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Research article

Demography and relatedness in multiple-foundress nests of the social sweat bee, *Halictus ligatus*

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Summary

Female sweat bees in the species *Halictus ligatus* exhibit a wide range of reproductive roles, ranging from typically foundress or queen-like to typically worker-like. Nests are founded in spring and most are haplometrotic, that is, founded by a single foundress. A few (up to 12%) are pleometrotic, founded by 2–6 foundresses. Variation in the proportion of multifoundress nests from year to year and from place to place suggests an adaptive basis for pleometrosis. We studied the demographic and social characteristics of 23 pleometrotic nests in an aggregation of 250–300 nests near Victoria, Ontario, in 1984, 1990, and 1991. In pleometrotic associations, dominant foundresses behaved in a manner typical of mid-summer, haplometrotic queens, while subordinates behaved like mid-summer workers. Dominant foundresses tended to be larger than subordinates. Pleometrotic nests were significantly more likely than haplometrotic nests to produce brood, and they also produced more workers. However, this early advantage did not result in the production of more reproductive brood per nest, nor did pleometrotic foundresses experience higher productivity per foundress than did haplometrotic foundresses. Relatively low relatedness among various categories of brood implied that subordinate foundresses were not closely related to dominants. We suggest that pleometrosis most likely results from accidental encounters between spring foundresses as they leave their hibernacula. Once formed, such associations confer a survival advantage on the nest as a whole, but do not result in greater reproductive brood productivity.

Introduction

The remarkable flexibility of halictine social behaviour is most dramatically revealed in socially polymorphic species such as *Halictus rubicundus* (Eickwort et al., 1996) and *Lasioglosum calceatum* (Sakagami and Munakata, 1972), both of which are social at low altitudes and solitary at high altitudes. More subtle but just as interesting, is the degree of flexibility observed in obligately social species such as *H. ligatus* (Michener and Bennett, 1977; Richards and Packer, 1994, 1995, 1996; Richards et al., 1995). A single *H. ligatus* female may exhibit reproductive behaviours that run the gamut from typically foundress or queen-like to typically worker-like. The choice of reproductive roles available to any particular female is dictated mainly by several important factors at the time of emergence: the social milieu of the nest, body size and fat stores at eclosion, and time of year (Michener, 1974, 1990; Richards and Packer, 1994). In *H. ligatus* nesting in southern Ontario, Canada (Packer, 1986a, Richards and Packer, 1995), females that emerge in mid-summer, that are small, have few or no fat stores, and whose nest-mates include a larger queen, are destined to become workers in their natal nests, assisting their mothers to raise the second, reproductive brood. Females that emerge in late summer, that are large and have large fat stores, are destined to mate, overwinter, and become foundresses of their own nests the following spring.

There are several exceptions to these rules. For instance, while some workers are altruistic, completely foregoing their own reproduction in favour of raising the queen's offspring, many workers lay eggs, raising their own offspring in addition to the queen's (about 50% of *H. ligatus* workers are inseminated and are capable of producing diploid eggs [Richards et al., 1995]). Variation in foundress behaviour is also observed. Typical foundress behaviour consists of solitary nest exavation and brood provisioning in the spring, followed by queen-type behaviour after the mid-summer emergence of workers. Multiple-foundress associations are exceptions to this pattern, because one foundress, often the largest, becomes dominant, ceases foraging, and begins to exhibit behaviour typical of a mid-summer queen with workers (Packer, 1993). The subordinate foundresses continue to forage, but their social role resembles that of mid-summer workers more than haplometrotic, spring foundresses.

In *H. ligatus*, the frequency of multifoundress nest-founding varies among populations (Chandler, 1955; Litte, 1977; Eickwort, 1985; Packer, 1986b, Packer and Knerer, 1986a), but haplometrotic nests always outnumber pleometrotic ones. In 1984, Packer (1986a, b) studied haplometrotic and pleometrotic nests in an aggregation near Victoria, in southern Ontario. Packer observed that very small haplometrotic foundresses experienced high rates of nest failure, but that small subordinate foundresses could contribute significantly to the enhanced reproductive success of pleometrotic nests. Packer proposed that as solitary foundresses, small females had a relatively low probability of successful reproduction, but that subordinates that assisted a related dominant foundress could gain inclusive fitness benefits. Thus subordinate behaviour could be explained by joiner subfertility or ergonomic synergism. Recently, we found that in single-foundress nests of Victoria *H. ligatus*, important social parameters such as body size, probability of nest failure, brood productivity, and patterns of genetic relatedness among nestmates change markedly from year to year (Richards and Packer, 1995, 1996; Richards et al., 1995). Since these parameters might also change in multifoundress nests, we decided to re-examine Packer's hypothesis.

Methods

Demographic data

This study is part of our examination of the links between environmental variation and the expression of social behaviour at an aggregation of 200–300 nests of

Halictus ligatus at Victoria, near Toronto in southern Ontario (Richards et al., 1995; Richards and Packer, 1994, 1995). This study includes data from 1984, 1990, and 1991; observations from 1984 were originally published by Packer (1986a, b).

At Victoria, mated foundresses emerge from their overwintering hibernacula in late May or early June. We have observed several methods of nest establishment. In the first, foundresses search for new nest sites in a typical slow meandering flight, inspecting cracks and holes in the soil. After finding an appropriate site, they excavate their burrows downward from the soil surface. A second method, less common than the first (Packer and Knerer, 1986b), is for foundresses to use the tunnels from which they emerged from their overwintering hibernacula as the basis for new nests. Occasionally they may refurbish their natal nests (from the previous summer) if tunnels still exist the following spring.

In early June, foraging foundresses with newly established nests were caught by placing clear plastic cups over the nest entrances, trapping departing females and preventing returning females from entering. Each forager was then caught in a hand net and held immobile so that individual colour marks (spots of enamel paint on the top of the head) could be applied with fine blades of grass or toothpicks. Pleometrotic nests were identified by the presence of at least one foraging foundress (the subordinate) and one non-foraging foundress (the dominant) which remained inside the nest, sometimes guarding the entrance. The head widths (HW) of foraging foundresses were measured in the field with an ocular micrometer accurate to 0.1 mm or in the laboratory with a binocular microscope accurate to 0.05 mm (as in Richards and Packer, 1996). HW was measured as the widest distance across the head, including the compound eyes. Because dominant foundresses did not forage, they were measured only if they were still alive at the time of excavation or if their bodies were found in the nest (so called "forensic apidology").

Several pleometrotic nests originally identified as haplometrotic, were recognized as pleometrotic at the time of excavation. These nests contained a subordinate foundress (an adult female with worn wings and mandibles and developed ovaries) smaller than the workers in that nest. These tiny foundresses must have been subordinates since haplometrotic foundresses invariably produce workers smaller than themselves (Richards and Packer, 1996). One exceptionally large nest, #157, was excavated on 13 August 1991 (see Fig. 2), and was probably pleometrotic, but since the foundresses were not found, this identification is not absolutely certain. The exclusion of nest #157 had no effect on the statistical significance of any comparisons between single and multifoundress nests.

Nests were excavated in spring and early summer during the period of worker brood development, or in mid to late summer during the period of reproductive brood development, using previously described methods (Packer, 1986a, 1986b; Richards, 1994). Excavation dates are given in terms of the number of weeks after mid-May, when foundresses begin to emerge from hibernal diapause. Pupae and larvae that had consumed their entire pollen masses were transferred from their brood cells to small chambers in wax-lined petri dishes, raised to adulthood in the laboratory, and then frozen at −80 °C. Adults, pollen masses, and small larvae were stored in separate microfuge tubes on ice in the field and then transferred to the freezer. Brood sizes were calculated as the total number of pollen masses, larvae, pupae, and callow adults present when a nest was excavated. Brood sizes underestimate maximum potential brood production because the earliest reproductive brood could emerge as adults and leave the nest before the youngest eggs were even laid, especially in nests with many workers. Therefore comparisons between haplo- and pleometrotic brood are for nests excavated during the same week. Only nests that were completely excavated were included in the data.

Behavioural observations

Behavioural data were collected during observations of foundresses at nest entrances. Intensive foraging observations began just before nest entrances were opened in the morning (about 10.00 h) and ended when the observed nests closed in the afternoon (by 17.00 h). Intensive observations were focussed on 4–8 nests per day. Alternatively, nests were surveyed daily at about 12.00 h to determine whether foundresses foraged on any particular day. Observations took place throughout the summers of 1984, 1990, and 1991.

Patterns of relatedness

Enzyme electrophoresis of two variable enzymes, *Hk* and *Gda*, was used as the basis for calculating genetic relatedness (Queller and Goodnight, 1989) among different classes of nestmates in 10 pleometrotic nests collected in 1991. Only three of these contained live foundresses at the time of excavation, so relatedness estimates involving queens are very imprecise. Details of the electrophoretic methods and relatedness calculations may be found in Richards (1994). The assumptions of Hardy-Weinberg equilibrium and lack of selection at these two loci, which are necessary for relatedness calculations, were satisfied (Richards et al., 1995). Nest #157 (see above) was not included in analyses of relatedness.

Statistical methods

Analyses based on linear models require that the data be drawn from a normal distribution. This condition was satisfied for the distributions of head width, but not for brood sizes, for which non-parametric analyses were required. A one-way analysis of variance (ANOVA) on ranked instead of raw data is formally equivalent to the Kruskal-Wallis *k*-sample test, a method for comparing the ranks of two groups. A one-way ANOVA on the rank of brood size was used to compare the reproductive brood sizes of haplo- and pleometrotic nests, because all the nests were excavated during the same week. To compare worker broods, which were excavated in two different weeks, we used a two-way ANOVA (essentially, a two-way Kruskal-Wallis test [Potvin and Roff, 1993]), according to the model

$$\text{rank of brood size} = B + \text{nest type} + \text{week excavated} + e.$$

Results

Nest development and productivity

In 1984, 13 of 130 nests (10%) marked in spring were pleometrotic. In 1990, only one multiple foundress nest was discovered among a total of 49 nests (2%), and in 1991, 9 of 78 (12%) nests were pleometrotic. In 1984 the number of foundresses per pleometrotic nest varied from two to four, whereas in 1991 it varied from two to six. Although the number of pleometrotic nests found in 1990 seems low, the proportion of multifoundress nests did not change significantly from year to year ($X^2 = 3.40$, df = 2, ns).

In 1984, all seven pleometrotic nests not excavated during the first brood period survived to produce reproductive brood. In 1990, the single pleometrotic nest survived to produce at least one worker and several reproductives. In 1991, 7/9 nests identified in spring survived to produce reproductive brood but two succumbed in early summer, only 3–4 weeks after the beginning of the foundress-foraging period. In one of these failed nests (M5), the subordinate foraged for pollen on 14 June 1991, was seen entering the nest without pollen on 15 June, and then no further activity was noted, although the nest was periodically observed until it was excavated on 2 August. The nest contained many short, interconnecting tunnels, one filled-in brood cell and two brood cells with moldy contents. There were no adults. The second nest, M3, was dug up on 16 August and contained three tunnels, one filled-in brood cell, and one empty cell. It appeared to have been destroyed by earthworms.

In 1991, the average size of the first (worker) brood was significantly greater in pleometrotic than in haplometrotic nests (Fig. 2; ANOVA on rank of brood size: $F = 4.37$, df = 4,9, $p < 0.05$). Although the first brood includes males, this implies that multifoundress nests produced more workers than single-foundress nests. This advantage did not translate into significantly larger second (reproductive) broods: a comparison of brood sizes during week 14 indicated no significant difference between the two types of nests ($F = 2.00$, df = 1,15, $p > 0.05$). Mean productivity per pleometrotic co-foundress was estimated based on two simplifying assumptions: 1) that nests discovered late in summer had had only two foundresses in the spring, and 2) equal rates of oviposition per foundress. These assumptions mean that productivity per pleometrotic foundress may be overestimated, but there was still no significant difference between pleometrotic and haplometrotic nests ($F = 2.01$, df = 1,15, ns).

Body size

The sizes (HW) of haplometrotic, dominant and subordinate foundresses from 1984 (n = 102) and 1991 (n = 64) are compared in Figure 1. Sizes are not known for the two foundresses of the only pleometrotic nest found in 1990. In 1994, Packer (1986 b) found that dominant, pleometrotic foundresses were significantly larger and subordinates were smaller on average than haplometrotic foundresses. The same pattern was evident in 1991: subordinates (mean HW = 2.6 mm, n = 16) were smaller than haplometrotic foundresses (mean HW = 2.8 mm, n = 35; t = 2.581,

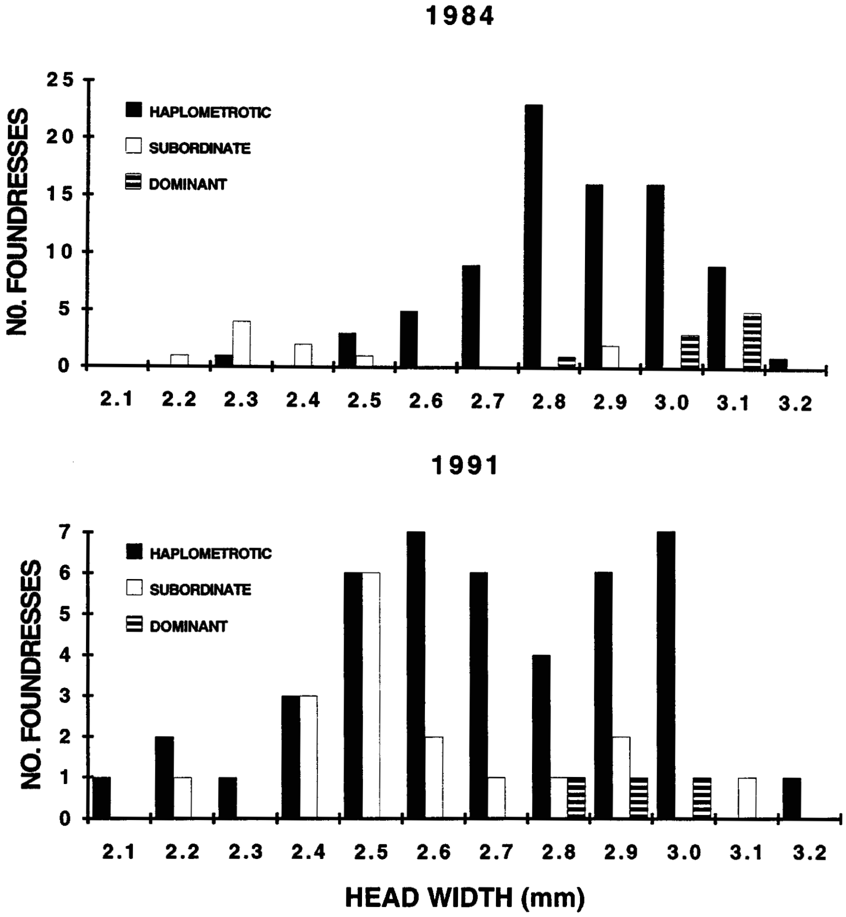

Figure 1. Comparison of head widths of dominant, subordinate and solitary *H. ligatus* foundresses in 1984 and 1991. The 1984 figure is reconstructed from Packer (1986 b)

df = 49, $p < 0.05$). Dominant foundresses (mean HW = 2.9 mm, n = 3) were significantly larger than subordinates (t = 2.2089, df = 17, $p < 0.05$), but not larger than solitary foundresses (t = 1.324, df = 36, ns). This lack of significance may be due to the very small number of dominant foundresses whose head widths were known.

Relatedness among nestmates

Average relatednesses among different classes of relatives within 1991 multi-foundress nests are given in Table 1. These estimates are compared with the values when a haplometrotic foundress lays all the eggs. It is likely that the average number of mates per foundress is two, and that sperm usage in diploid eggs is random (Richards et al., 1995).

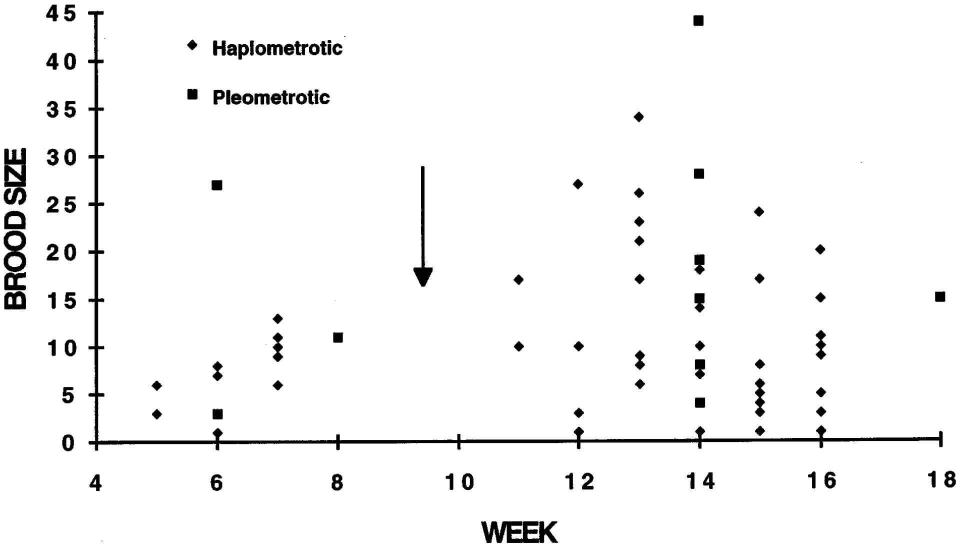

Figure 2. Total brood sizes in single and multiple foundress nests excavated at Victoria in 1991. The arrow indicates the approximate commencement of reproductive brood production. Nest # 157 (the largest nest found) was identified as pleometrotic because of its large brood size, but this identification is not completely certain

Table 1. Patterns of relatedness in *Halictus ligatus* nestmates from haplometrotic and pleometrotic nests in Victoria, Ontario in 1991. Asterisks indicate significant deviation of the observed value of relatedness from that expected (see text). Foundresses may be multiply (probably twice) mated, but sperm usage in diploid eggs appears to be random. Data for haplometrotic nests are from Richards et al. (1995)

Relationship	Haplometrotic nests observed R + SE	Expected *r*	Pleometrotic nests observed R ± SE	N
Foundress-worker	0.38 ± 0.15	0.5	−0.040 ± 0.218	3,13
Foundress-male	1.00 ± 0.00	1.0	0.285 ± 0.602	3,12
Foundress-gyne	−0.18 ± 0.19	0.5	0.153 ± 0.423	2,25
Worker-worker	0.49 ± 0.11	0.5	0.016 ± 0.096*	28
Worker-male	0.40 ± 0.18	0.25	0.045 ± 0.026*	21,30
Worker-gyne	0.23 ± 0.13	0.5	0.282 ± 0.603	10,40
Gyne-gyne	0.28 ± 0.08	0.5	0.257 ± 0.153	41

The 95% confidence interval around the observed value of worker-to-worker relatedness in pleometrotic nests does not include 0.5 (Table 1). If dominant foundresses completely monopolize oviposition, then relatedness among workers should be about 0.5, approximately the same value observed in single foundress nests (Richards et al., 1995). This is evidence that subordinate foundresses share in oviposition of the worker brood. In the one pleometrotic nest in which the dominant foundress was still alive at the time of excavation, average foundress-worker relatedness was 0.27±0.26 (R±1 s.e.). In contrast, in the two nests with surviving

Table 2. *Hk* (hexokinase) and *Gda* (guanine deaminase) genotypes found among the workers of one multiple foundress nest excavated in 1991. This array of genotypes indicates multiple paternity of the workers of this nest, but also supports the hypothesis of multiple maternity. *f* = fast allele, *s* = slow allele, *vf* = very fast allele

Hk	*Gda*	No. workers with genotype
f/f	*f/f*	2
f/f	*s/s*	3
s/f	*f/f*	1
f/vf	*f/f*	1
f/vf	*s/f*	2
s/vf	*s/f*	1

subordinates (and no dominant) foundress-worker relatedness was −0.13 ± 0.18. Although relatedness estimates for individual nests are exceedingly imprecise (Queller and Goodnight, 1989), the rank order of these estimates supports the hypothesis that dominant foundresses secure the greatest share of oviposition.

Further evidence for oviposition by subordinates comes from an examination of genotype arrays within nests. If multiple paternity alone were the reason for the large number of genotypes sometimes observed among the workers of a single colony (Table 2), then many foundresses would have to have mated more than twice and we would again expect that relatedness among workers would be about 0.5 (Richards et al., 1995). More likely, multiple maternity of workers and early males is due to oviposition by subordinate foundresses. In reproductive broods, multiple maternity of gynes and late males could also be due to egg-laying by workers (as occurs in single foundress nests [Richards et al., 1995]).

Behaviour of pleometrotic foundresses

The dominant foundress was still alive at the time of excavation in only three pleometrotic nests, one excavated during week 12 in 1990, and one each during weeks 8 and 14 in 1991. In two other 1991 nests, a subordinate foundress that had been marked in spring, had outlived the dominant, and was still alive when the nest was excavated. Both of these subordinates had mated and had developing ovaries, one with 4 oocytes and one with 6. These subordinates, which had definitely been observed foraging in the spring, did not resume foraging after worker emergence. In contrast, in pleometrotic nests in which the dominant foundress survived to worker emergence, the subordinates also continued foraging after worker emergence (see below).

The behaviour of both dominant and subordinate foundresses differed in several respects from that of haplometrotic foundresses. Haplometrotic foundresses foraged on about two out of every three days of suitable (not rainy or cold) weather, and spring foraging activity continued for several weeks until the first brood was completely provisioned in mid to late June (Richards, unpubl. data). Thereafter, foraging activity in haplometrotic nests ceased until the emergence of the workers. In pleometrotic nests, subordinates foraged every suitable day, but unlike the haplometrotic foundresses, they continued to forage up to and beyond the emergence of their workers. This difference between the two types of nests may be due to aggressive behaviour by dominant foundresses. In both 1984 and 1991, we observed dominant queens as they physically ejected subordinates from the nest, and then pushed them out the entrance when the subordinates tried to re-enter the nest. On one such occasion in 1991, a dominant forced a small subordinate to forage past the point of exhaustion. The subordinate completed almost twice as many foraging trips as most of the surrounding haplometrotic foundresses. On her last three foraging trips of the day, she literally fell out of the air and then crawled weakly to the nest, rather than landing right at the entrance as is customary with *H. ligatus* foragers. This subordinate was never seen again and probably died soon after this incident took place. The dominant foundress did not resume foraging after the subordinate's disappearance.

Dominant foundresses may experience difficulty adjusting to the disappearance of their subordinates. In the sole multifoundress nest of 1990, the subordinate disappeared about two weeks after the nest was founded. The dominant foundress, who had earlier been observed pushing the subordinate out the nest entrance to forage, spent at least three days sitting in the nest entrance, waving her antennae and occasionally half-emerging before going back inside. She eventually resumed foraging herself, but this delay cost her at least three days of foraging activity.

Discussion

It is difficult to assess the adaptiveness of multifoundress nest founding in *Halictus ligatus* because so few nests are of this type. At Victoria, up to 12 % of 200–300 nests were pleometrotic, and the proportion varied from year to year. In some other *H. ligatus* populations, pleometrotic nests do not occur at all (Chandler, 1955; Eickwort, 1985). The rarity of pleometrotic nests in *H. ligatus* suggests that in proximate terms, multifoundress associations are probably formed by accident when young foundresses encounter each other as they emerge from hibernation. Such encounters are made more likely by *H. ligatus* nest architecture, because young gynes hibernate in tunnels under their natal nest (Packer, 1986 b; Packer and Knerer, 1986 b), sometimes in the same tunnel and separated only by thin soil partitions (M. Richards, unpubl. data). Occasionally, small, worker-destined females also overwinter, rather than foraging in their natal nests (Richards and Packer, 1994), and such small workers may be the source of very small subordinates. The tendency to retain worker-like characteristics is supported by an unusual nest excavated in mid-June, 1991. This nest contained a single small foundress and several young brood. At this time of year, nests should contain round, worker-brood pollen masses, but the pollen masses in this nest were shaped like those that produce gynes (Boomsma and Eickwort, 1993). This exceptional occurrence could be explained if the nest was founded by a former worker and if workers are behaviourally programmed to produce gyne pollen masses, and sometimes do so even when they have become foundresses.

Pleometrotic nest-founding is known in other sweat bee species (Packer, 1993), including *H. scabiosae* (Knerer and Plateaux-Quénu, 1966; Gogala, 1991), *Lasioglossum lineatulum* (Eickwort, 1986), and *L. comagenense* (Batra, 1990). Pleometrosis has been particularly well studied in the vespine wasp genus *Polistes*, in which nests are often initiated by a single female who is joined by others during the earliest stages of colony development (Reeve, 1991). As in *H. ligatus*, joining or subordinate behaviour by foundresses is facultative, and the number of foundresses and the frequency of multifoundress nests varies from place to place or among species. Reeve (1991) listed seven adaptive explanations for joining and subordinate behaviour and concluded that for *Polistes* the evidence most convincingly supported enhanced defence against usurpation by conspecifics, survivorship insurance, and nest site limitation. We examine Reeve's hypotheses as adaptive explanations for multifoundress behaviour in *Halictus ligatus*.

Ergonomic synergism could explain pleometrotic nest-founding in *H. ligatus*, if pleometrotic colonies produced brood more efficiently than haplometrotic ones, and if subordinates were closely related to the dominant foundresses that monopolize oviposition. Since most pleometrotic associations in *H. ligatus* are digynous (Litte, 1977; Packer, 1986b; this study), subordinates would have to gather provisions at more than twice the rate of haplometrotic foundresses in order to achieve the same productivity per foundress as in haplometrotic colonies. Subordinate foundresses tend to forage every day that the weather is favourable, while haplometrotic foundresses tend to forage during two out of every three days (Richards, unpubl. data). A provision mass is constructed from the pollen gathered in a single day's foraging effort (Richards, unpubl. data), so a subordinate in a digynous nest can provision three brood for every two provisioned by a solitary foundress. This explains why pleometrotic nests produce more workers than haplometrotic nests. Nevertheless, ergonomic efficiency cannot explain subordinate behaviour. Even if co-foundresses are natal nestmates, average relatedness among *H. ligatus* gynes from haplometrotic nests is only $R = 0.29$ (Richards et al., 1995), and pleometrotic foundresses experience lower brood productivity than haplometrotic foundresses (Table 3, Fig. 2). In fact, in some pleometrotic nests, the subordinates may actually have a negative effect on brood production: in 1991, two nests with four and five foundresses each had very low brood productivities. Some of the subordinates in these nests were as large as average haplometrotic foundresses, so the dominant females may have had trouble controlling their behaviour (Richards and Packer, 1995). A similar pattern of lower productivity in multifoundress nests was also noted by Litte (1977), who studied a nesting aggregation of *H. ligatus* in New York, and may be especially common when associations contain more than two foundresses (Packer, 1993). In contrast, in the allodapine bee *Exoneura bicolor*, brood productivity per foundress was higher in multifemale groups than in single-foundress colonies (Silberbauer and Schwarz, 1995).

Nest survivorship insurance (Reeve, 1991) is likely an important advantage for pleometrotic nests. If one foundress dies, another is available to care for the nest. At Victoria, the rate of nest failure (in which a nest produces no brood that survive to adulthood) was much higher in haplometrotic than in pleometrotic nests (Table 3). In the three years 1984, 1990 and 1991, only two of the total 25 multifoundress nests marked in spring produced no reproductive brood, whereas 30–50% of haplometrotic nests failed in that time (Richards and Packer, 1995). Usually, nest failure in *H. ligatus* is associated with the disappearance of the foundress, and is strongly affected by local weather conditions, especially prolonged periods of rain

Table 3. Comparison of demographic and reproductive quantities relevant to the fitnesses of foundresses in haplometrotic and pleometrotic nests. Demographic data for haplometrotic foundresses summarized from Richards and Packer (1995). The size of the reproductive brood is compared during week 14 of 1991

	Haplometrotic	Pleometrotic
Nest survival to worker brood emergence	61%	92%
Foundress survival to worker brood emergence[a]	45%	dominant 33%, subordinate 67%
No. workers per nest[a]	≥8.5	≈15.0
Worker-worker relatedness[a]	0.49	0.02
Maternity of worker brood	foundress only	shared, dominant > subordinate
Nest survival to production of reproductive brood	57%	90%
Foundress survival to production of reproductive brood	50–70%	dominant 33%, subordinate 33%
No. reproductive brood per nest[a]	12.6 ± 12.3	13.7 ± 8.9
No. reproductive brood per original foundress[a]	12.6 ± 12.3	5.6 ± 4.8
Maternity of reproductive brood	shared, queen > workers	shared, foundress < workers?

[a] Estimates based on 1991 only.

(Richards and Packer, 1995). Multifoundress nests may be less likely to fail, because in poor weather more nest maintenance, such as excavation of "aerating" tunnels (Packer and Knerer, 1986 a), may be required. Interestingly, this advantage of pleometrosis applies equally to dominant and subordinate foundresses, since nest failure is not associated with foundress body size.

The remaining adaptive explanations for subordinate behaviour are subfertility, enhanced nest defence, and nest site limitation (Reeve, 1991). Packer (1986 b) proposed that subfertility was the reason why some females become subordinates, because in 1984, small, haplometrotic foundresses experienced relatively high rates of nest failure and low reproductive success. However, our examination of haplometrotic foundress size in 1984, 1990, and 1991 indicates no overall effect of foundress size on nesting or reproductive success (Richards and Packer, 1995, 1996). The survival of several small subordinates well past mid-summer, together with the early disappearance of several dominant females, also indicated that foundress size may have little direct effect on survival or productivity.

Multifoundress nests should be more resistant to predators and parasites, because the dominant female is always available to guard the nest entrance while the subordinate forages. At Victoria, the main allospecific brood parasites were bee flies (*Bombylius pulchellus*), but parasitism frequency did not differ between multiple and single foundress nests (Packer, 1986 b, 1988; Richards, unpubl. data).

Nest usurpation by *L. leucozonium* occurs very rarely. There is also no behavioural evidence for intraspecific brood parasitism at Victoria despite hundreds of hours of observations of marked bees at nest entrances (Richards and Packer, unpubl. data). In general, protection against predators or parasites seems unlikely to bestow any significant advantage on pleometrotic nests.

Nest site limitation could encourage females to nest together, but at Victoria, only a small portion of the apparently desirable nesting area was used, and areas that were used successfully one year were not always used the next. Soil hardness, a critical factor affecting pleometrosis in the presocial sphecid wasp *Cerceris antipodes* (McCorquodale, 1989), is not relevant at Victoria, since there is substantial rainfall in spring (Richards and Packer, 1995).

We suggest that the existence of multifoundress associations in *H. ligatus* is best explained by a combination of coincidence and nest survivorship. Multifoundress associations are probably formed by accident as females encounter each other in spring, but they have the advantage of enhanced nest survivorship relative to haplometrotic nests. However, for pleometrosis to be adaptive, this advantage would have to outweigh the strong disadvantage of decreased individual reproductivity. It is possible that maternity of worker brood may provide sufficient genetic benefit to co-founding, because worker-brood males may have high reproductive value and many workers themselves produce reproductive brood (Richards et al., 1995), but we do not yet have sufficient data to evaluate this possibility.

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