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Life History and Social Evolution of the Primitively Eusocial Bee *Augochlorella striata* (Hymenoptera: Halictidae)

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ABSTRACT: Life history parameters of the primitively eusocial bee *Augochlorella striata* (Hymenoptera: Halictidae) are summarized for a population in central New York, and analyzed with respect to the evolutionary maintenance of eusociality in this species. High mortality (39%) of solitary foundresses and low mortality (12%) of social colonies indicate severe ecological constraints limiting independent (solitary) reproduction. Extreme relatedness asymmetries (3:1, due to singly-mated queens) and female-biased reproductive broods create genetic incentives favoring worker behavior (helping). In addition, workers appear to capitalize on relatedness asymmetries by biasing the sex ratio towards their more closely related sisters and away from their more distantly related brothers, because eusocial colonies (headed by a mother queen; relatedness asymmetry present) consistently produce more female-biased sex ratios than parasocial colonies (headed by a sister queen after queen supersedure; relatedness asymmetry absent). Both intrinsic factors inherent in the haplodiploid system of sex determination (relatedness asymmetries in conjunction with female-biased sex ratios) and extrinsic factors (ecological constraints) therefore appear to modulate eusocial evolution in *A. striata.*

Augochlorella striata (Provancher) is an ubiquitous bee in eastern North America, ranging from Texas to Nova Scotia and from the central plains to the east coast (Ordway, 1966a, b; Packer Jessome et al., 1989). It is the northernmost representative of the Augochlorini, a strictly New World tribe of mostly brilliantly metallic green-blue bees with the center of distribution in the Neotropics (Eickwort, 1969). Most augochlorine bees are solitary or semisocial, but bees in one clade that includes the genus *Augochlorella* are eusocial (Danforth and Eickwort, in press).

The annual life cycle of *A. striata* follows the typical pattern of primitively eusocial, temperate halictine bees (Ordway, 1966a, b; Michener, 1990; Packer, 1993). During the *foundress* phase in spring, foundresses construct a nest in the soil and provision a first brood of both sexes. The emergence of the first brood in early summer marks the beginning of the *worker* phase, as first-brood females remain with their mother as workers. Foundresses now cease all foraging, become queens, and, with the help of their workers, produce a second brood of male and female reproductives. The emergence of the second (reproductive) brood in late summer marks the beginning of the *reproductive* phase. Reproductives mate in late summer and early fall, but only inseminated females overwinter to complete the colony cycle. In some colonies, the foundress dies during the worker phase, and one of her daughters assumes the position of a replacement queen. Colonies undergoing queen supersedure are called "parasocial" (queen and workers are from the same generation), to distinguish them from "eusocial" colonies (queen and workers are from different generations) that are headed by the foundress queen throughout the season.

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Because of its eusocial life history and abundance, *A. striata* had been selected for an experimental study of queen-worker conflict over the colony sex ratio (Mueller, 1991; Mueller et al., 1994). This paper summarizes the life history of *A. striata* in central New York, compiled over the four seasons (1989 to 1992) when the experiments on sex-ratio conflict were conducted. Previous reports on this bee include accounts of nesting and nest architecture (Knerer and Atwood, 1962; Ordway, 1961; Ordway, 1966a; Packer, Sampson et al., 1989), systematics (Ordway, 1966b; Eickwort, 1969), natural enemies (Ordway, 1964), caste differentiation (Ordway, 1965; Packer, Jessome et al., 1989), allozyme variation (Packer and Owen 1990), and intrapopulation variation in social organization (Packer 1990).

Materials and Methods

Study populations: A. striata was studied at two sites (Sites 1 and 2) on the campus of Cornell University, Ithaca, New York, USA, where it is one of the most common bees of the local apifauna. The main study site (Site 1) was selected to conduct the field experiments (1989–1991) that are described in Mueller (1991). The following analyses of the life history of *A. striata* are based on only those nests that were not experimentally manipulated. Unless stated otherwise, therefore, experimental parasocial colonies (induced by the removal of colony foundresses) are excluded from the analyses.

All behavioral observations on marked bees were collected at Site 1. Nests at Site 1 were excavated only if this was required by the field experiments (mostly during the worker phase). Consequently, the records of excavated nests from Site 1 do not cover the entire nesting season. To obtain a detailed picture of the nesting behavior throughout the season, a second population (Site 2) was studied in 1991 by excavating nests at intervals of ten days, beginning at nest initiation in early May and ending with the emergence of the last individuals of the second brood in late summer.

The main study population (Site 1) consisted of two nest aggregations located on the grounds of the old Fisheries Laboratory at Cornell University. *A. striata* was observed at this site throughout the active seasons of 1989–1992. The two aggregations (measuring 9 × 7 m^2 and 12 × 2 m^2, respectively) were located on the grassy embankments of two ponds and were separated by about 45 meters. A second population (Site 2) was studied during the season of 1991 at a steep (about 30°) south-facing slope just east of the Wilson Synchroton Facility on the campus of Cornell University. This population consisted of multiple, more diffuse aggregations dispersed over an area of about 30 × 50 m^2. The slope was patchily covered with dense shrubs and some small trees, and the aggregations were located in the open grassy areas in between.

Nests were located either by observing returning foundresses as they entered their nests, or by carefully searching through the grass that covered the sites (nests of *A. striata* are readily identified by their characteristic entrance tubes called "turrets"; Ordway 1966b). Each nest was marked by placing a small plastic stake about 4 cm away from the nest's turret. At Site 1, special efforts were made to locate nests during the time of nest initiation. The great majority (>80%) of the nests at Site 1 therefore were discovered during the early foundress phase. At Site 2, nests were located throughout the season by searching. The number of nests monitored over the four seasons at Site 1 were $n = 155$ (1989), $n = 211$ (1990), $n = 140$ (1991), $n = 41$ (1992), and at Site 2 $n = 119$ (1991).

Capture of bees: During 1989–1991, but not 1992, virtually all bees associated with the nests at Site 1 were captured and code-marked during the foundress and worker phases. Bees were captured by inverting clear plastic cups over the nest entrances. The bottom of these cups had been cut out and replaced with a nylon screen to allow ventilation. Bees leaving their nest were trapped inside these cups and could be transferred to an insect net for further handling. To facilitate size measurement, evaluation of wing wear, and marking, bees were placed into small vials and immobilized by brief chilling on ice.

Size measurement and code-marking: The head width and wing wear of each bee was measured following the methods described in Mueller et al. (1992) and Mueller (1993). Head width measurements are accurate to about ±0.02 mm (about 1% of a bee's head width). To facilitate marking, each bee was placed in a small restrainer as described by Mueller et al. (1992) and then marked under a microscope (10× magnification). Bees were code-marked with unique color combinations of Testors® enamel: two small dots on the scutum and a third dot on the abdominal terga. After drying of the enamel, bees were transferred to a small clear plastic tube (4 mm inner diameter) and placed back into their nest by carefully holding one end of the tube to the nest's turret and gently prodding the bee into the turret with the aid of a pipe-cleaner inserted through the other end of the tube. The numbers of bees marked at Site 1 were 88, 153, and 94 foundresses as well as 252, 422, and 324 first-brood females in 1989, 1990, and 1991, respectively. Males of the first brood were measured and marked only in 1989 ($n = 50$), but released unmarked after measurement during 1990 ($n = 17$) and 1991 ($n = 19$). Individuals of the second brood (reproductives) were not marked.

Behavioral observations: During the foundress and worker phases of 1989–1991, the activity of marked bees was monitored almost daily between 0900 and 1500 (except during inclement weather) by recording their behavior at nest entrances (e.g., guarding, building the turret) or when leaving for or returning from foraging. To facilitate simultaneous observation of several nests during the bees' activity period, clear plastic cups (see above) were placed (for 20–30 minutes) over individual nest entrances, allowing bees to exit their nests and hover inside the cups, or to find their nests and hover outside the cups. Bees attempting to leave or enter their nests were then identified and permitted passage by temporarily removing the cup from the entrance.

Excavations: Nests were excavated between 0530–0800 by first digging a hole at 5–10 cm distance from the nest and then digging laterally toward the subterranean cavity. During excavation, the nest's entrance was obstructed with a small piece of foam-rubber to prevent the escape of bees. Since the cooler morning temperatures prevented the bees from flying away, resident bees could be captured during excavation as they tried to scuttle away through the breach in the cavity wall. All recesses of the cavity, any side branches of the upper tunnel, and any blind terminal tunnels were traced to locate resident bees. Occasionally a bee managed to escape; however, such a bee generally could be captured later during the day as she hovered at the spot of the excavated nest and tried to relocate her nest's entrance. The number of nests excavated at Site 1 was $n = 104$ (1989), $n = 111$ (1990), and $n = 52$ (1991), and at Site 2 $n = 119$ (1991).

Cell clusters (combs) generally were encountered at a depth of 5–15 cm. The intact comb was carefully extricated by cutting the rootlets that suspended the comb or by dislodging the comb from support pillars. Combs excavated at Site 2 were opened and brood contents censused. Older larvae and pupae were placed into individual wax-depression dishes and reared to adulthood, but younger brood was discarded. Combs collected at Site 1 were brought to the laboratory, placed intact into individual petri dishes, and maintained at 23°C and close to 100% humidity. Mould growing in cells and on the comb was a problem if cells had been damaged during the process of excavation. To prevent speading of the mould, such cells were opened and the contents removed.

Sex ratio: Combs were inspected daily for males and females that had emerged from their cells. These bees were measured for head width and weighed to the nearest 0.01 mg before freezing them at −70°C for DNA fingerprinting analysis (Mueller et al., 1994). Investment sex ratios (henceforth called "allocation ratio") were then calculated from wet weights. Wet weights minimally overestimate female investment (Boomsma 1989), but the extent of this bias should be negligible in the case of *A. striata,* because such a bias is significant only in species with extreme size dimorphism between the sexes (Helms, 1994; Boomsma, pers. comm.). Second-brood allocation ratios were determined for only those nests that (a) had not been experimentally manipulated in the field; and (b) were excavated no earlier than the end of the worker phase. At Site 1 where experiments were conducted, only 6 eusocial and 10 parasocial nests in 1989, 18 eusocial and 8 parasocial nests in 1990, and 10 eusocial and 5 parasocial nests in 1991, met these two criteria. At Site 2 (no experiments; excavations only in 1991), 28 eusocial and 24 parasocial colonies were excavated during the worker phase and early reproductive phase and used in the sex-ratio analyses. At Site 1, nests were collected in the fourth week of the worker phase (about one week before the end of provisioning of the second, reproductive brood), to ensure collection of reproductives emerging from cells that had been provisioned early in the worker phase (developmental time from oviposition to emergence is 28–30 days; Ordway, 1966a; Mueller, 1993). Because the sex ratio of reproductives provisioned during the last week of the worker phase is female-biased (see Results), the allocation ratios of reproductives emerging in the laboratory slightly underestimate the extent of the female bias. The error amounts to about 1–5% only, however, as few reproductives are produced during the last week of provisioning (see Results).

Results and Discussion

GENERAL LIFE CYCLE: Table 1 summarizes the dates of the main stages in the life cycle of *A. striata* in Ithaca, New York. Mated spring foundresses emerged from their winter hibernacula during the first week of May. After about a two week period of nest initiation (selection of nest site; construction of tunnel, cavity, and first cell), foundresses began provisioning cells during the third week of May. The first males and females of the first brood emerged almost synchronously during the last week of June. This marked the beginning of the worker phase. Foundresses ceased to forage and became primary reproductives (queens), while their daughters became workers and provisioned cells for the production of a second brood. Males left the nest on the day of their emergence and did not return to their natal nest. First-brood males mated with workers and replacement re-

Table 1. Phenology of *Augochlorella striata* in Ithaca, New York, during 1989–1992.

Date of	1989	1990	1991	1992
First sighting	5/04	5/01	4/28	5/02
First pollen foraging	5/20	5/12	5/11	5/20
Emergence of first worker	6/30	6/28	6/12	7/01
Emergence of first male	6/30	6/28	6/14	7/02
Emergence of 2nd brood	8/05	8/04	7/16	?
Last pollen foraging	8/11	7/31	8/06	?
Last sighting	9/23	10/04	9/16	?

productives of the first brood, and, if they lived long enough, possibly also with female reproductives of the second brood. Workers provisioned cells for about 4–5 weeks, but provisioning by workers generally decreased at about the time of the emergence of the first reproductives (second-brood offspring) at the beginning of August. The last *A. striata* (male and female reproductives) were generally sighted during late September. Only females entered hibernation and probably overwintered in burrows below their natal nest.

NEST FOUNDING: *Nest initiation:* The great majority of nests were initiated *de novo* in the spring, and only a few nests were reactivated burrows of nests of the previous season. Of the 211, 140, and 41 nests located at Site 1 in 1990, 1991, and 1992, respectively, only 1.8%, 2.8%, and 4.8% represented such reactivated burrows. Since the total number of nests at Site 1 remained high throughout the study (except for 1992) in spite of high natural nest mortality (see Results) and extensive excavations at the end of each worker phase, it appears that some foundresses immigrated into the aggregation during the time of nest initiation in spring.

Single and multiple foundresses: Virtually all spring nests of *A. striata* in Ithaca were founded by single females. Only one foundress was present in all of 50 nests excavated during the first three weeks of the foundress phase in 1989 at Site 1. Similarily, of 45 nests excavated during the foundress phase in 1991 at Site 2, only one nest (2.2%) had two co-foundresses (excavated May 26). The cell-cluster of this nest contained twice as many provisioned cells (14 cells) as the average number of provisioned cells (6.9 ± 2.87 cells/nest) found in the sample of 12 nests excavated on the same day (Fig. 1). No other nest showed an equally extreme brood size at Site 2 in 1991, although two nests (excavated later, June 5 and June 15 in 1991) were almost as extreme (1.7 times the average brood size). No nest excavated during the foundress phase in 1989 had more than 1.5

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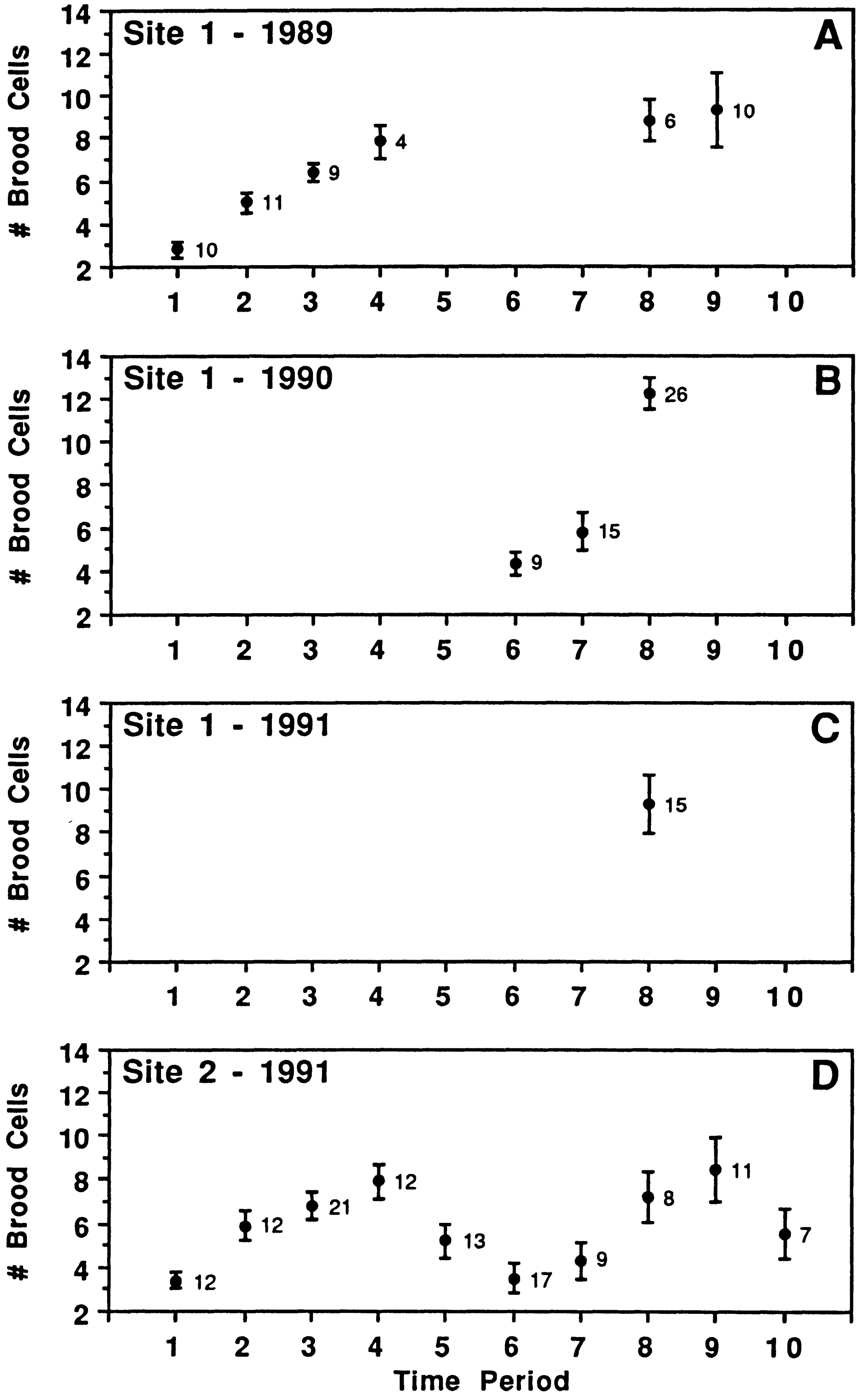
Fig. 1. Number of cells with developing brood found in nests excavated during 1989–1991 at Site 1 and 1991 at Site 2. For each year, the entire season was divided into ten-day time periods, and synchronized between years as follows: Time period 1 marks the beginning of provisioning in May. The worker phase (emergence of first brood) begins with time period 5, the reproductive phase (emergence of second brood) begins during time period 8. The most complete excavation record (Site 2—1991) shows the bimodal progression of provisioning with the first peak toward the end of the foundress phase and a second peak toward the end of the worker phase. Brood sizes averaged 7 to 9 cells for the first brood and 9 to 11 cells for the second brood. Error bars represent one standard error; numbers indicate sample sizes (number of nests excavated).


Site 1 - 1989
A
10
11
9
4
6
10
Site 1 - 1990
B
9
15
26
Site 1 - 1991
C
15
Site 2 - 1991
D
12
12
21
12
13
17
9
8
11
7
Brood Cells
2
4
6
8
10
12
14
1
2
3
4
5
6
7
8
9
10
Time Period

times the average brood size of contemporary nests. Both of these two methods (direct observation at excavation, and indirect inference based on large comb size) indicate a very low frequency (2%) of multiple foundress associations.

Detailed behavioral observations of over 450 nests at Site 1 (1989–1991) during the foundress phase revealed only one nest with two co-foundresses. This nest was discovered early in the founding phase (May 15 1990) and observed until it failed during the third week of the worker phase. The two co-foundresses were significantly smaller in size (1.84 and 1.86 mm head width) than the average size of solitary foundresses (head width = 1.964 ± 0.061 mm; t = 2.63, d.f. = 149, P = 0.009) in the same population, but not significantly different in size from first-brood females of the previous year (head width = 1.897 ± 0.062 mm; t = 1.08, d.f. = 201, P = 0.283). Both females showed strict division of labor, the larger female guarding and the smaller one foraging. The forager died or abandoned the nest during the first week of June, whereupon the guard began foraging. The nest produced at least 3 first-brood females, all of which were seen collecting pollen, but the nest finally failed for unknown reasons during the third week of the worker phase.

Division of labor between the two co-foundresses also was true for the nest excavated on 29 May 1991 at Site 2. The two females of this nest measured 1.99 and 1.95 mm head width (not significantly different from the average head width of foundresses in the same population, head width = 1.972 ± 0.071 mm; t = 0.036, d.f. = 84, P = 0.972; but significantly different from the average head width of first-brood females from the previous year, head width = 1.897 ± 0.062, t = 2.13, d.f. = 3.92, P = 0.034). Only the larger of the two had fully developed ovaries and showed no wing wear, while the smaller one had only slightly enlarged ovaries but showed some wing wear. Both females were inseminated and had comparable mandibular wear and Dufour's gland development. It appears, therefore, that the large female functioned as the primary reproductive and the smaller one as the primary forager.

Nest switching and usurpation: Like pleometrosis, nest switching and nest usurpation occurred rarely in the population studied. Of 335 foundresses marked over three seasons, only one foundress (spring 1989) was seen to abandon her first nest and switch to a second nest. The switch occurred three weeks after the beginning of provisioning, and the female's new nest was discovered in an area that had been carefully searched before on several occasions, suggesting that the new nest was founded in mid-season and was not usurped from another female. The reasons for the switch were unclear. The turret of the first nest quickly disintegrated and finally became obstructed, indicating that the female had not left a nest with multiple foundresses. The female provisioned her second nest for at least ten days, but her second nesting attempt failed after 24 days, well before any brood of her second nest could have developed to adulthood.

No foundress was ever seen to usurp a nest, although one incident of successive occupancy of a single nest by two foundresses occurred in 1991. In this case, the first foundress had died or abandoned the nest during the third week of the foundress phase (indicated by the gradual deterioration of the nest's turret) and a second female (head width = 1.88 mm) became associated with the nest after two weeks, shortly before the emergence of the first workers in the general population. The female's wings were extremely worn (no original wing margin left), indicating a history of substantial flight activity before occupying the nest. This female provisioned the nest for only a short period (6 days) and reared at least one male and one female that emerged at the beginning of the reproductive phase.

Although these two exceptional cases indicate that foundresses possess the behavioral plasticity to switch to a new nest late in the foundress phase, the frequency of nest switching and nest usurpation in the Ithaca populations appears extremely low. Some cases of nest switching and usurpation occurring during the first two weeks of the foundress phase (before marking) may have been missed, however, since a considerable proportion of foundresses were marked during the second half of the foundress phase.

QUEEN SUPERSEDURE: On average, 42.2% (62.5% in 1989; 30.8% in 1990; and 33.3% in 1991) of the marked foundresses heading reactivated nests at Site 1 died during the first four weeks of the worker phase and were superseded by one of their daughters. A similar supersedure rate of 46.2% was observed at Site 2 in 1991. The majority of nests (eusocial) produced two broods of the same generation, and an average of 44.4% of the nests (parasocial) produced two broods of successive generations. *A. striata* in Ithaca therefore is partially bivoltine.

Loss of the queen and subsequent supersedure by one of the daughters is expected to depress a nest's work force by one worker. Indeed, colonies headed by replacement queens had an average of 3.1 (1989), 2.5 (1990), and 3.2 (1991) workers, compared to 3.2 (1989), 3.2 (1990), and 4.6 (1991) workers in colonies headed by the foundress queen throughout the season (paired $t = 1.95$, d.f. $= 2$, $P = 0.19$). The lower work force, together with a four-day lapse in foraging activity in orphaned colonies immediately following queen loss (Mueller, 1993), therefore is expected to result in differences in brood sizes between parasocial and eusocial colonies (see Brood Sizes).

BROOD SIZES: The average number of cells with developing brood in nests excavated in 1989–1991 is represented in Fig. 1. Cell contents of nests excavated at ten day intervals at Site 2 in 1991 are given in Table 2. On average, foundresses completed between 7 and 9 cells during a 3–4 week period of intense provisioning and then slowed down or ceased provisioning for the remainder of the foundress phase. At the end of the foundress phase, average sizes of the first brood were 7.7 (SE = 1.5) in 1989 at Site 1 and 7.9 (SE = 2.4) in 1991 at Site 2 (these are the only two years where nests were excavated during the end of the foundress phase), yielding an overall average of 7.8 cells in the first brood of *A. striata.*

Average brood sizes decreased temporarily at the beginning of the worker phase (Fig. 1B, D) because emergence rates of the first brood exceeded provisioning rates of the second brood during this period. As work forces gradually increased, however, average sizes of the second brood showed a corresponding increase to average brood sizes (8–12 cells) greater than those of the first brood (Fig. 1A, D). However, because provisioning of the second brood spans about 35–45 days (Table 1), and because developmental time from oviposition to adult emergence is only about 30 days (Mueller, 1993), the observed average brood sizes at excavation late in the season underestimate the total number of brood produced during the *entire* worker phase (that is, reproductives provisioned early in the worker phase emerge, and males leave, at a time when the last brood is provisioned). When calculating total brood production for Site 2 in 1991 (using a developmental time of 30 days, which is about ¾ of the time span over which

Table 2. Contents of cells in nests excavated at Site 2 in 1991 at intervals of ten days (±1 day).

Excavation date	5/16	5/26	6/05	6/15	6/25	7/05	7/15	7/25	8/04	8/14
Time period	1	2	3	4	5	6	7	8	9	10
# of nests excavated	12	12	21	12	13	17	9	8	11	7
Av. # cells with brood	3.4 ± 1.38	5.9 ± 2.35	6.8 ± 2.77	7.9 ± 2.90	5.2 ± 2.91	3.5 ± 2.65	4.3 ± 2.55	7.2 ± 3.27	8.5 ± 4.81	5.5 ± 3.60
Empty with wax lining	18.0%	2.7%	3.3%	5.4%	5.7%	9.8%	2.7%	5.0%	3.4%	1.7%
Egg on provision	36.0%	9.6%	1.4%	8.1%	6.8%	6.5%	1.8%	2.1%	1.7%	—
1st instar larva	28.0%	11.0%	0.7%	0.9%	3.4%	1.6%	0.9%	2.1%	2.6%	—
2nd instar larva	16.0%	16.4%	0.7%	0.9%	3.4%	0.8%	1.8%	1.4%	2.6%	—
3rd instar larva	—	24.7%	4.1%	—	3.4%	0.8%	2.7%	2.1%	1.7%	—
4th instar larva	—	26.0%	8.1%	—	5.7%	2.4%	5.5%	5.0%	6.8%	5.2%
Prepupa	—	6.9%	13.5%	4.5%	4.6%	3.2%	2.7%	3.6%	5.1%	10.3%
Pupa	—	2.7%	64.9%	77.5%	46.6%	25.2%	19.1%	21.7%	35.0%	48.3%
Rhipiphorid parasite	2.0%	—	2.0%	1.8%	—	2.4%	4.6%	5.0%	6.8%	3.5%
Mouldy content	—	—	—	—	2.3%	4.1%	—	0.7%	3.4%	—
Empty with exuvium	—	—	—	0.9%	18.2%	26.8%	10.9%	5.0%	4.3%	3.1%
Filled with soil	—	—	—	—	—	16.3%	45.5%	46.0%	26.5%	29.6%

brood is provisioned), the number of cells provisioned during the entire worker phase is 11.3 cells (8.5/3 = 2.8 cells more than the maximal average brood size of 8.5 cells observed; see time period 9 in Table 2). A similar problem of underestimating total second-brood sizes pertains to estimates for Site 1. At Site 1, nests were excavated about one week before the end of provisioning, and the observed average brood sizes need to be corrected for additional offspring produced during the last week of provisioning. A correction of about 2.6 offspring is suggested by the fact that colonies produced an average of about 10.3 offspring in almost four weeks of provisioning (2.6 offspring per week; Fig. 1A–D). The corrected total second-brood size at Site 1 then averages 12.9 reproductives (11.9 in 1989; 14.8 in 1990; 11.9 in 1991). Across Sites 1 and 2, therefore, the overall average second-brood size is 12.8 reproductives (averaging first the two values from 1991, then across years).

The variance in brood size during the worker phase greatly exceeded that of the foundress phase (Fig. 1A, D). Some colonies provisioned more than twice as many cells as the average colony in the population. At the upper extreme, brood sizes of up to 20–25 cells per single nest were occasionally found shortly before the emergence of the first sexuals (second brood). Queenright colonies (foundress present) had larger brood sizes during the worker phase than did colonies that had lost the foundress ($t = 7.5$, d.f. $= 9$, $P < 0.0001$; Fig. 2A–D). In the latter colonies, one of the foundress' daughters assumed the role of the primary reproductive (see 'Queen Supersedure' above) and provisioning continued after a lapse of 3–5 days. The lower productivity of supersedure nests therefore was a direct consequence of several factors: (a) the lapse in provisioning immediately after foundress loss and before queen replacement, (b) the reduced work force resulting from queen supersedure (a daughter that would have functioned as a worker, if the foundress had survived, became the replacement queen in the orphaned nest), and (c) cessation of provisioning in some orphaned colonies that lost the foundress late in the season.

COLONY MORTALITY: *Mortality rates:* To control for the possible role of the marking procedure in causing foundress death, mortality rates were calculated only for those marked foundresses that were resighted at least once after marking (bees were only marked at Site 1 and mortalities are therefore calculated only for that site). Of those resighted foundresses, 8.2% (1989), 8.1% (1990), and 12.9% (1991) died during the remainder of the foundress phase. These values greatly underestimate mortality rates during the foundress phase, since foundress deaths prior to marking (e.g., during nest initiation) are not included in this analysis. Nest failure rates based on nests discovered early in the foundress phase therefore may yield a more accurate estimate of foundress mortality. Of 47 (1989), 58 (1990), and 99 (1991) nests located during the early foundress phase (no later than the first week of provisioning), 31.9%, 46.5%, and 37.4%, respectively, failed during the foundress phase and did not rear any first-brood offspring. Nest failure rates appear to estimate foundress mortality rates accurately, because secondary nesting attempts after loss of a first nest are exceedingly rare (see Nest Founding). On average, about 39% of the foundresses therefore perish during the foundress phase in *A. striata.*

Colony mortality during the worker phase is more difficult to estimate, since colonies that failed because of death of all adult colony members early during the worker phase could not be reliably distinguished from colonies that were not reactivated (colonies rearing first-brood females, none of which became a worker). Of the colonies with at least one first-brood female, 30.8% (1989), 17.1% (1990), and 25.0% (1991) did not produce any second-brood offspring, either because of death or because of non-reactivation. Of the reactivated colonies (colonies with workers foraging for pollen), 13.3% (1989), 12.9% (1990), and 10.0% (1991) failed because all adult colony members disappeared. Overall, failure rates of colonies during the worker phase (mean = 12.1%) therefore are significantly lower than the failure rates of solitary nests during the foundress phase (mean = 38.6%) (paired $t = 6.097$, d.f. = 2, $P = 0.026$).

Causes of mortality: Predatory carabid beetles and conopid fly parasites were the only known causes of adult mortality. Together these two causes accounted for less than 20% of all nest failures observed in 1989–1991. It appears therefore that most bees die from other causes while foraging. Of all the nests observed at Site 1 during 1989–1991, 1.2% ($n = 6$ observations) perished when being attacked by a predatory carabid beetle (*Scarites subterraneus*). These beetles appeared to force themselves into the nest burrow, drive out or kill all females present, and consume brood and provisions.

Conopid parasitism was a slightly more important cause of mortality. 4.0% (Site 1, 1989) and 2.4% (Site 2, 1991) of the foundresses in nests excavated during the foundress phase had a conopid larva or puparium developing in their abdomens, but none of a total of 122 foundresses in colonies excavated at Site 1 and Site 2 during the worker phases of 1989–1991 was parasitized by a conopid. However, a few workers present in the same colonies were always parasitized during the worker phase (Site 1: 1.4% in 1989, 1.1% in 1990, 2.5% in 1991; Site 2: 1.5% in 1991). In addition, 2.5% of the workers found in colonies excavated at Site 2 during the reproductive phase in 1991 showed evidence of conopid parasitism. Since conopids attack foraging bees (Smith, 1966; Schmid-Hempel and Schmid-Hempel, 1990), the presence of parasites in workers and the absence of parasites in foundresses during the worker phase underlines the risk taken by foragers when collecting provisions. Three marked workers were found alive at the time of excavation with older conopid larvae developing in their abdomens. These workers had been active foragers early in their lives, but had ceased foraging completely 10 days prior to excavation. Because unparasitized workers forage throughout their lives, this suggests that the parasite may inhibit foraging behavior. On two occasions, a worker with a conopid puparium was found dead

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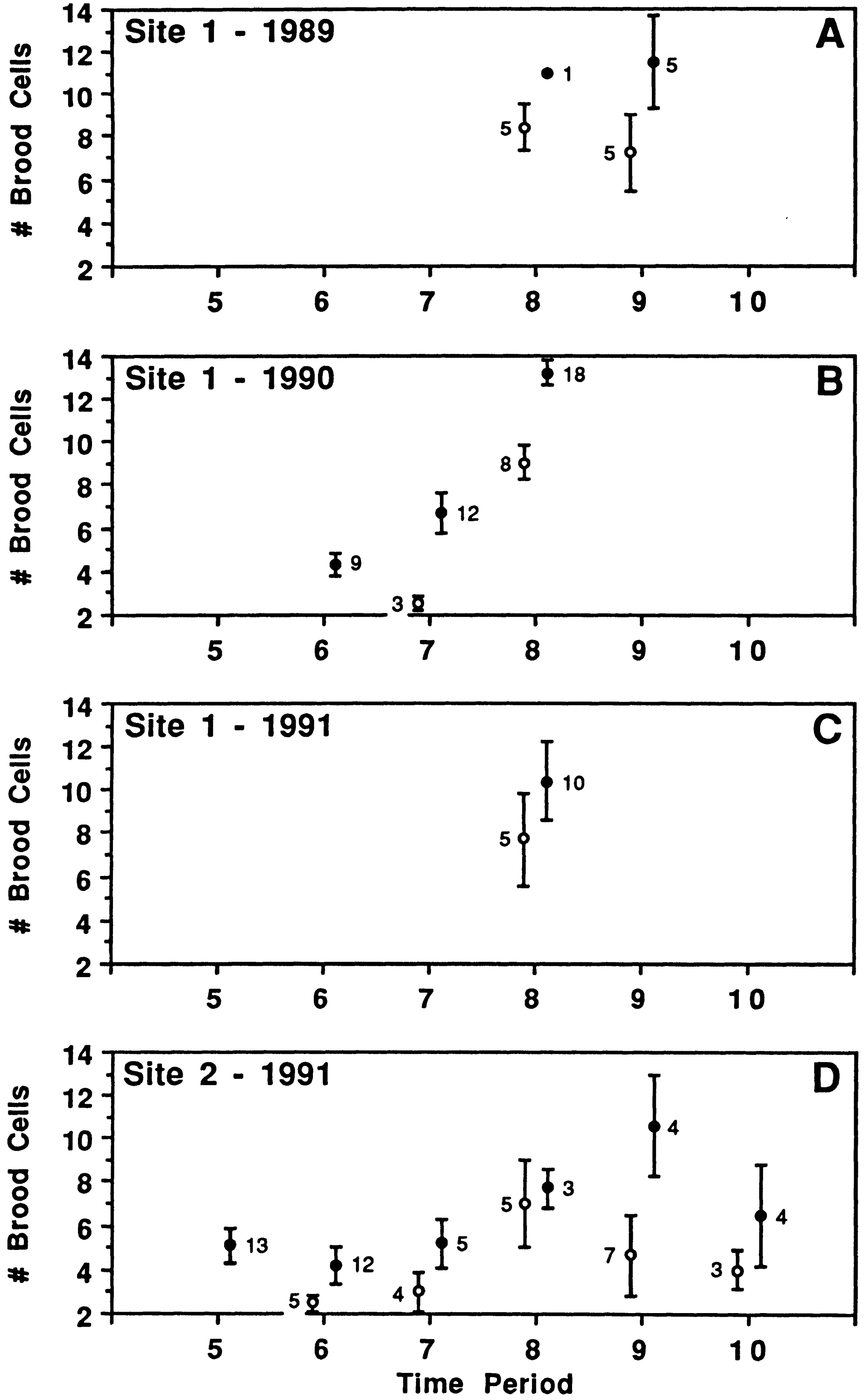
Fig. 2. Number of cells with developing brood found in colonies headed by the original foundress (eusocial; closed circles) and colonies headed by a daughter replacement reproductive after the death of the foundress (parasocial; open circles). Time periods are defined as in Fig. 1. Eusocial colonies showed significantly higher productivities than supersedure colonies ($t = 7.54$, d.f. = 9, $P < 0.0001$; paired t-test, comparing average brood sizes of the ten time periods during which at least one eusocial and one supersedure colony was excavated). This difference reflected the fact that superseding colonies interrupted provisioning for about 3–5 days immediately following the death of the foundress (time necessary for full ovarian development of a replacement reproductive) and had fewer workers because of queen supersedure. Error bars represent one standard error; numbers indicate sample sizes (number of nests excavated).


Site 1 - 1989
A
Site 1 - 1990
B
Site 1 - 1991
C
Site 2 - 1991
D
Brood Cells
14
12
10
8
6
4
2
5
6
7
8
9
10
Time Period
1
5
5
5
18
8
12
9
3
10
5
13
12
5
5
4
5
3
4
7
4
3

just outside its nest's entrance, apparently having been pushed out by its nestmates. If parasitized bees generally are removed from colonies in this manner, the above frequencies of conopid parasitism probably underestimate actual rates of parasitism.

CASTE: *Size differences:* In all three years when bees were measured (Site 1), foundresses were significantly larger (1.9–3.7%; all $P < 0.0001$) than first-brood females (workers). Average head widths for foundresses and first-brood females, respectively, were 1.970 ± 0.061 ($n = 88$) and 1.897 ± 0.062 ($n = 252$) in 1989, 1.963 ± 0.058 ($n = 153$) and 1.896 ± 0.062 ($n = 422$) in 1990, 1.972 ± 0.071 ($n = 84$) and 1.934 ± 0.058 ($n = 324$) in 1991. Even though workers were about 2–4% smaller on average than foundresses, there was considerable size overlap between the two castes. In some cases, one or several daughters were actually larger than their mother. Size therefore does not reliably discriminate the two castes in a given nest, and other criteria, such as the size of the Dufour's gland and the number of ovarian yellow bodies, allow precise differentiation between foundresses and workers (see Mueller, 1993 for details of this method). Foundresses did not differ in size between the three years ($P > 0.4$). First-brood females in 1991 were significantly larger than those in the two previous years (both $P < 0.001$). The increased size of first-brood offspring in 1991 may have been related to the unusually warm spring in 1991, allowing foundresses to forage more hours per day, or to collect provisions more efficiently because of the accelerated flowering of plants.

Insemination: All foundresses examined during the foundress and worker phases of 1989–1991 were inseminated. In the presence of a foundress (eusocial colonies), 40.0% (1989, $n = 20$), 15.8% (1990, $n = 95$), 45.7% (1991, $n = 35$) of the workers were inseminated. In contrast, a consistently larger proportion of the workers in parasocial colonies were inseminated (45.5% in 1989; 26.7% in 1990; 81.8% in 1991) (paired $t = 1.64$, d.f. $= 2$, $P = 0.242$ after arcsine transformation of percentages). In addition to the greater proportion of inseminated workers in parasocial colonies, replacement reproductives were virtually always inseminated [83.3% (1989, $n = 6$), 85.7% (1990, $n = 7$), 100% (1991, $n = 4$)]. Overall, only 2 of a total of 17 replacement reproductives (11.8%) examined during 1989–1991 had not mated, and their colonies therefore produced a 100% male brood. Since replacement reproductives and workers in parasocial colonies are both first-brood offspring of the deceased foundress, the overall rate of insemination of first-brood females in parasocial colonies was significantly larger than the one in eusocial colonies (paired $t = 5.25$, d.f. $= 2$, $P = 0.03$ after arcsine transformation of percentages). This implies that either (a) inseminated first-brood females in eusocial colonies were more likely to leave their colonies than were inseminated first-brood females in superseded colonies, or (b) first-brood females in superseded colonies responded facultatively to foundress loss by mating, while first-brood females in eusocial colonies remained unmated.

Reproductive options of first-brood females: The majority of first-brood females stayed in their natal nest and became workers. Of 56 (1989), 73 (1990), and 56 (1991) marked first-brood females (all from nests that were excavated toward the end of the worker phase), 91.1%, 93.2%, and 83.9%, respectively, had been resighted at least once after marking. Of these resighted females, 78.4% (1989), 88.8% (1990), and 80.8% (1991) had been observed to forage and thus had become workers in their natal nest by the time of excavation, while 13.7% (1989, $n = 7$), 1.5% (1990, $n = 1$), and 12.2% (1991, $n = 5$) never were observed to forage, but were present in the nest when excavating colonies at the end of the worker phase. Most first-brood females therefore remained in their natal nest to become workers. However, if a significant number of first-brood females left their natal nest before marking (see below), it may be that a smaller percentage of first-brood females actually became workers.

Of the marked first-brood females from nests excavated toward the end of the worker phase, a significant proportion [16.1% (1989, $n = 9$ females), 17.8% (1990, $n = 13$), and 32.1% (1991, $n = 18$)] "disappeared" within a week after marking either (a) because they died of natural causes or the effects of marking; or (b) they opted to leave their natal nest to reproduce independently during the same season or the following year. An average of 1.03% of all marked first-brood females were actually observed to found their own nests, either in mid-summer during the same season [0.8% (1989, $n = 2$ females), 0.9% (1990, $n = 4$), 0.3% (1991, $n = 1$)] or during the following spring along with regular (second brood) foundresses [0.8% (1989, $n = 2$ females), 0% (1990, $n = 0$), 0.3% (1991, $n = 1$)]. Disappearance rates of first-brood females therefore overestimate mortality rates. This problem is particularly acute if first-brood females emigrate to attempt nesting outside the study area. However, all first-brood females that were observed to attempt independent nesting did so in their natal aggregation, that is, no migration of first-brood females was seen in three years of observation between the two aggregations at Site 1 (45 meters distance). Emigration of first-brood females from their natal nest site therefore seems low, and "disappearance" rates appear to approximate mortality rates. Thus, independent reproduction during the same summer or the following spring is a reproductive option for first-brood females, but it appears to be exceedingly rare (1% of first-brood females).

Becoming a replacement reproductive was a second option for first-brood females to produce offspring. Of 66 (1989), 100 (1990), and 87 (1991) first-brood females from nests for which the type of sociality was known (that is, these nests were excavated at the end of the worker phase), 9.1%, 6.0%, and 4.6%, respectively, became replacement reproductives after the death of the nests foundresses. For any particular first-brood female, the chance of superseding the foundress (on average 6.57%) was therefore significant.

Worker reproduction, in contrast, was a less important reproductive avenue for first-brood females. For 12 eusocial and 12 parasocial colonies of the 1990 season, genetic fingerprinting analyses indicate that worker reproduction was absent in the presence of the foundress, but that workers are occasionally successful in producing a son in colonies that had lost the foundress (Mueller et al., 1994). In parasocial colonies, worker reproduction accounted for 9% and 0% of the males and females, respectively. Thus, 6.1% (9% of an average allocation ratio of 67.8% of the fingerprinted parasocial nests; Mueller et al., 1994) of all reproductive effort in parasocial colonies is directed towards worker reproduction. This implies that an "equivalent" of $2.64\% = 6.1\% \times 0.432$ (0.432 is the average supersedure rate, that is, the probability that a first-brood female will be in a parasocial nest) of all first-brood females are functional "reproductives" as laying workers. [This value changes to $2.44\% = (0.09 \times 62.8) \times 0.432$ when assuming that the allocation ratio of the second brood is overestimated by as much as 5%; see Sex

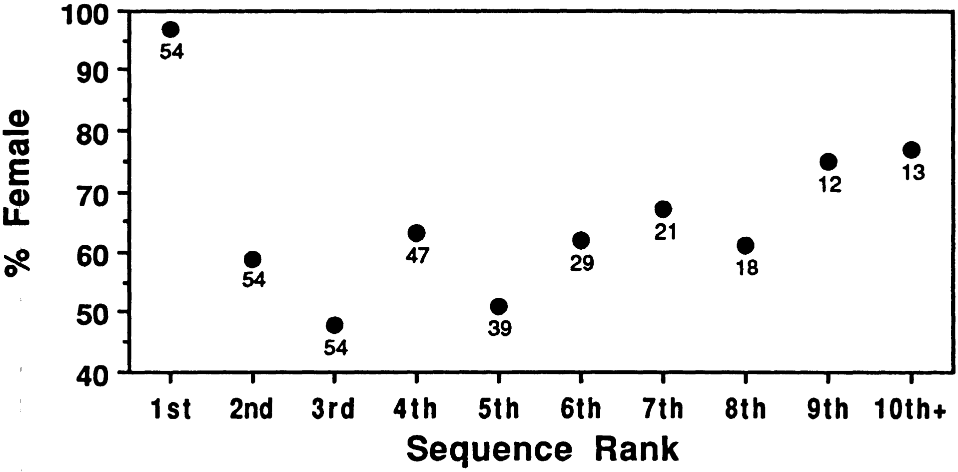


Fig. 3. The percentage of female offspring emerging in sequence (1st to 10th + cell) from combs of 54 nests excavated during the foundress phase of 1991 at Site 2. Numbers indicate the number of nests that produced a male or female of a particular sequence rank. The great majority of foundresses (96%) produced a female as their first offspring. Subsequent offspring were produced at a more balanced ratio, with a gradual increase towards more and more female-biased ratios.

Ratio.] Worker reproduction (2.6%) therefore appears to be a less important reproductive option than becoming a replacement queen (6.6%), but more important than independent nest founding (1.0%).

SEX RATIO: *First-brood sex ratio:* The first offspring produced by a foundress is virtually always a daughter (Fig. 3). Subsequent offspring of the first brood are produced at a more equal male to female ratio, with the ratio gradually rising from about 1:1 for the second offspring to about 1:3 for the tenth offspring. A similar drastic shift from a highly female-biased to a more male-biased sex ratio, and a subsequent monotonic trend towards more and more female-biased sex ratios was also described by Packer (1990) for a population of *A. striata* in Nova Scotia. Production of a female as the first offspring may be a strategy of the foundresses to gain a worker at the earliest possible opportunity.

Overall, the allocation ratio of the first brood appears female-biased with an average of 32.9% male investment (34.6% in 1989, 27.9% in 1990, 36.3% in 1991 at Site 1; 36.2% in 1991 at Site 2; using values from time periods 5–7 and averaging first within 1991; see Table 3). However, the actual ratio of investment in first-brood reproductives must be more male-biased, because the great majority of first-brood females become sterile workers. A more accurate value of the allocation ratio of the first brood (corrected for the production of sterile workers) would take into account the exact probability of reproduction by first-brood females either (a) as an independent reproductive (1.03%), (b) as a laying worker (2.64%), or (c) as a replacement reproductive after queen supersedure (6.57%) (see "Caste" for derivation of these percentages). Mueller (in preparation) outlines a method to correct the first-brood sex ratio for the production of sterile workers, applies this method to parameter estimates from *A. striata,* and concludes that the corrected first-brood sex ratio is about 80% and highly male-biased.

Second-brood sex ratio: Emergence of second-brood offspring (sexuals) was

Table 3. Number of males and females emerging during 10-day periods from combs of non-experimental colonies, and their numerical and allocation sex ratios (% male) for Site 1 (1989–1991) and Site 2 (1991). Time periods are arranged such that the stages in the life cycle correspond between years and sites: Time period 5 begins with the emergence of the first brood; time period 8 includes a mix of the last emergences of the first brood and the first emergences of the second brood; time periods 9–12 include only individuals of the second brood.

Year Site	Time period	# of Females	# of Males	Numerical sex ratio	Allocation sex ratio	
1989						
Site 1	5	47	26	35.62	31.23	
	6	14	13	48.15	43.72	1. brood
	7	—	—	—	—	
	8	—	—	—	—	———
	9	6	20	76.92	71.50	
	10	32	26	44.83	40.02	2. brood
	11	23	6	20.69	19.15	
	12	—	—	—	—	
1990						
Site 1	5	—	—	—	—	
	6	27	21	43.75	37.59	1. brood
	7	30	7	18.92	15.32	
	8	27	18	40.00	33.42	———
	9	34	85	71.43	64.25	
	10	83	58	41.14	34.05	2. brood
	11	13	7	35.00	29.16	
	12	—	—	—	—	
1991						
Site 1	5	—	—	—	—	
	6	—	—	—	—	1. brood
	7	—	—	—	—	
	8	11	18	62.07	61.02	———
	9	19	24	55.81	52.93	
	10	14	23	62.16	55.59	2. brood
	11	13	13	50.00	46.52	
	12	—	—	—	—	
1991						
Site 2	5	47	43	47.78	43.44	
	6	70	39	35.78	31.70	1. brood
	7	22	12	35.29	32.02	
	8	13	16	55.17	49.92	———
	9	4	9	69.23	68.81	
	10	17	26	60.47	53.34	2. brood
	11	29	17	36.96	33.12	
	12	8	5	38.46	34.89	

protandrous, with males predominating during the first two weeks (50–70% male investment) and females during the last three weeks (20–40% male investment) of the reproductive phase (Table 3). Overall, the estimated population allocation ratio of the second brood was slightly female-biased with an average of 44.5% male investment (Site 1: 41.4% in 1989 for TP9–11; 43.6% in 1990 for TP8–11;

54.2% in 1991 for TP8–11; Site 2: 43.0% in 1991 for TP8–12; averaging first between the two measures from 1991; see Table 3; TP = time period as explained in Table 3). [When deleting brood emerging in time period 8 (a mix of emergences from first and second brood), affected values change minimally to: 45.1% in 1990 and 52.4% in 1991 at Site 1; 43.3% in 1991 at Site 2. The overall average across years changes to 44.8%.] However, colonies at Site 1 were excavated about 1 week before the end of provisioning. While relatively little brood is provisioned during this time, investment in sexuals is female-biased at the end of the season (Table 3); omission of the last few emergences therefore will slightly underestimate female investment. The second-brood investment ratio over the entire worker phase therefore must be more female-biased than indicated by the above estimates. Indeed, the second-brood investment ratio at Site 2, calculated over the entire worker phase (Time Periods 8–12), was 43.0% male investment, but 44.0% if reproductives produced in the last week of provisioning were deleted. The error in the allocation-ratio estimate for colonies excavated one week before termination of provisioning therefore appears to be 1–5%. The actual average allocation ratio of the second-brood probably falls within the range of 41%–45% male investment, suggesting a value of 43% for further analyses.

Variation in sex ratio between colonies: Allocation ratios of the second brood differed markedly between colonies. Allocation ratios of both eusocial and parasocial colonies were protandrous, but, overall, colonies headed by the original foundress produced significantly more female-biased allocation ratios (mean male investment = 39.5%; 32.2% in 1989, 40.3% in 1990, and 48.3% in 1991 at Site 1; 43.8% in 1991 at Site 2) than colonies headed by a daughter replacement reproductive after supersedure of the foundress (mean male investment = 58.4%; 48.6% in 1989, 69.1% in 1990, and 67.7% in 1991 at Site 1; 47.2% in 1991 at Site 2; paired $t = 3.2$, d.f. = 3, $P = 0.047$). [The allocation ratios, corrected for the few sexuals that would have been provisioned after excavation, are probably 1–5% more female-biased; see above.] The sex-ratio differences between eusocial and parasocial colonies confirm predictions derived from split sex-ratio theory (Boomsma and Grafen 1990, 1991) that allocation ratios should be more female-biased in the presence of a relatedness asymmetry (eusocial colonies) than in the absence of a relatedness asymmetry (parasocial colonies). This suggests that workers are at least in partial control of the allocation ratio and capitalize on the relatedness asymmetry in eusocial colonies by biasing the allocation ratio towards their more closely related sisters (Trivers and Hare 1976; Boomsma 1991; Mueller 1991).

Female to male weight ratio: Both female and male weights of the second brood were significantly higher than corresponding weights of the first brood (paired $t = 4.61$, d.f. = 3, $P = 0.044$ for females; paired $t = 5.43$, d.f. = 3, $P = 0.032$ for males; Fig. 4). The reasons for these differences are unclear but could

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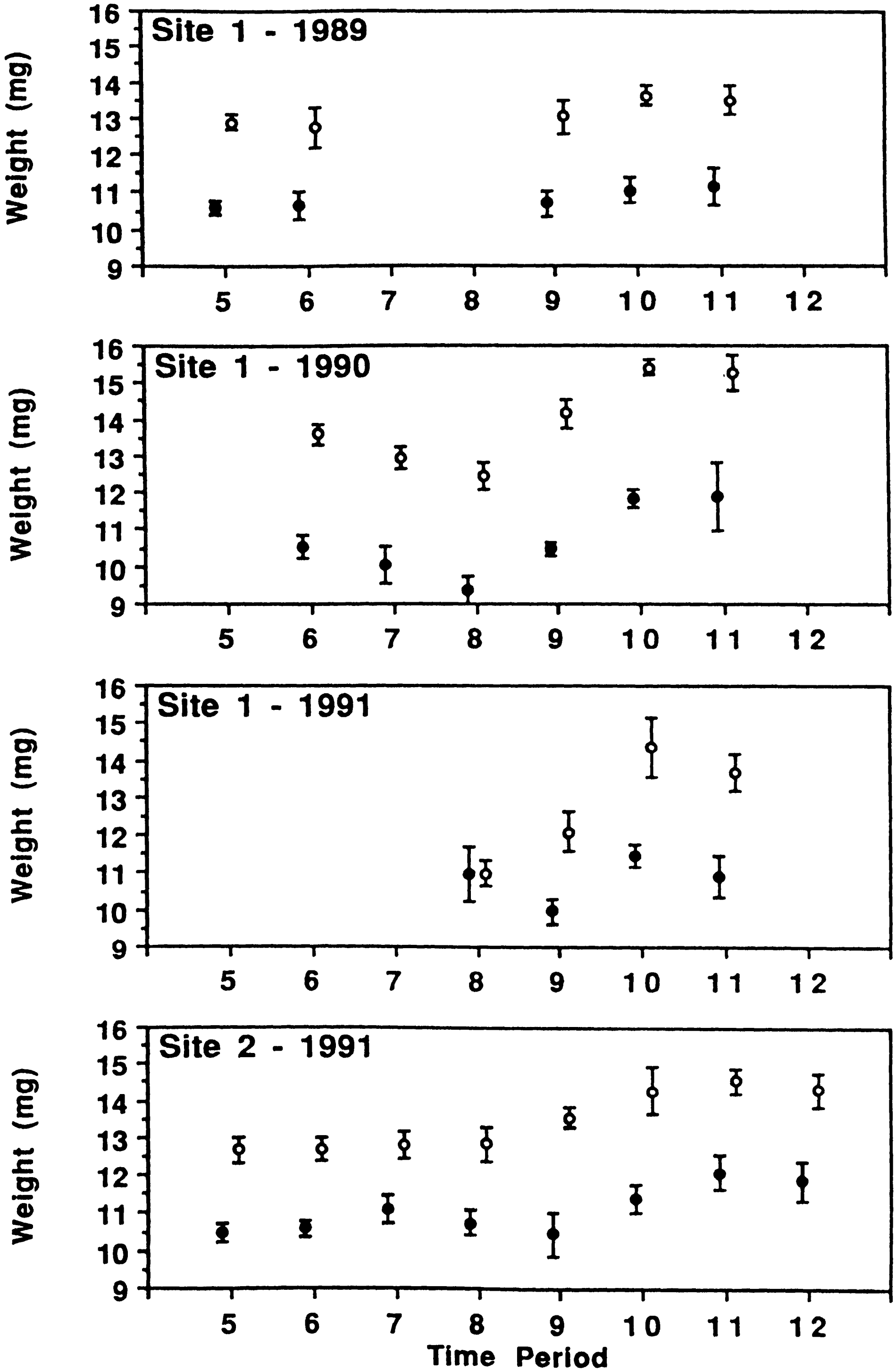
Fig. 4. The average wet weight (mg) of males (closed circles) and females (open circles) emerging from combs of experimental and non-experimental colonies during ten-day periods in the laboratory. Time periods are arranged such that the stages in the life cycle correspond between years and sites. The average wet weight of both males and females increased from the first brood (time period 5–7) to the second brood (time period 9–12).


Site 1 - 1989
Site 1 - 1990
Site 1 - 1991
Site 2 - 1991
Weight (mg)
9
10
11
12
13
14
15
16
5
6
7
8
9
10
11
12
Time Period

include (a) constraints such as scarcity of forage or low average temperatures in spring that force foundresses to produce males and females of suboptimal size; (b) optimal allocation of resources to worker vs. reproductive brood; (c) "parental manipulation" of the size of first-brood females to induce "subfertile" first-brood females to become workers (Alexander, 1974). While the first hypothesis could explain the increase in weight for males and females, the latter two hypotheses could do so only for females, but not for males. This suggests that the lower weights of first-brood females may not necessarily be due to parental manipulation as has been suggested by Alexander (1974), but may be the mere consequence of ecological factors constraining foraging options of foundresses.

Although the absolute weights of both male and female offspring increased over time, the weight ratio (male : female) remained relatively constant throughout the entire colony cycle (Fig. 5). In both the first and second brood, females weighed 1.2–1.3 times more than males (average = 1.238 ± 0.052). The ratio increased slightly from the first to the second brood (Fig. 5), but the increase was not significant (paired $t = 2.94$, d.f. = 3, $P = 0.097$). The slight increase in the male : female weight ratio for sexuals may reflect the fact that the sexual brood consisted entirely of reproductives, while the first brood consisted predominantly of sterile female workers and male reproductives.

MALE BEHAVIOR AND MATING: Males were present in high numbers from the beginning of the worker phase until the end of the season (Tables 1, 3). This reflected the foundress' tendency to produce a male as one of her first few offspring (Fig. 3). All first-brood females therefore had the possibility of mating and were not reproductively constrained by the absence of males, contrary to what has been suggested for other halictines (Yanega, 1988, 1989). As shown above, 100% of the foundresses, 90% of the replacement reproductives, and about 40% of the workers were inseminated. Indeed, the existence of unmated replacement reproductives in *A. striata* clearly indicates that matedness is not a necessary condition for queen development as envisioned in Yanega's (1988, 1989) model of caste determination.

Males frequently attempted to mate with first-brood females during the worker phase. Mating attempts generally occurred on flowers while females were foraging, but males would also try to grab females in mid-air. In either case, the pair generally fell to the ground, and the female struggled to free herself from the male. Most mating attempts therefore resulted in the rejection of the male. Of 47 mating attempts recorded during 1989–1992, only one resulted in a mating (lasting 4 sec), while all other pairs separated after a short grapple of about 1 sec. Given that about 40% of first-brood females become inseminated (see above 'Caste: Insemination'), this indicates that (a) unmated females reject mating attempts, and/or that (b) inseminated females refuse to mate with more than one or

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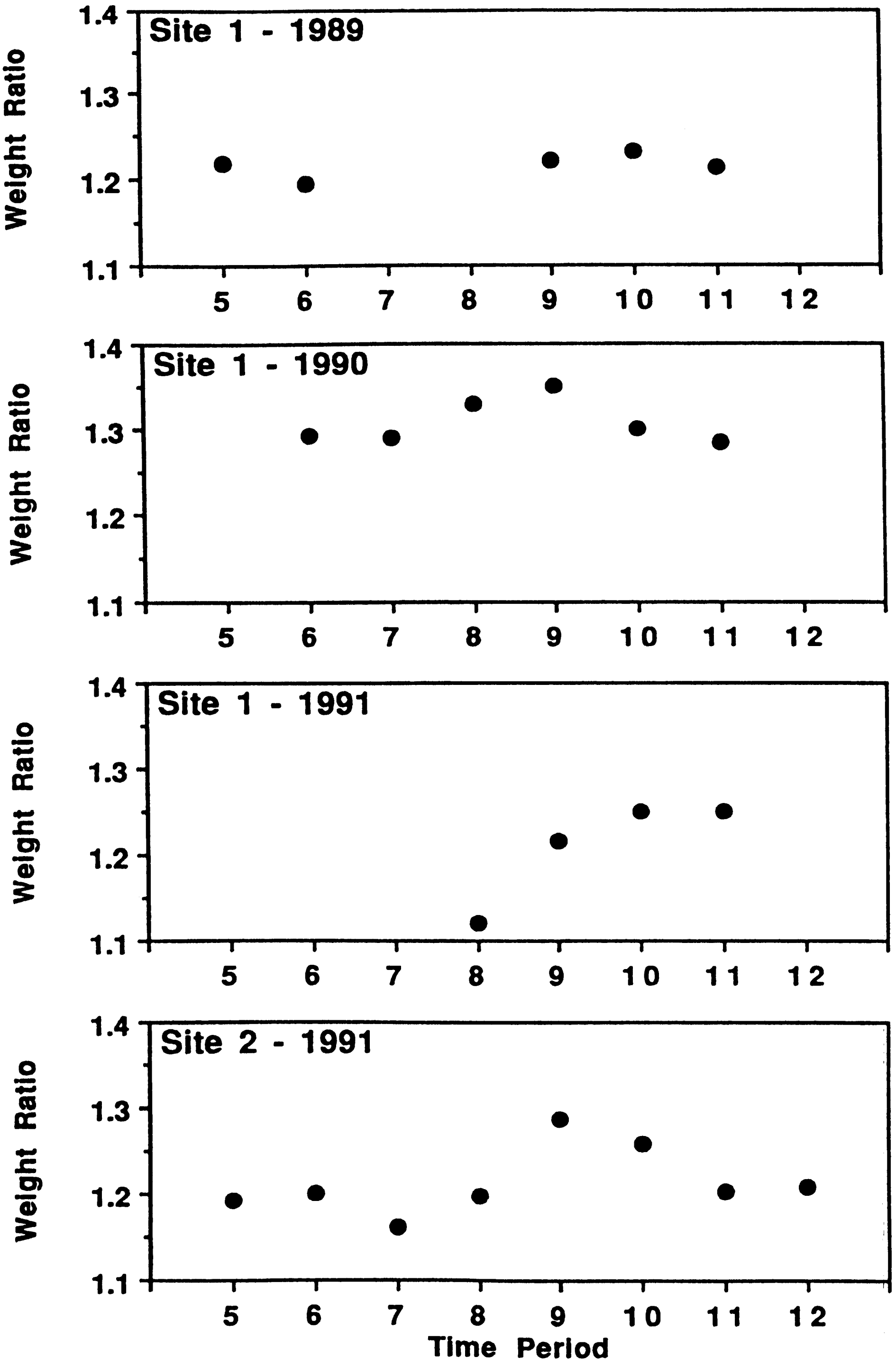
Fig. 5. The male to female weight ratio for sexual reproductives emerging from combs of experimental and non-experimental colonies during ten-day periods in the laboratory. Time periods are arranged such that the stages in the life cycle correspond between years and sites. Although the absolute weight of both male and female offspring increased from the first brood (time period 5–7) to the second brood (time period 9–12) (see Fig. 4), the weight ratio remained relatively constant throughout the entire colony cycle.


Site 1 - 1989
Site 1 - 1990
Site 1 - 1991
Site 2 - 1991
Weight Ratio
1.4
1.3
1.2
1.1
5
6
7
8
9
10
11
12
Time Period

with only a few males. The finding of an effective mating frequency of one in *A. striata* (Mueller et al., 1994) is consistent with the latter hypothesis.

Males left their natal nest on the day they emerged, did not return, and appeared to drift gradually out of their natal aggregation. Of 50 males marked at Site 1 during the worker phase of 1989, only 12 (24%) were resighted after marking while hovering about the nest aggregation. Only two males were sighted for longer than 15 days, and only one for 30 days. This suggests that either the average lifespan of males was limited, or, as seems more likely, males were highly vagrant and thus likely to drift out of the aggregation. The latter scenario is consistent with DNA fingerprinting evidence of outbreeding in *A. striata* (Mueller et al., 1994). One mixed aggregation of five males of *A. striata* and one male *Lasioglossum* sp. was discovered on a rainy day in a dry, rolled-up leaf of a small alder partially overhanging one of the nest aggregations.

Evolution of Eusociality in Augochlorella striata

Evans (1977) categorized the evolutionary causes of eusociality into intrinsic (genetic) and extrinsic (ecological) factors and suggested that an analysis of eusocial evolution should attempt to weigh the relative contribution of these factors in the selective process. For *A. striata,* the life-history parameters above suggest that both genetic factors (relatedness asymmetry and sex-ratio biases) and ecological factors (ecological constraints) contribute to the maintenance of eusociality. Intrinsic factors are implicated by (a) extreme relatedness asymmetries (3:1; due to singly mated queens; Mueller et al., 1994) in conjunction with female-biased sex ratios at a time when worker altruism is expressed (see Seger, 1983); and (b) the coexistence of eusocial and parasocial colonies during the worker phase, each specializing on an opposite sex-ratio strategy, thus undoing each other's effects on the population sex ratio and allowing eusocial workers to capitalize on relatedness asymmetries more than they could if the population consisted only of eusocial colonies (Boomsma and Grafen, 1990, 1991). Extrinsic factors are implicated by (a) the high mortality rates of independently nesting females during the foundress phase, compared to more moderate mortality rates of colonies during the worker phase, thus guaranteeing immediate and assured fitness returns to females opting to become workers rather than attempt independent reproduction (Queller, 1989; Gadagkar, 1990; Alexander et al., 1991); and (b) plasticity in reproductive strategies of first-brood females, suggesting adaptive responses to ecological variables modulating fitness functions of workers and independent reproductives (West-Eberhard, 1981; Alexander et al., 1991).

Even though both intrinsic and extrinsic factors appear to operate in the evolutionary maintenance of eusociality in *A. striata,* it is unclear at this point which of the two is the more important selective factor. A sequel analysis (Mueller, in preparation) attempts to weigh the relative importance of these two factors. This sequel study concludes that intrinsic factors (relatedness asymmetries and sex-ratio biases) contribute less than 10% to the fitness of workers, that intrinsic factors play nevertheless an important role in modulating decisions of second-brood females when choosing between a strategy of independent reproduction or worker behavior, but that, overall, the evolution of eusociality in *A. striata* is driven largely by ecological constraints, with relatedness asymmetries (and female-biased sex ratios) playing a numerically less critical role.

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