Solitary and eusocial nests in a population of *Augochlorella striata* (Provancher) (Hymenoptera; Halictidae) at the northern edge of its range

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Summary. *Augochlorella striata* was studied at the northern limit of its range. The study population contained a mixture of solitary and social nest foundresses. Eusocial foundresses produced 1 or 2 workers before switching to a male biased brood. Solitary foundresses produced males first. Cells vacated by eclosed offspring were reused late in summer. A female biased brood resulted from cell reuse in both solitary and eusocial nests. Workers were slightly smaller than their mothers and were sterile although most of them mated. In comparison to published data from a Kansas population of this species, the Nova Scotia population had i) a lower proportion of multiple foundress nests, ii) a smaller worker brood and iii) a briefer period of foraging activity but iv) comparable overall nest productivity.

Introduction

Geographically distinct conspecific populations of Halictine bees often exhibit markedly divergent social organisations. Sakagami and Munakata (1972) showed that a population of *Lasioglossum calceatum* at high elevation was solitary even though nearby lowland populations were eusocial like those in France (Plateaux-Quénu 1974, 1979). In *Halictus ligatus* there is a decrease in the degree of sociality towards the equator (Michener and Bennett 1977; Packer and Knerer 1986). Other examples of geographic variation in sweat bee social biology have been provided by Eickwort (1985) and Eickwort and Eickwort (1969).

The halictine tribe Augochlorini has its centre of distribution in Central and South America: only a few species reach the temperate Nearctic (Eickwort 1969). *Augochlorella striata* (Provancher) occurs further north than any other member of the tribe (Ordway 1966b). This species is known to be eusocial in Kansas (Ordway 1965, 1966a; Michener 1974). In September 1986, an aggregation of this species was found on Cape Breton Island (45.47° N, 60.37° W), well beyond the previously

known northern limits of its range. This marginal population was studied throughout its period of flight activity in 1987.

The following account of the biology of the Kansas population is taken from Ordway (1965, 1966a). *Augochlorella striata* was active from the beginning of April until late September and pollen ball construction occurred from the second week of May until mid August. Although multiple foundress associations were common (with a mean of over 2 females per nest in spring) all overwintered females foraged and appeared fecund. Some new nests were initiated late in spring, apparently due to multiple foundress associations splitting up. Queens did no foraging after the emergence of the female-biased first brood, this activity was left to worker daughters which averaged 4.2% smaller than foundresses and had low levels of ovarian development. If a nest was orphaned early in summer, a daughter became replacement queen and foraging recommenced after a period of inactivity. The mean number of brood cells increased gradually during the summer, reaching a peak of 12. Only a few cells were used twice and the number of offspring produced per nest averaged between 14 and 15, slightly greater than the number of brood cells.

Under the rigours of a maritime Canadian climate, *A. striata* should exhibit the following differences: 1) a reduced duration of brood production, resulting in; 2) fewer workers per nest and; 3) fewer reproductives; 4) nest foundresses may produce a mixture of workers and reproductives as a result of their own foraging – such "brood divalency" has been described for *Halictus rubicundus* by Yanega (1988, 1989). Similar production of reproductives along with workers is known in an arctic bumble bee (Richards 1973) and a montane paper wasp (Lorenzi and Turilazzi 1986).

Methods

In the period June 24–26, over 300 *A. striata* nests were discovered by locating turrets at nest entrances (Ordway 1966a; Packer et al.

1989b). Dense nest patches were observed in detail during provisioning phases and females were given individually distinctive patterns of Testors PLA enamel paint. This allowed the number of foundresses and workers per nest to be counted. During the eusocial phase, a previously uninvestigated part of the nest site was searched for active nests. The relative frequency of more populous nests was probably overestimated in the latter sample as it was easier to find more active nests.

Nest productivity and brood cell content data were obtained by excavation. Entire brood cell clusters were removed from the soil for dissection. Cell contents were either censused and discarded (if unlikely to be reared successfully) or placed in individual depressions in wax-filled petri dishes and reared to adulthood. Sex ratios were estimated by counting male and female brood and measuring the dry weight of reared adults. Pupae were sexed and their head widths measured (± 0.05 mm). Recently eclosed adults were dried in an oven at 80° C and weighed. Female mean weight (but not male) varied significantly among time periods. Consequently, average investment in males and females was estimated for each time period separately. The population investment ratio (proportional investment in males) was calculated as:

$$\frac{\sum_{i=1}^{6} Nm_i \cdot Wm_i}{\sum_{i=1}^{6} (Nm_i \cdot Wm_i + Nf_i \cdot Wf_i)}$$

Where Nm_i = mean number of males per nest in time period i; Nf_i = mean number of females per nest in time period i; Wm_i = mean dry weight of males in time period i and Wf_i = mean dry weight of females in time period i.

The population numerical sex ratio was calculated as above but with the weight variables omitted. In ants, dry weight investment estimates exaggerate the degree of female bias in comparison to energetic cost ratios, the degree of overestimation being correlated with the degree of sexual size dimorphism (Boomsma 1987, 1989). Sexual size dimorphism in *A. striata* is significant (Fig. 4) but small: the individual dry weight ratio (male:female) was 1:1.13. Investment estimates are unlikely to be heavily biased by sex differences in energetic costs per unit adult dry weight.

For ease of statistical analysis, some data are presented grouped in 10 day time periods. Time period (t.p.) 0 began on the first day that nests were excavated – 24 June, and lasted until 2 July; t.p. 1 lasted from 3 July to 12 July etc. Methods for nest excavation, assignment of wing and mandibular wear scores and ovarian condition etc. follow Packer (1986). Terminology for female categories

is from Eickwort and Kukuk (1987) and Yanega (1989). Means are presented along with standard deviations, the adjusted G test is used for analysis of 2×2 contingency tables and non-parametric tests are employed where sample sizes are too small for variance estimates to be accurate. Note that some brood cells were reused late in summer and the number of offspring produced in nests exceded the number of brood cells in some cases.

Results

Description of colony cycle

Nest initiation occurred in mid June. Two nests excavated on 24 June contained 1 and 2 completed pollen balls with eggs. The productivity (number of brood cells plus the number of brood cells used twice) of nests excavated at different times during the summer (Fig. 1) suggests a low frequency of multiple foundress association. For discussion of the limited evidence for multiple foundress nests see Packer et al. (1989a).

Rainfall in July was 80% lower than average. This resulted in drought conditions towards the end of the month, after more than 5 brood cells had been provisioned. Dry soil conditions made brood cell construction increasingly difficult as indicated by the extreme fragility of the few cells constructed at this time. Despite the continued abundance of flowers and foraging by other halictine species with a nest architecture involving less soil manipulation, *A. striata* ceased provisioning before the end of July (compare brood productivity figures for time periods 2 and 3 in Table 1). Nest excavations revealed that most brood cells contained pupae at this time (Fig. 2) and these were mostly male. This seemed unusual for a supposedly social insect for which a brood of workers would be expected at this time. It was concluded (prematurely) that this was a solitary population and large numbers of nests were excavated to ensure accurate estimation of the sex ratio. Pollen foraging began again in early August.

Of 43 marked nests in which the foundress was still alive in August, 30 (70%) became reactivated for a sec-
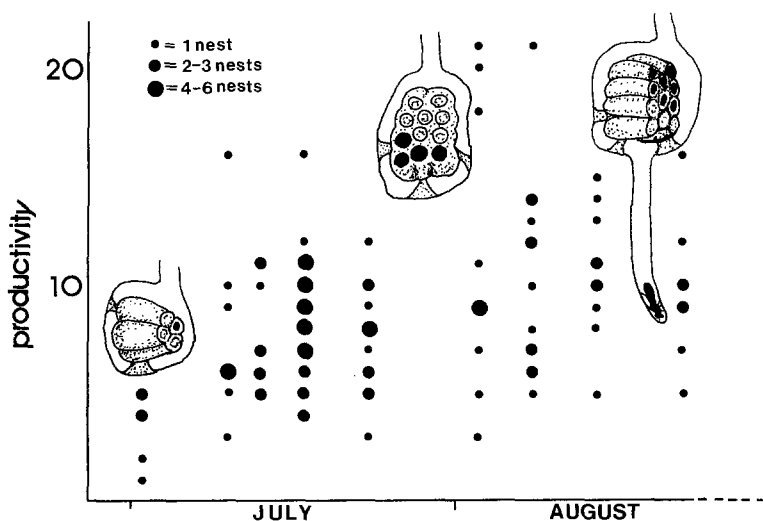

Fig. 1. Productivities of *A. striata* nests at various times during the summer. Six outlying points with very high productivity may represent multiple foundress associations. The drawings represent blood cell clusters as they appear at the appropriate times

ond bout of pollen foraging. However, the average number of brood cells did not increase significantly after reactivation (mean number of cells in t.p. $2 = 7.21 \pm 2.5$, $n = 34$; t.p. 4 mean $= 8.09 \pm 3.28$, $n = 25$; $t = 1.15$, $P > 0.2$), even though there was an average of 3.3 ± 2.22 recently provisioned cells in reactivated t.p. 4 nests. Furthermore, the number of brood cells was not significantly greater in reactivated nests than in non-reactivated nests within t.p. 4 (Mann-Whitney U test, $U_s = 41$, $P < 0.1$). These data suggest that new cells were not constructed for brood produced in August but that cells vacated by eclosed offspring were reused.

Table 1 presents data on nest productivity at different times during the summer for nests with different categories of adult occupancy. Figure 2 shows seasonal variation in nest contents. The division of foraging into two phases is indicated by the almost complete absence of pollen balls in time periods 2 and 3. Offspring of both sexes were first found as callow adults within their natal brood cells on July 17th.

The second bout of provisioning involved both old (the original foundresses) and young foragers (workers). The two could be distinguished easily: wings of ageing mothers were yellowish-brown and frayed and their bodies were bronzy in colour whereas more recently emerged females had hyaline, unworn wings and a deep blue-
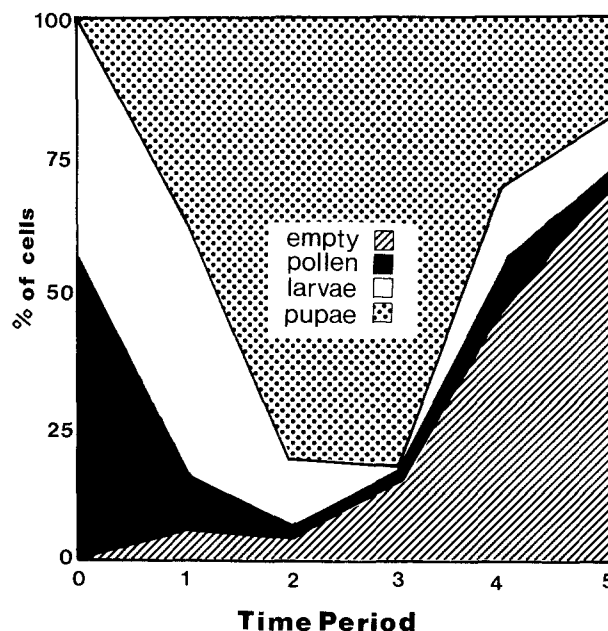

Fig. 2. Contents of cells in nests within different ten day time periods

green integument. This nest reactivation resulted in an average of 4.5 (± 4.1, $n = 32$) additional offspring per nest.

No orphaned nests were reactivated: females emerging in these nests excavated overwintering burrows, as did some daughters in nests with surviving foundresses. Early in t.p. 4, 5 females in 4 orphaned nests excavated overwintering burrows beneath the natal brood cell cluster whereas 8 of 9 females in 7 nests with surviving foundresses became workers in matrifilial societies. This difference is significant if daughter females or nests are analysed ($G_{adj} = 11.44$, $P < 0.001$; $G_{adj} = 10.06$, $P < 0.005$ respectively).

Only one pollen ball was found in t.p. 5 nests, indicating that provisioning had effectively finished by mid August.

Foundress variation

Foundress mortality was high in the early stages of brood production. Of 46 dead foundresses found in their natal nests, 21 (46%) had puparia of parasitic conopid flies within their abdomina. Surviving foundresses in

Table 1. Productivity and social status of nests of *A. striata* at various times during the summer

Time period 1st day	Productivity – mean number of offspring[a] (SD) sample size				
	All[b] nests	Nests with some brood survival	Nests with foundress present	Foundress-right non-reactivated	Reactivated nests
0 24.6	3.57 (1.18) 7	3.57 (1.18) 7	3.8 (1.17) 7		
1 3.7	3.31 (2.39) 16	4.42 (1.56) 12	5.2 (1.3) 5		
2 13.7	4.76 (3.65) 100	6.26 (2.83) 78	7.21 (2.5) 34		
3 23.7	4.23 (3.59) 34	5.92 (2.74) 25	6.38 (2.5) 13	5.73 (2.09) 11	10.0 (1.0) 2
4[c] 1.8	6.36 (6.07) 53	7.67 (3.82) 36	9.0 (3.97) 16	6.33 (2.75) 6	10.6 (3.72) 10
5 11.8	5.52 (4.75) 42	8.29 (3.19) 27	9.37 (2.78) 19	8.11 (2.42) 9	10.5 (2.58) 10

[a] Number of offspring surviving, for reactivated nests this includes the estimated number of eclosed adults, i.e. reused cells are counted twice
[b] Includes nests with no living occupants
[c] Does not include a sample of nests discovered by observing returning foragers

Table 2. Variation in foundress mandibular, wing and total wear during the summer. Sample sizes as in fourth column of Table 1. Data not available for time period 3 females

Time period	Mandibular wear score	Wing wear (# of nicks)	Total wear
0	1.80 ± 0.40	0.80 ± 0.74	2.60 ± 1.01
1	2.87 ± 0.78	1.50 ± 1.32	4.37 ± 1.49
2	3.00 ± 0.75	1.85 ± 1.72	4.85 ± 2.23
4	4.00 ± 1.10	6.34 ± 4.17	10.34 ± 4.52
5	4.45 ± 0.73	7.85 ± 6.48	12.30 ± 6.50

reactivated nests averaged larger than those censused earlier in summer (mean head width of foundresses from time periods $0-2 = 1.91$ mm ± 0.06, $N = 27$; for t.p. 4–6 mean $= 1.97$ mm ± 0.07, $N = 41$; $t = 3.33$, $P < 0.01$). This is probably due to higher mortality rates of smaller foundresses (mean head width of foundresses found dead in nests $= 1.90$ mm ± 0.07, $N = 13$; mean head width surviving foundresses as above, $t = 3.14$, $P < 0.01$).

Variation in foundress wing and mandibular wear (Table 2) supports the observation of two brood rearing periods, with a lull in activity in late July. The large increase in wing wear between time periods 2 and 4 suggests a non-linear relationship between wing fraying and amount of foraging.

Eusocial nests

Sixteen nests were studied in detail after reactivation and all active females marked and observed for at least 2 days. The foundress was the only forager in seven nests, while five nests had 1 and 4 had two workers. Foundress and worker foraged from the same nest in one instance. In all cases, workers appeared as active as foraging solitary foundresses; they were not young, overwintering females preparing for diapause.

Slight thickening of some worker ovarioles was observed, but only one individual (out of 18) contained even one-quarter of a developed oocyte and none had yellow bodies – nurse cell break-down products indicative of past oviposition (Billen 1985). Conversely, all foundresses had well developed ovaries or, during periods of inactivity when ovaries had regressed, yellow bodies. In time period 4, 64.2% of workers (9 of 14 whose spermatheca was found) were mated compared to 72.2% (13 of 18) for non-working daughters ($G_{adj} = 2.15$, $P > 0.1$). All daughter females found in nests were inseminated by time period 5 ($n = 18$).

Workers averaged 2.7% smaller than their mothers (mean wing length of 11 workers $= 4.6$ mm, mean wing length of their 9 mothers $= 4.73$ mm), but were statistically more likely to be the smaller bee than expected by chance (sign test, $P < 0.05$). In contrast, non-working daughters were not significantly more likely to be smaller

than their mothers. Daughter bees observed working were more likely to be worn than non-working bees within nests ($G_{adj} = 12.68$, $P < 0.001$) and had a mean index of wear of 2.54 (± 2.4, $n = 9$) whereas only 1 of the 18 non-working daughter bees had an index of wear above zero.

Queens were no larger than solitary foundresses that reactivated their nests themselves (mean head width $= 1.98$ mm ± 0.05 for both groups, $N = 10$ and 16 respectively). Indicating that size played no role in determining which surviving foundresses would become queens.

For 16 nests excavated within a 5 day period, the mean number of recently produced offspring in eusocial nests was significantly greater than in those reactivated solely by foundresses (mean $= 5.1 \pm 1.96$, $N = 8$, mean $= 2.6 \pm 1.22$, $N = 8$ respectively; Mann-Whitney U test, $U_s = 55.5$, $P < 0.02$). The additional brood productivity per worker was less than 2. Comparatively little foraging occurred within the aggregation after these nests were excavated. This suggests that workers do not augment productivity by a large amount, but they do so at a time when a highly female–biased sex ratio is being produced (see below).

Sex ratio and sequence of production of the sexes

The numbers of pupae excavated at different times during the summer are shown in Table 3. Nests produced a disproportionate number of males before reactivation ($3:1$ – 523 out of 694 censused pupae), but afterwards the reverse bias was observed (9 out of 45 pupae were male). In this population, males were produced and emerged earlier, on average, than females. This is unexpected in a social hymenopteran where earlier offspring are typically worker females. Closer inspection of the data reveals an interesting pattern.

Figure 3 shows the sex of first, second and subsequent individuals produced in nests where each of the first five offspring (at least) could be sexed and their sequence of production unambiguously determined. The first individual was more likely than expected by chance to be female (taking the overall first brood sex ratio as the expectation) and approximately half of the foun-

Table 3. Calculations of the sex ratio for time periods 1 to 6 inclusive

Time period	N. of nests	N. of males	N. of females	Investment per nest[a]		Sex ratio[b]	
				males	females	numerical	investment
1	14	44	10	120.72	29.94	81.48	80.13
2	78	344	99	172.70	62.50	77.65	73.43
3	25	89	29	143.08	59.09	75.42	70.77
4	36	46	33	50.09	45.40	58.23	52.46
5	27	9	30	13.08	50.23	23.08	20.66
6	7	0	6	0.00	40.60	0.00	0.00
Total	187	532	207	499.67	287.76	72.00	63.46

[a] Calculated as mean number of males or females multiplied by the mean estimated dry weight of the subsample of that sex from that time period. Mean male weight for t.p. 5 estimated as average male weight from t.p.'s 1–4, mean female weight for t.p. 6 estimated as mean female weight for t.p.'s 1–5

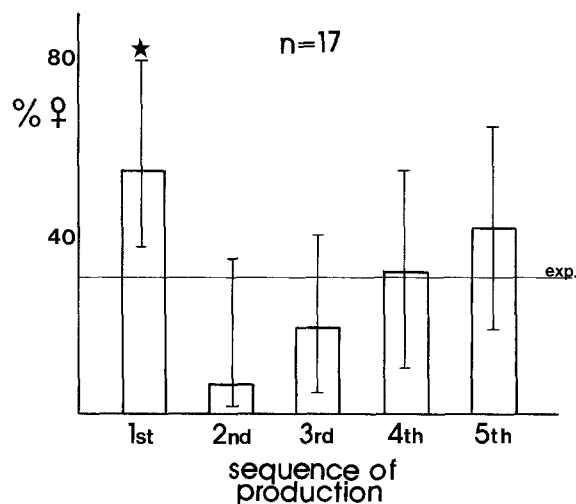[b] Calculated as male investment as a percentage of total

Fig. 3. Proportion of females produced on the first to fifth pollen balls for each of 17 nests, 95% confidence intervals also shown. In time period 1, significantly more females were produced than expected from the overall first brood sex ratio
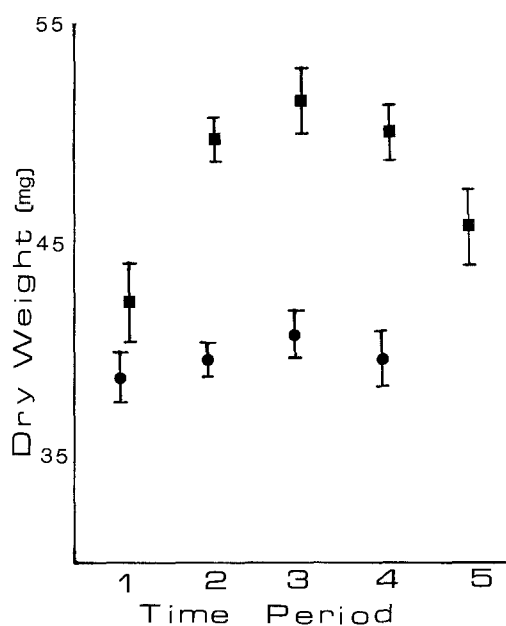

Fig. 4. Mean dry weight of adult males and females upon eclosion according to the time period in which their nests were excavated. *Squares* represent females, *circles* males. Points with non-overlapping interval lines are significantly different at the 0.01 level. Females from t.p.'s 1 and 5 are significantly different at the 0.05 level

dresses produced a female as their first offspring. Thereafter, the probability of a daughter being produced was low but increased monotonically. Foundresses which did not produce a female first remained unlikely to produce one until, on average, the third or fourth pollen ball had been constructed.

Regression equations relating the cube of individual pupal head width (x) with dry weight (y) of the adult it produced were as follows: for males $- y = 4.73x + 10.98$ ($R^2 = 0.28$, $n = 129$, $P < 0.000001$), for females $- y = 6.41x - 1.28$ ($R^2 = 0.58$, $n = 44$, $P < 0.000001$). These equations predict the weight of adults for which only linear measurements (head widths) were available. Variation in predicted average male and female weights in

different time periods is shown in Fig. 4. Analysis of variance of the subset of this data for which maternal dry weight could be estimated revealed significant effects of foundress size ($P < 0.0001$), time period ($P < 0.0001$), sex of offspring ($P < 0.0001$) and time period/sex interaction ($P < 0.05$) upon individual offspring dry weight. In all, 45% of total variation was explained by the model. Gabriel's method for unplanned comparisons among means (Sokal and Rohlf 1981, p. 249) for the entire data set indicates that the earliest females weighed significantly less than those produced at the end of the summer, which in turn weighed less than those found as pupae in time periods 2, 3 and 4 (Fig. 4). These small females were the workers produced at the beginning of foraging in June. There are no significant differences in male weights among time periods, but males consistently weighed less than females.

Table 3 provides details of the calculation of sex ratios in different time periods and over the whole season. The calculated numerical and investment proportion of males is 0.72 and 0.63 respectively. Workers in eusocial nests should be discounted from calculations of investment in reproductives. The numerical and investment proportion of males then become 0.75 and 0.66 respectively.

Discussion

The data support 3 of the 4 initial predictions. First, the duration of foraging activity in the Cape Breton population lasted two months compared to three months in Kansas. Second, an average of 0.5 workers was produced per nest in Cape Breton while mid-summer nests in Kansas averaged 2 workers (probably an underestimate of the total produced because mortality during the long eusocial phase was not taken into consideration in Ordway's study). Third, queens in the Cape Breton population produced both worker and reproductive brood as a result of their own foraging, although only half of them produced any workers.

The drought conditions that prevailed for the last 2 weeks of July could not have caused these results. The duration of brood production was diminished because of late nest initiation – late also in comparison to other sympatric halictines (Packer et al. 1989a), but which occurred one month before drought conditions began. Similarly, the small number of workers produced and the polymorphism between social and solitary nests could not have been influenced by drought in July because the first five offspring had been produced before the end of time period 1 before the drought–induced decrease in rate of brood cell construction occurred (Table 1).

The outcome of one prediction was affected by drought conditions: total brood productivity was certainly decreased by the cessation of foraging for 2 weeks in July. As outlined below, this interruption of activity probably resulted in the loss of between 2.5 and 3 additional brood per nest. Thus, reactivated nest productivity should have averaged between 13 and 14 individuals, comparable to the number which pertained in Kansas (Ordway 1966a). With similar brood sizes being pro-

duced in three rather than two months of foraging, the rate of brood production in Kansas was only two-thirds that in Cape Breton.

The small proportion of nests that became eusocial and the small number of workers in these nests makes the Cape Breton population the most primitively eusocial halictine studied to date; although very small colony sizes are known for a few tropical halictine species (Eickwort 1989; Michener et al. 1979). Interestingly, none of the Cape Breton *A. striata* workers had any appreciable ovarian development making this population more advanced in its caste differentiation than many species with a more populous worker brood. Nonetheless, the great majority of workers were mated and the size difference between castes was small, two features indicative of a primitive social organisation (Packer and Knerer 1985).

How is caste determined in this population? Only overwintered females that produced small, early females could become queens but the mechanism resulting in eusocial and solitary foundresses remains unknown. The fact that orphaned, early females excavated overwintering burrows suggests that the continued presence of the queen is required to promote summer foraging over diapause initiation in daughters.

The heavily male biased sex ratio (c. 2:1) appears to demand explanation but may not be usual. Drought conditions precluded cell construction and offspring production for about two weeks immediately before nest reactivation. Nests in which the foundress survived until the very end of the foraging period produced approximately 10 or 11 offspring over an estimated 55 days for which brood production was possible (subtracting the drought period from the total active season duration). Based upon this production rate, the drought may have caused a reduction in brood size of 2.5 to 3 offspring. Foraging was precluded at the time when nests were switching to female production. If this lost productivity had resulted in offspring with a similar sex ratio to that produced just after reactivation (ie as in t.p. 5), the per nest investment in males would have decreased to 0.57 (a ratio of 1.35:1). In the absence of additional samples from less unusual years, further application of these data to theories of sex ratio evolution seems unwarranted.

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