 11 were digynous, and 1 each contained three and four foundresses. Wade (1985) has argued that the harmonic mean is a more useful measure of the degree of pleometrosis. The harmonic mean number of females in spring nests was 1.08.

Chandler (1955) claimed that multifemale spring associations of *H. ligatus* in Indiana broke up before foraging commenced and that there was no pleometrosis in the population that he studied. Eickwort (1985), with rather small sample sizes, found no evidence for pleometrosis in this species in California. Other authors have found pleometrotic associations during the spring provisioning phase (Litte 1977; Knerer and Plateaux-Quénu 1966; Knerer 1980). The number of overwintering foundresses per nest at Victoria (mean = 4.25, SD = 3.31, N = 8) averages much higher than the 1.18 females found during the spring provisioning period. Some individuals disperse and found new nests, although nest initiation by independent vertical excavation from hibernal burrows is also possible (Sakagami and Fukuda 1972; Packer and Knerer 1986b). All marked individuals either returned to the nest at which they were originally observed or initiated a new one: no individuals were seen joining already established nests. It would appear that pleometrosis arises when more than one female remains associated with the natal nest. However, because comparatively few observations were made during the preforaging period, low frequencies of joining may have been missed.

Pleometrosis in this species has been observed by Litte (1977) and Knerer (Knerer and Plateaux-Quénu 1966; Knerer 1980). Litte provided sufficiently detailed data to allow statistical comparison. The mean number of females in spring associations in New York State was 1.35, somewhat higher than that found at Victoria. However, the proportions of haplometrotic and pleometrotic nests did not differ significantly between the two localities (χ^2 = 2.02, p > 0.1). Knerer and Plateaux-Quénu

(1966) state that 60% of spring nests in Toronto were pleometrotic. Although exact data were not reported, this may represent a real difference.

Differences between dominant, subordinate, and solitary-nesting females

Figure 1 shows the variation in size of dominant, subordinate, and solitary-nesting females. As may be expected, dominant females in pleometrotic nests were larger than those that nested alone (mean head width of haplometrotic foundresses = 2.85 mm, SD = 0.26, N = 77; of dominant females in pleometrotic nests = 3.04 mm, SD = 0.11, N = 8; t = 1.84, p < 0.05).

Subordinate females (as defined by differences in survivorship and foraging activity) in these nests were significantly smaller than the dominant female (mean head width of subordinates = 2.50 mm, Mann–Whitney U test, U_s = 68, p < 0.005). The mean size difference between a subordinate and its corresponding dominant female was 17.2%, which is greater than the difference of 12.6% between queens and workers in haplometrotic nests (Packer 1986). Subordinate foundresses were significantly smaller than the workers that they helped to rear (mean head width of the sample of subordinates for which worker head widths are available = 2.30 mm, SD = 0.06, N = 6; for workers = 2.62 mm, SD = 0.20, N = 19; t = 6.49, p < 0.001; the subsample of subordinate females was normally distributed allowing the use of a parametric test). This surprising result is supported by the finding that workers in pleometrotic nests were larger than those in haplometrotic ones (mean head width of workers from haplometrotic nests = 2.51 mm, SD = 0.10, N = 105; from pleometrotic nests = 2.58 mm, SD = 0.10, N = 40; t = 3.61, p < 0.0005). However, there was no difference in queen–worker size dimorphism between haplometrotic and pleometrotic nests: workers in the latter nests averaged 12.7% smaller than their respective queens and those from haplometrotic colonies were 12.6% smaller (SD = 0.05 and 0.04, N = 33 and 100, respectively; t = 0.05, p > 0.9).

Forty workers were found in eight pleometrotic nests. The proportion with ovarian development was not significantly different from that in haplometrotic nests (χ^2 = 0.36, p > 0.5) but they were less likely to have mated (χ^2 = 5.35, p < 0.05). However, the latter result is due to the disproportionate number of workers that were excavated from pleometrotic nests in the early stages of the summer provisioning phase when few workers are mated (Packer 1986). Comparisons of females from haplometrotic and pleometrotic nests within individual 10-day periods revealed no significant differences in the proportion of mated workers.

Nest productivity and survival

Productivity differences can arise from variation in the number of pollen balls provisioned or from different levels of brood mortality.

Pleometrotic nests of *H. ligatus* at Victoria had larger worker broods than haplometrotic ones. Single-foundress nests averaged 6.65 first brood offspring (SD = 2.6, N = 20) with a mean of 5.65 workers per nest; males made up 14.6% of this brood. Pleometrotic nests averaged 17.1 first brood individuals (SD = 10.2, N = 7). The digynous nests averaged 12.4 first brood offspring (6.2 per foundress), the trigynous nest had 37 (12.3 per foundress), and the quadrigynous nest had 21 (5.25 per foundress). To test whether there was any departure from equal productivity per foundress in nests initiated by different numbers of females, a logistic analysis of variance was performed using the statistical package GLIM 3.77 (Royal

Statistical Society 1985). The result showed that, despite the apparently great productivity of the trigynous nest, there was no departure from homogeneity in productivity per foundress when all nests were considered ($G^2 = 0.78$, $p > 0.5$).

The difference between haplometrotic and pleometrotic nest first brood productivity is significant ($t = 3.77$, $p < 0.001$) as is that between digynous and the other two pleometrotic nests (Mann–Whitney U test, $U_s = 10$, $p = 0.05$). The proportion of males in the first brood of polygnous nests (17.3%) did not differ significantly from that in haplometrotic nests ($\chi^2 = 1.11$, $p > 0.1$).

Clearly there is increased first brood productivity in pleometrotic nests at Victoria. However, Litte (1977) found no first brood productivity differences between haplometrotic and pleometrotic nests. As a result, productivity per female was lower in pleometrotic nests in New York State, a feature that has been reported for other halictine species (Michener 1974).

In addition to producing more workers, pleometrotic nests produce a larger number of reproductive brood individuals. Two pleometrotic nests were excavated on August 9, 1984. On the same day, five haplometrotic, queenright nests were excavated. The former had a larger number of reproductive brood cells with healthy immatures (mean = 32.5, more than twice the number for haplometrotic nests, 15.2). This difference is significant (Mann–Whitney U test, $U_s = 10$, $p = 0.05$). Thus, pleometrosis does result in a significantly larger reproductive brood.

Nine haplometrotic nests failed to produce a worker brood and one such nest produced workers but no reproductives. All 13 pleometrotic nests produced reproductive broods. However, this difference is not statistically significant (Fisher's exact test, $p = 0.27$).

Smaller foundresses were less likely to raise a worker brood than their larger conspecifics. Of five solitarily nesting females that were of similar size to the small subordinates (i.e., with a head width of less than 2.6 mm) only one succeeded in raising a worker brood whereas 65 of 83 larger foundresses succeeded in raising worker broods. The difference in probability of success between these two groups is significant (Fisher's exact test, $p = 0.012$). Thus, solitarily nesting subordinate-sized females are approximately one-quarter as likely to raise a worker brood as larger individuals.

Bombyliid flies are the most important mortality factor affecting *H. ligatus* at Victoria (Packer and Knerer 1986*b*). Females of *Bombylius pulchellus* were active during the spring provisioning phase and would flick their eggs down the entrances of host burrows. In New York, the pleometrotic nests are guarded for a significantly greater proportion of the time than are haplometrotic ones (Litte 1977). Although detailed data on the time spent guarding were not collected at Victoria, subjective impressions suggest that the same is true at this locality. However, the frequency of parasitism by bombyliids did not differ significantly between haplometrotic and pleometrotic nests ($\chi^2 = 2.43$, $p > 0.1$). Additionally, when all brood mortality factors are taken together, there is no significant difference in immature survivorship between haplometrotic and pleometrotic nests ($\chi^2 = 0.74$, $p > 0.1$). This indicates that pleometrosis does not result in improved brood survival in this species.

Gibo (1978) studied the productivity and survival of nests with different numbers of foundresses in *Polistes fuscatus*. His study is of particular interest here because the locality is only 32 km from the Victoria site and this population of *P. fuscatus*, like

H. ligatus nearby, has only one worker brood per year. He found that first brood productivity per foundress was fairly constant, whereas reproductive brood productivity per foundress (in those nests that survived) was smaller in the pleometrotic nests. In sites where the nests were exposed to predation, nest survival was much greater for pleometrotic nests and when combined with productivity differences, resulted in a markedly increased final productivity for multiple-foundress colonies. Differences in survival of whole colonies and productivity per colony were less marked in sites where the nests were protected from predation by a mesh screen. This study indicates the importance of brood predation on the biology of polistine wasps, species that make their nests in open, exposed situations. In contrast, *H. ligatus* nests in the ground and their colonies are less susceptible to destruction by predators.

The selective advantages of subordinate behaviour in pleometrotic nests

Assuming that subordinates produce no reproductives directly, subordinate behaviour is selected for if

$$[1] \qquad P_c > P_q + \frac{1}{r_i} P_i$$

(West 1967), where P_c is the productivity of a digynous colony, P_q is the productivity of the colony of the dominant female when unaided, P_i is the productivity of the subordinate female nesting alone, and r_i is the coefficient of relatedness between the subordinate female and the helped dominant individual. Alternatively, r_i could be taken as the ratio of relatedness between the brood raised by the subordinate in a pleometrotic nest to that raised by her when nesting alone. However, assuming that colony foundresses are singly mated, in the present situation, r_i is likely to be 3/4 in both cases unless the subordinates result from worker-laid eggs in which case r_i will be 3/8. The above equation assumes that subordinates do not have a direct contribution to the reproductive brood. This assumption may not hold in the situation under discussion here.

In addition to direct contributions to the reproductive brood, there are three ways in which subordinate behaviour could be selectively advantageous. Two of these advantages involve increased inclusive fitness benefits through helping the dominant relative. Thus, improved colony survival or productivity when more than one foundress is present could select for subordinate behaviour. The remaining mechanism implies that subordinates are less fecund or otherwise less able to raise a brood alone. Under these circumstances, aiding relatives may be particularly advantageous. These four hypotheses (direct reproduction, improved colony survival, increased productivity, and subfertility) are considered in turn in the following discussion.

Direct reproduction by subordinates

This can occur either by "sneaky oviposition" while the dominant foundress is still alive, or as a result of the subordinate becoming dominant after queen death.

Only two subordinates from Victoria were dissected. Both were very much smaller than the dominant female, were in nests with recently emerged workers, and had no ovarian development. More data are available from nest aggregations within the Toronto city limits (G. Knerer, unpublished data). In 1963 and 1964, 11 subordinates were excavated from seven nests before adult workers had emerged. Ovarian development in these subordinates was substantial and two of them contained a fully developed oocyte. All but one of the seven dominant individuals

in these nests had 1 or more fully developed oocytes, giving a total of 10 oocytes in dominant females. Thus, it is possible that subordinates in pleometrotic nests lay as many as 17% (2 out of every 12) of the worker brood eggs. However, these are likely to result in worker individuals, or worker brood males.

An additional two subordinates from Toronto were excavated from nests that contained adult workers and were thus producing reproductives (Packer 1986). One, like the two subordinates from Victoria, had no ovarian development; the other contained one fully developed oocyte, indicating that subordinates may survive long enough to lay a few reproductive brood eggs. However, it is quite possible that subordinate-produced eggs are eaten by nest mates: oophagy was not uncommon at the Victoria site (L. Packer, manuscript in preparation).

The data from Victoria in 1984 indicate that two dominant females might have died before their reproductive broods were produced. In one nest (B2), excavated before the emergence of the worker brood, a tiny (head width 2.3 mm) female was the sole adult occupant. The brood consisted of three pollen balls, two larvae, and one prepupa which, upon pupation, resulted in a female with a head width of 2.35 mm. Not one haplometrotic nest produced a worker that was larger than the foundress, and so it seems probable that this observation represents a pleometrotic nest in which the dominant female had died.

The enigmatic contents of one other nest may represent an example of the early death of a dominant individual. Nest 33 was excavated at a time when all nests had adult workers. It contained four females of approximately equal size, one of which had been marked earlier in spring. The brood consisted of one male and six female pupae and 18 cells that had been filled in, perhaps as a result of pollen contents becoming mouldy. The small size difference between the spring female and the three workers in this nest plus the large number of cells suggest that this had been a pleometrotic nest in spring.

Neither of the above two nests were included in the other analyses because the interpretation that they had been pleometrotic may be incorrect.

To summarize, subordinates are unlikely to make a substantial direct contribution to the reproductive brood.

Improved colony survival

As discussed above, pleometrotic nests were no more likely to survive the period between initiation and worker emergence than were haplometrotic nests. This is in contrast to the situation found in polistine wasps in which the exposed colonies often suffer predation from birds, particularly just before worker emergence (Gibo 1978). Under these circumstances, pleometrotic colonies are more likely to be reestablished than are single-foundress nests (Gibo 1978).

Increased colony productivity

This refers to the number of reproductive generation individuals produced by the colony. It can result from increased foraging activity and (or) reduced brood mortality.

Let us assume that subordinate and dominant females have equal potential productivities ($P_q = P_i$) and that they are full sisters ($r_i = 3/4$). Then, from Eq. 1, subordinate behaviour is selected for if the productivity of two-foundress nests exceeds 7/3 times that of single-foundress colonies. If the subordinates are nieces, produced by worker oviposition ($r_i = 3/8$), then two-foundress nests would have to have more than 11/3 times the productivity of haplometrotic nests for increased productivity alone to explain subordinate behaviour. The observed reproductive brood productivity of two-foundress nests was

double that of haplometrotic colonies, not quite enough to select for subordinate behaviour if the females concerned are sisters. If subordinates are worker-produced females, then increased productivity falls far short of selecting for such behaviour.

Subfertility of subordinates

It was shown previously that small foundresses (head width < 2.6 mm) are only one-quarter as likely to successfully raise a brood in comparison to larger foundresses. Thus, from Eq. 1, P_i is one-quarter P_q, and the value of P_c that must be exceeded if subordinate behaviour is to be selectively advantageous is 4/3, assuming that the two females are full sisters. The observed productivity of digynous nests was twice that of haplometrotic nests. Thus, the increased productivity of digynous nests plus the decreased probability of successful nest initiation by the smaller subordinates more than compensates for the reduced coefficient of relatedness between subordinates and the brood that they help to rear. If subordinates are worker-produced females, then r_i is 3/8 and, for Eq. 1 to hold, the productivity required of digynous nests must be 5/3 times that of a dominant female nesting alone. Again, the threshold value above which subordinate behaviour is selected for is exceeded if the reduced productivity of subordinates nesting alone plus the increased productivity of helped relatives are considered together.

Unfortunately, the two larger subordinates found in this study were not captured for dissection. Based upon size criteria alone, these individuals would be expected to be capable of successful independent nest founding. Therefore, increased productivity of pleometrotic nests, by itself, does not explain their subordinance. It remains possible that parasitism by conopids or nematodes had reduced their potential productivity, making subordinate behaviour their best strategy. Alternatively, these females may have had a better chance of surviving long enough to lay some reproductive brood eggs than the smaller subordinates.

Digynous nests are twice as productive as single-foundress colonies and subordinates have approximately one-quarter the potential productivity of their larger conspecifics. If these values are substituted into Eq. 1, subordinate behaviour is selected for if r_i is greater than 1/4. This indicates that under the conditions described here, high coefficients of relatedness amongst founding females are not necessary to explain pleometrotic foundress associations.

In his study of *Polistes fuscatus*, Gibo (1978) found that, assuming that all foundresses have equal potential productivity, parental manipulation was the most likely explanation of subordinate behaviour. However, if the equal fecundity condition was relaxed, kin selection, parental manipulation, and individual selection (whereby subordinates produce some offspring themselves) could all explain subordinate behaviour. As shall be demonstrated below, parental manipulation is an unlikely explanation for subordinate production in *H. ligatus*.

Possible disadvantages associated with being a dominant female in a pleometrotic nest

Dominant individuals obtain a worker brood without running the risks of active foraging. They also obtain a larger worker brood because the subordinate individual(s) continue to forage for a longer period or more intensely than do females that nest alone. Thus, subordinate females would forage every day when the weather was suitable, whereas haplometrotic nests were active only intermittently resulting in a widely spaced emergence period for the worker brood (Packer 1986). Litte (1977) also observed higher activity levels in multiple-foundress nests

of this species and in laboratory colonies of *Lasioglossum (Dialictus) zephyrum*, individuals in multifemale nests are more active than solitary females (Michener 1974). Given the obvious advantages to being a dominant female in a pleometrotic nest it is somewhat surprising that most females in this population that overwinter initiate nests solitarily.

The overwintering behaviour of *H. ligatus* gynes may preclude the establishment of pleometrotic associations in spring for many females. In the autumn, each female excavates a hibernaculum near the bottom of the natal nest. Hibernaculae from one nest are often widely dispersed within the soil (Packer and Knerer 1986b), decreasing the chances that females will encounter sisters when they become active the following spring. It is unlikely that searching for the burrows of relatives is a viable alternative for females that have overwintered, for several reasons. Firstly, nest entrances at this locality are normally hidden under the basal rosettes of various weeds (Packer and Knerer 1986b) making them difficult to locate. Secondly, there are disadvantages associated with searching for another individual's burrow because this exposes the female to predation risks and, if unsuccessful, may delay independent nest initiation resulting in a reduction in time available for colony development. Moreover, being a dominant individual in a pleometrotic nest may not be the best strategy available to a foundress that has overwintered. This is because of increased intranidal competition for oviposition in more populous colonies. The proportion of oocytes that a queen has to resorb is positively correlated with the number of workers in the nest (L. Packer, manuscript in preparation). Thus, the larger worker population in pleometrotic nests may cause the queens to lose reproductive dominance to such an extent that haplometrosis results in a higher final reproductive output for them.

Studies of *Lasioglossum (Evylaeus) lineare* (Knerer 1983) indicate that queens may have difficulty in maintaining dominance over unusually large worker broods. Pleometrotic nests of this species provisioned up to 24 cells in the worker brood. However, a maximum of eight adult workers was found later in the year and Knerer concluded that many workers had left (or had been forced out of?) the nests.

Further evidence that the presence of subordinates is not necessarily entirely advantageous for their dominant nest mates comes from field observations of *Halictus scabiosae* (Knerer and Plateaux-Quénu 1966), a species closely related to *H. ligatus* (Pesenko 1985). In this species, the largest female becomes the dominant individual in pleometrotic nests but the subordinates are aggressively excluded before the first workers emerge. This behaviour may keep the number of workers low enough to ensure their effective domination by the queen in addition to removing any competition that may arise from the subordinates themselves. Additionally, if the excluded subordinates establish a nest solitarily the queens may gain inclusive fitness benefits by expelling them. Ousted subordinates have been observed to usurp the nests of *Lasioglossum (Evylaeus) nigripes* and to raise broods therein (Knerer and Plateaux-Quénu 1967).

The establishment of pleometrotic associations

Most subordinates in the Victoria population of *H. ligatus* were much smaller than the average female that had overwintered, and even smaller than the average worker. It is possible that small females were produced as a result of the accidental fertilization of eggs that were laid upon the small, male-producing provision masses. The smaller average size of male-producing pollen balls (average weight 38.2 mg) com-

pared with worker ones (43.9 mg) supports this possibility. This hypothesis is of interest because it is an alternative to parental manipulation. However, if the fertilization of eggs laid upon these small pollen balls is not accidental, it may reflect the attempts of queens to increase their number of grandoffspring by producing some malnourished females that will stay in the natal nest the next spring and help a larger, dominant sister. The "accidental" fertilization of eggs that are laid on small provision masses may be selectively advantageous to queens under these circumstances.

Will a queen increase her number of grandoffspring if she produces a mixture of larger than average dominant females, and smaller than average subordinates? Accurate estimates of the weight of pollen required to produce the large dominant individuals and the small subordinate females are not available. However, worker pollen balls averaged 43.9 mg in weight and gyne provision masses 66.3 mg, i.e., worker pollen balls weigh approximately 66% as much as those that produce a gyne. The cube of the mean head width of workers is 16.6 mm^3, and that of gynes 23.1 mm^3. Thus, the "volume" of a worker is 71% that of a queen. The estimates of relative queen/worker volume ratios are similar to those obtained for pollen ball weights; therefore, estimates of the relative cost of producing individual bees may be obtained from the cube of their mean head width. These estimates are 23.2 units per haplometrotic foundress, 28.1 units per dominant foundress, and 15.6 units per subordinate. Thus, to produce one dominant and one subordinate costs 43.7 units, barely any less than the 46.3 units required to produce two females the size of the average haplometrotic foundress. Additionally, it would be difficult to ensure that one large and at least one small individual remain together in their natal nest in spring. Thus, it seems unlikely that the production of small subordinate females is a result of parental manipulation. These small individuals may result from worker oviposition or they may be surviving worker brood individuals.

Evidence that subordinates are surviving worker brood individuals comes from nest No. 16 in 1983. This nest was digynous and produced 19 first brood females that were individually marked. Many of them were subsequently observed foraging. However, two were seen again only after the nest was excavated on August 22. One of them showed no signs of having worked: it had no mandibular or wing wear. The other had no wing wear but a mandibular wear index of 1, indicating that it had performed a minimal amount of excavation; mandibular wear scores are a good indication of the amount of excavation performed (Packer and Knerer 1986b). Two different unmarked and unworn females excavated at this time also appear to have been worker brood individuals, judging by their size. At this late date, there was almost no pollen ball construction taking place in the population at large and it seems highly likely that these females were going to overwinter.

Evidence that subordinates may result from worker-laid eggs is as follows. First, it seems likely that workers lay most of the male-producing eggs in this population (L. Packer, manuscript in preparation); therefore, most male-sized provision masses receive worker-laid eggs. Secondly, the proportion of workers that mate increases as the summer provisioning phase progresses (Packer 1986) indicating that workers should be capable of producing diploid eggs. Thus, small overwintering females could result from worker oviposition, perhaps late in the summer or after the death of the nest foundress. Subordinate females resulting from this behaviour would only have a coefficient of relatedness of 3/8 to the dominant individuals.

The large size difference between the dominant individuals

and most of the subordinates indicates that dominance relationships are probably determined on the basis of size. Foundresses of this species have been observed interacting underground in thin sandwiches of soil held together by sheets of glass (Packer and Knerer 1985). Large individuals were observed to grab hold of smaller ones by the neck with their mandibles. The small females were then taken to the bottom of the burrow and repeatedly pumelled into the earth at the end or bashed from side to side against the burrow walls. In many wasps, aggressive interactions have been ritualized into overt signalling behaviour (reviewed by West-Eberhard 1982). This is unlikely to be an option for halictine bees which must interact in the gloomy depths of their subterranean burrows. Overt displays of violence may be necessary to establish dominance relationships on the basis of size in sweat bees.

Dominance in polistines has been thought to be based upon size (Haggard and Gamboa 1980; Sullivan and Strassmann 1984), and differences in ovarian condition (Dropkin and Gamboa 1981). However, Röseler et al. (1984), in a study of Polistes gallicus, found that size did not affect dominance relationships and that juvenile hormone levels affected both ovarian development and levels of aggression. Thus, the correlation between ovarian development and dominance may result from the effects of juvenile hormone upon both features. It is unlikely that initial ovarian condition can be a factor in the establishment of dominance in sweat bees because these are mass-provisioning species that oviposit once after each cell has been provisioned. Additionally, halictine foundresses undergo ovarian development in few ovarioles at a time in spring, and produce a maximum of two eggs per day. Polistines, however, feed their larvae progressively and lay eggs before foraging. The ability to communicate potential fecundity may be more important in species that lay eggs first and forage later. A correlation between ovarian development and dominance may be advantageous in such circumstances. However, a correlation between juvenile hormone titre and aggression may not result in the establishment of dominance hierarchies in spring associations of Halictus ligatus: size differences appear to be more important and these may determine the outcomes of dominance interactions.

Pleometrosis and the evolution of social behaviour in halictine bees

There are two major hypotheses that seek to explain the route taken in the evolution of hymenopteran eusociality (see Brockmann 1984 for a review). (i) The semisocial hypothesis assumes the establishment of dominance relationships amongst females of the same generation before the origin of matrifilial societies. (ii) The subsocial hypothesis suggests that sociality arose because offspring stayed with their mother to raise a brood.

The semisocial hypothesis has been championed by West-Eberhard and other students of sociality in vespoid wasps. Studies of the selective advantage accruing to subordinate individuals in wasps have demonstrated that nest survival is the most important factor (Metcalf and Whitt 1977; Gamboa 1978; Gibo 1978; Gibo and Metcalf 1978; Noonan 1981; Strassmann 1981). This may perhaps be expected in organisms that make nests in exposed situations and in which the developmental period from egg to adult is long. Additionally, biogeographic and phylogenetic evidence suggest that vespoid sociality arose in the tropics where predation and parasite pressure may be expected to be particularly great.

More data are available on the social organisation of bees that are at the very earliest steps of social evolution than for wasps at a similar stage. Several species that are on the threshold of sociality have been studied: Euglossa cordata (Garófalo 1985), Halictus (Seladonia) confusus (R. Tuckerman, work in progress), and Lasioglossum (Dialictus) lineatulum (G. C. Eickwort 1986). Each of these three species has been shown to have solitary, subsocial, semisocial, and eusocial colonies within the same population. As yet, detailed investigations as to the relative costs and benefits to each type of social organisation have not been made for these species. Nonetheless, their importance for theories of the origin of eusociality are clear: in populations where eusociality is an emergent property, all types of social organisation may be present. Two prerequisites for this social diversity may be mentioned: tolerance of conspecifics and the ability to establish dominance relationships. Once the former has been established, associations between individuals of the same generation and between parents and offspring may both be expected. The fact that many normally solitary animal species exhibit dominance interactions indicates that the establishment of a hierarchy (perhaps consisting only of one dominant and one subordinate) may be a comparatively easy step (Michener 1985). The evolution of well-organised eusocial societies, whatever the precise mechanism, may only be possible after a protosocial insect could expect to have a group of conspecifics as part of its normal environment. Thereafter, the selective forces that result in pleometrosis and matrifilial associations may be expected to differ depending upon the relative advantages of each to the constituent members of the society. However, in the very beginning, both semi- and sub-social societies may be expected and the distinction between the two routes that may have been taken in social evolution may not be very clear in halictine bees.

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