Nomadic behaviour and colony fission in a cooperative spider: life history evolution at the level of the colony?

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The concept of colony-level life history evolution is introduced for the cooperative spiders by describing the life cycle and demography of *Aebutina binotata* (Araneae: Dictynidae), a species living in groups containing up to several dozen adult females plus their offspring. In a life cycle remarkably similar to that of army ants, the colonies of *A. binotata* were found to reproduce by fission and to alternate nomadic and sedentary phases in tight association with their internal demography. Colonies of other cooperative spiders, on the other hand, remain stationary as they grow for a number of generations before producing propagules that are relatively small subsets of the maternal colony. It is suggested that *A. binotata*’s peculiar life cycle may have unfolded as a consequence of the two-dimensional architecture of its nests. Expanding two-dimensional nests may fragment more easily than the three-dimensional nests characteristic of other species. A long distance group migration or nomadic phase, described here for the first time for a spider, may have followed as a mechanism to cope with potential disadvantages of fission while selecting for strict synchronization of individual life cycle stages within the nests. It is shown, however, that, as in other cooperative spiders, *A. binotata*’s sex ratio is also highly female biased. The theoretical implications of biased sex ratios in a species with fissioning colonies are briefly discussed.

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The possibility that social groups may exhibit life history strategies, as do individual organisms (Stearns, 1992), has only recently been explicitly explored in the literature (reviewed in Bourke & Franks, 1995). The cases discussed so far have involved species of the social insects which often form highly integrated social groups that could, in some instances, be considered superorganisms (e.g. Franks, 1989; Seeley, 1989). Here, I will argue that the concept of a colony-level life history strategy can also be applied to organisms, such as the cooperative spiders, that constitute less integrated societies. I will do so by contrasting the colony life cycle of *Aelurina binotata* Simon (Araneae: Dictynidae), a spider recently reported to be social (Avilés, 1993a), with that of other spider species of a similar level of sociality.

*A. binotata* is a cribellate spider of bright yellow coloration and about 5 mm in length (see cover of Choe & Crespi, 1997), currently placed in the family Dictynidae (Perunkevitch, 1928; Millot, 1933, but see Lehtinen, 1967). Avilés (1993a) reported that this neotropical species forms colonies containing from at least a dozen to just over a hundred adult females plus their offspring. Its nests consist of a thin sheet of silk laid on both surfaces of one or a few contiguous leaves and their connecting branches. Egg sacs and young are kept on the underside of the leaves where older spiders remain except during web repair and prey capture activities. Several individuals participate in subduing and transporting prey items on which communal feeding takes place. Brood care, which involves sac guarding and the sharing of captured prey, is apparently communal as the offspring in a nest intermix freely and are cared for by a declining number of surviving females. No division of labour among colony members, other than on the basis of age, is apparent in this species. In particular, females appear to lay a single egg sac each (Avilés, 1993a).

Social behaviour involving communal prey capture, feeding, and brood care has been described for 17 spider species in eight genera (for a recent review see Avilés, 1997). With a few exceptions, the colonies of these cooperative spiders (technically labelled as non-territorial permanent social) constitute not only social groups but also relatively closed intrabreeding populations. This situation, which notably differentiates these spiders from most insect societies, arises because colony members remain within their natal nest throughout their lives and mate with other members of their colony to produce successive generations (e.g. Lubin & Crozier, 1985; Roelofs & Riechert, 1988; Smith & Engel, 1994; Smith & Hagen, 1996). This process repeats itself generation after generation until the colonies either give rise to daughter colonies or become extinct. It has been suggested that the highly female-biased sex ratios that characterize the cooperative spiders (reviewed in Avilés, 1997) may have arisen because the isolation of the colony lineages and their relatively fast rate of turnover would have allowed the operation of intercolony selection for faster colony growth (Avilés, 1986, 1993b, 1997).

Previously described cooperative spiders produce more or less stationary nests that are inherited from parental to offspring generations. Their usual mode of colony proliferation involves the production of daughter colonies that are small subsets of
Table 1. Sizes of *A. binotata* individuals by instar and sex. The specimens belong to three completely-collected colonies and samples from periodically-censused colonies. Total length measured to the nearest 0.1 mm; interocular distance measured to the nearest 0.025 mm. Instar 1 corresponds to spiderlings prior to their emergence from the sac

<table>
<thead>
<tr>
<th>Instar</th>
<th>Sex</th>
<th>Total length mm Mean ± 95% c.i.</th>
<th>Interocular distance (anterior lateral eyes) mm × 10 Mean ± 95% c.i.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (in sac)</td>
<td>?</td>
<td>1.39 ± 0.04 (N=11)</td>
<td>1.76 ± 0.10 (N=9)</td>
</tr>
<tr>
<td>2</td>
<td>?</td>
<td>1.61 ± 0.08 (N=10)</td>
<td>2.25 ± 0.05 (N=11)</td>
</tr>
<tr>
<td>3</td>
<td>?</td>
<td>1.82 ± 0.07 (N=11)</td>
<td>2.98 ± 0.11 (N=23)</td>
</tr>
<tr>
<td>4</td>
<td>female</td>
<td>2.16 ± 0.08 (N=23)</td>
<td>2.65 ± 0.19 (N=31)</td>
</tr>
<tr>
<td></td>
<td>male</td>
<td>2.30 (N=2)</td>
<td>3.25 (N=2)</td>
</tr>
<tr>
<td>5</td>
<td>female</td>
<td>2.65 ± 0.19 (N=31)</td>
<td>3.95 ± 0.13 (N=11)</td>
</tr>
<tr>
<td></td>
<td>male</td>
<td>2.77 ± 0.24 (N=2)</td>
<td>3.58 ± 0.16 (N=3)</td>
</tr>
<tr>
<td>6</td>
<td>female</td>
<td>2.96 ± 0.14 (N=10)</td>
<td>4.84 ± 0.18 (N=10)</td>
</tr>
<tr>
<td></td>
<td>male</td>
<td>2.99 ± 0.08 (N=7)</td>
<td>4.34 ± 0.16 (N=6)</td>
</tr>
<tr>
<td>7</td>
<td>female</td>
<td>3.85 ± 0.11 (N=10)</td>
<td>6.12 ± 0.13 (N=10)</td>
</tr>
<tr>
<td></td>
<td>male</td>
<td>3.45 ± 0.01 (N=2)</td>
<td>4.5 (N=2)</td>
</tr>
<tr>
<td>8</td>
<td>female</td>
<td>4.74 ± 0.16 (N=7)</td>
<td>7.31 ± 0.24 (N=8)</td>
</tr>
</tbody>
</table>

the parental colony (reviewed in Avilés, 1997). Here, I will present evidence that *A. binotata* departs from this basic pattern in incorporating a nomadic phase in its life cycle and in giving rise to new colonies by fission, a life cycle remarkably similar to that of army ants. As in other cooperative spiders, however, *A. binotata*’s sex ratio was found to be highly female-biased. In the discussion, I speculate about the factors that could have led to the evolution of *A. binotata*’s peculiar colony-level life history pattern and point to the evolutionary implications of a sex ratio bias in a species whose colonies reproduce by fission.

**METHODS**

*Instars, sex, and sex ratio determination*

*A. binotata* specimens were initially sorted into distinct age/size classes—here assumed to correspond to instars—according to differences in their size, body proportions, and the state of their genitalia. The degree of enlargement of the palpi was used to distinguish males of different instars from each other and from females of the equivalent instar. Undifferentiated juvenile and female instars were separated primarily based on size and the correspondence of that size to the previously determined male instars. A discriminant function analysis based on four measurements—total body length, carapace length, sternum length, and interocular distance—was used to revise the original classification in instars. Only two specimens out of 109 measured were found to have been initially misclassified according to this method. I have used the interocular distance and total body length, which produced the best separation of the size classes, to define the various instars (Table 1). Sex ratios were estimated among intermediate instars in three completely-collected colonies and among late instars in seven colonies censused in the field.
Field observations

I followed the history of naturally-occurring colonies of *A. binotata* at a 3500 m² tropical rainforest area by the Tarapuy River in eastern Ecuador (Sucumbios Prov., 00°08' S, 76°16' W, 210 m above sea level). I initially tagged and mapped the position of 24 colonies whose history I followed at two to four-week intervals for a period of 4 months (February to May 1984). I surveyed the site again 2 and 4 months later when I recorded 21 additional colonies. During each visit to the field I recorded changes in the size, position, and internal demography of all colonies (number of egg sacs, adult and subadult males and females, and approximate number of juveniles) and inspected their surroundings (within a 5 m radius) for the presence of any previously unrecorded nest that may suggest a colony reproduction event.

I obtained direct evidence of colony relocation from (a) observing a complete relocation process (*N* = 1), (b) observing colonies before and after their relocation was completed in a few hours or in consecutive days, when silk lines still connected the old and new sites (*N* = 5), (c) noting short distance (<0.5 m) relocation events that had taken place in between visits to the field (*N* = 3), (d) observing the initiation of the process, without identifying the final destination of a colony (*N* = 2), and (e) observing migrating groups of spiders (*N* = 3). I obtained indirect evidence of relocation from noting the disappearance of a colony from its original location and either (f) tentatively identifying its new location within a 5 m radius (*N* = 3) or (g) assuming that it had moved beyond the searched area (*N* = 8). Identification of a colony's new location in (f) was based on a correspondence in size and age-structure between the missing colony and a newly-appeared colony within the searched area. Because I considered this identification only tentative, I have performed all statistical tests under the alternative assumption that the three colonies in this category had moved beyond the searched area. I also considered the alternative possibility that the colonies in (f) and (g) had gone extinct rather than relocated. There was, however, no indication of destruction of the marked nest sites or *in situ* deterioration of these colonies that would suggest extinction. In my experience with other cooperative spiders, unless a catastrophe hits a colony, extinction tends to be a gradual process that can be documented.

A preliminary assessment of the minimum distance traveled and duration of the migratory phase of colonies with mature individuals was obtained by following one of three migrating groups of spiders (case e) for 13 hours of two consecutive days and by observing the relocation process of a captive colony in the laboratory (see below).

Laboratory observations

Following the periodic observations above described, the area of the forest where this study was performed was cut for cattle grazing. No additional colonies could be located until August 1995, when G. Cañas collected by the Guyabeno River (Ecuador, Sucumbios Prov., 00°02' S, 76°19' W) a colony containing 13 adult males and 56 adult females. This colony was maintained at the University of Arizona for a period of 8 months. During this time the spiders were kept under tropical rainforest conditions (12 hour photoperiod, 21–26°C, and 60–80% humidity) and provided with water and a daily supply of insect prey. The spiders were placed in a
Figure 1. Distribution of *A. binotata* colonies and their life cycle stage as seen on the fifth census date at the study site by the Tarapuy River in eastern Ecuador. In addition to the colonies present this date, shown are also three colonies that had recently disappeared from their recorded location (## 3, 5 and 7) and two colonies recorded in the next census date (## 22,23). The stage in a colony’s life cycle is symbolized by partially-filled circles. Circles become filled as the offspring generation develops from egg sacs (empty circles) to adults (7/8-filled circles). Colonies whose nearest neighbour is in identical stage as themselves are marked with an asterix. If we exclude the two colony pairs known to be the product of fission (colonies 8–17 and 16–19), 8 of the remaining 17 colonies—or 47.1%—had an identical nearest neighbour.

183 × 65 × 46 cm terrarium containing a variety of tropical plants and marked on the top with a 10 cm grid. The location of the spiders within the terrarium was recorded daily from September 6 through September 27 and at irregular intervals before and after this period.

**Statistical tests**

I developed a permutation test to investigate whether the spatial distribution of colony life cycle stages in the field might reflect the occurrence of fission events other than those observed (see Manly, 1997 for a general description of randomization methods). The test consisted in permuting the colony life cycle stages, as shown in Figure 1, while maintaining the spatial distribution of the colonies fixed. I performed 30,000 replicate permutations to test the hypothesis that the proportion of colonies having as their nearest neighbour a colony in identical stage in their life cycle as themselves was higher than expected by chance. This hypothesis was based on the observation that the products of two fission events recorded became each other’s nearest neighbours.

Unless otherwise indicated, means are reported ± 95% confidence intervals. Categorical data were analysed using contingency tables and the likelihood ratio chi-square test (G test).
Table 2. *A. binotata* sex ratios among intermediate- (instars 4–6) and late-instar individuals (instar 7 males, instar 7–8 females) in four completely-collected (colonies 7, 17, 43, and 45) and six field-censused colonies (remaining colonies). The colonies with late-instar individuals shown did not yet contain egg sacs and, thus, are unlikely to be affected by early male mortality.

| Colony | Instars 4–6 | | Instars 7,8 | | |
|--------|-------------|---|-------------|---|
|        | Females | Males | Females | Males |
| 7      | 60 | 9 | 57 | 9 |
| 17     | 9 | 1 | 62 | 1 |
| 45     | 93 | 5 | 50 | 2 |
| 41     | 106 | 4 | 93 | 8 |
| 33     | 89 | 3 | 60 | 1 |
| 34     | 32 | 8 | 436 | 20 |
| Total  | 162 | 15 | 456 | 28 |
| % males | 8.5 | | 5.8 | | |
| 95% c.i. | 4.3–14.2 | | 3.6–8.6 | | |

RESULTS

Life cycle and colony demography

*A. binotata* clutch sizes ranged from 11 to 17 eggs (mean = 14.9 ± 1.9, N = 7 field-collected sacs). Including a first instar spent within the egg sacs, *A. binotata* males were found to become adult in their 7th and females in their 8th instar (Table 1). Starting in their 4th instar, males could be distinguished from females by their increasingly enlarged palpi. The sex ratio among instars 4–6 was heavily and significantly female biased—8.5% males (G² = 142.7, 1 df, P < 0.0001; Table 2). A sex ratio bias at this stage would indicate heavier maternal investment in females given that instars 4–6 are still subject to maternal care (see below and Fig. 2B) and males and females of these instars are not significantly different in size (Table 1) (F = 0.47, 3 df, P = 0.70 for the effect of sex on log-transformed body length, with sex nested within instar). The proportion of males among instars 7–8 females and instar 7 males was lower—5.8% males—but not significantly different from that of the younger individuals (G² = 1.5, 1 df, P = 0.23).

Egg-laying and offspring development were highly synchronized within the nests. In the laboratory, 23 out of the 26 egg sacs produced were laid over the span of one night. In the field, the colonies contained only a subset of individual life cycle stages—either adult females plus egg sacs, adult females plus spiderlings of two or three contiguous instars, or subadults and young adults in the absence of females of the maternal generation. Only two out of the 44 nests seen in the field contained individuals that were out of phase with other members of their colony: (a) a colony with 5 early-instar juveniles, out of phase with 102 adult females, 7 egg sacs, and 1 adult male and (b) a colony with 2 subadult females in a nest that otherwise contained only adult females and juveniles. Based on their age composition, I have defined eight colony life cycle stages (I–VIII) that I will use throughout the paper to refer to various aspects of the biology of this species (Fig. 1).
I obtained an estimate of the average female reproductive success—a combined measure of the number of eggs laid per female and of offspring survival to an intermediate instar—in six colonies seen from at least the tail end of the egg-laying period (when the original number of females could be recorded). In these colonies, average female reproductive success was $9.6 \pm 1.8$ offspring per female. If seen as a function of the number of females originally in the nest, these data are suggestive of a non-linear relationship between reproductive success and colony size (Fig. 2A). Because of the small number of points involved, however, any trend suggested by these data can only be considered tentative and is discussed here for heuristic purposes only (see Discussion).

As their offspring developed, a decreasing number of maternal females were present in the nests (see Fig. 2B for an example) and none were seen in colonies containing subadults and young adults (old maternal females could be distinguished from young adults by their noticeably darker coloration). Nonetheless, females overlapped with their progeny during a significant portion of their life cycle (Figs 2B and 3). Males, on the other hand, were absent from the field nests once egg laying had been completed and appear to have a much shorter life span. In the laboratory, 11 out of the initial 13 males died during the observed 5-week relocation period. The two surviving males settled with the females but wandered away from the nest (and died soon thereafter) 1 and 13 days after the eggs had been laid. In contrast, the adult females in the laboratory lived for another 6 months.

By combining data from the observed fractions of the life cycles of four field colonies, plus the 5-week nomadic period observed in the laboratory, I estimate that a complete cycle from eggs to eggs of two consecutive generations would last between
Figure 3. Diagramatic representation of colony and individual life cycles in *Aebutina binotata*. A complete cycle from eggs to eggs is estimated to last between 28 and 31 weeks, with a 15–18 week overlap between maternal and offspring generations (see text for details).
Table 3. Relocation distance of *A. binotata* colonies as a function of the stage in their life cycle (instar composition). All colonies observed during a given developmental stage are included in each category. Colonies seen for more than one stage, therefore, may be included in more than one category. The number of colonies for which the only evidence of relocation is disappearance from a site are noted within parentheses*, with those in column ‘>0–5 m’ corresponding to colonies whose new position was identified with some uncertainty (see Methods).

<table>
<thead>
<tr>
<th>Colony life cycle stage</th>
<th>Instars present</th>
<th>Number of colonies per relocation distance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0 m</td>
<td>&gt;0–5 m</td>
</tr>
<tr>
<td>first half (I–V)</td>
<td>8,1–8,4,5</td>
<td>23</td>
</tr>
<tr>
<td>second half (V–I)</td>
<td>8,4,5–8,1</td>
<td>3</td>
</tr>
</tbody>
</table>

* The association between colony life cycle stage and relocation distance (see text) stands even if we assume that the colonies within parentheses in the ‘>0–5 m’ column were misidentified following relocation—i.e., we subtract these colonies from column ‘>0–5 m’ and add them to column ‘>5 m’ (G² = 18.4, 2 df, *P* = 0.001) or if we assume that all colonies within parentheses went extinct rather than relocated (G² = 17.9, 2 df, *P* = 0.0001). This lack of synchronization appeared surprising given how close in space the colonies were to each other, with a mean distance to their nearest neighbour of only 3.45 ± 2.13 m (N = 16 colonies as seen on the fifth census date). As I show below (see ‘Colony fission’), however, the spatial distribution of life cycle stages was not entirely random, apparently reflecting patterns of colony reproduction.

### Colony relocation and the nomadic phase

None of the colonies under study remained at their original location for more than one generation cycle. As the stage in their life cycle progressed, the colonies occasionally relocated to nearby sites (<5 m) and eventually entered a phase of long distance migration that I will refer to as the nomadic phase. There was a significant association between the stage in a colony’s life cycle and the distance moved (G² = 18.1, 2 df, *P* = 0.0001, Table 3). With only one exception, colonies that contained egg sacs or young juveniles did not move or moved for less than a meter when damage to their nest had occurred. The only colony that moved beyond a 5 m radius at this stage had just started the egg-laying period and contained only two egg sacs. Colonies that contained older instar individuals, on the other hand, moved more readily and farther away. For instance, following a major storm that triggered several relocation events, two colonies that contained individuals approaching reproductive maturity moved beyond a 5 m radius, while two colonies containing young juveniles moved to locations within 5 m of their original site. Six of the twelve short distance (>0–5 m) relocation events recorded were triggered by nest damage.
One occurred after the leaf supporting the nest dried up and five others followed strong rains. The trigger in the remaining six cases was not identified.

Colonies containing individuals nearing sexual maturity, on the other hand, entered a nomadic phase that may apparently last several weeks. Evidence of such nomadic phase came from observing the repeated relocation of the laboratory colony, noting the disappearance from their recorded location of all colonies (5 out of 5) that reached colony life cycle stages VII and VIII, and observing in the field three groups of migrating adult spiders. The colony maintained in the laboratory was on the move for 5 weeks following its placement in the terrarium. During the 21 days when daily records were maintained (see Methods), the spiders moved back and forth within the terrarium, establishing temporary nests that lasted for 1–4 days (mean = 2.7 days, N = 6 relocation events recorded in this period). Throughout this period, the males sought matings and copulated with the females. All spiders that survived the 5-week relocation period—55 females and 2 males—finally settled under a 11 x 6.5 cm leaf. The females laid their eggs 4 days after settlement and remained together under the same leaf for the following 6 months. (The laboratory colony eventually failed because the eggs did not develop or were eaten by the females).

In the field, I observed three migrating groups of adult males and females. I followed a group of 57 females and 9 males for 13 hours of two consecutive days (12:00 to 18:00 hours and 7:00 to 14:00 of the following day, with no displacement having taken place during the night). During this period, the spiders followed each other single file along bridges of silk cast inside the forest. The bridges ranged in length from 0.1 to 7.0 m (median = 0.9 m, N = 49 segments), for a total of 51 m in zigzag and a net displacement of 20 m in a northeasterly direction. In 25 out of the 30 displacements for which group composition was recorded, the entire group started out in a single direction. In the remaining five cases, a few spiders started out in a different direction but within 1 to 10 minutes re-joined the majority. By the end of the observation period, only one spider had become separated from the group. If the spiders moved a similar distance every 3–4 days for a period of 5 weeks, as did the laboratory colony, this rate of migration would result in 0.4–0.6 km of group travel and 0.14–0.18 km of net displacement in a 5-week period.

**Colony fission**

On two occasions I obtained direct evidence of colony fission. In one case, a colony containing 27 adult females and just over 300 instar 4–6 juveniles became reduced to 1/3 that size (9 adults and around 135 juveniles) while a new colony of around 2/3 the size of the original colony (13 adults and around 190 juveniles of similar instar) appeared 30 cm away from it. On a different occasion, the 10 cm separating two parts of a colony increased to a 40 cm gap, with no connecting lines, after one of the parts moved. The original colony contained 23 adult females and 190 instar 5–6 juveniles. After fission, the part that had moved contained eight adult females and 86 juveniles.

Because the products of these fission events became each other’s nearest neighbours, I hypothesized that the spatial distribution of life cycle stages among the remaining colonies might reflect the occurrence of other recent fission events. A permutation test (see Methods) supports this hypothesis. While 47.1% of the
remaining colonies had nearest neighbours in identical stage in their life cycle as themselves (Fig. 1), only 14.8% were expected to do so under the null hypothesis of a random distribution of represented life cycle stages. The probability of observing 47.1% or higher identical nearest neighbours just by chance is $P = 0.009$.

Finally, the size distribution of colonies at intermediate and early stages in their life cycle is consistent with the occurrence of colony reproduction by fission. On the one hand, colony division in two or more parts would explain the size discrepancy between colonies in an intermediate stage (IV–V) (range 100–650, median = 245, $N = 8$) and those starting a new generation cycle (range 14–106, median = 40, $N = 19$). On the other hand, the absence of colonies containing less than 14 adult females suggests that colony foundation by just one or few females, a method of colony proliferation common in other cooperative spiders (Avilés, 1997), does not occur in $A. \text{binotata}$.

**DISCUSSION**

The observations described above point to some unusual features in $A. \text{binotata}$’s colony life cycle when compared with those of other cooperative spiders (Fig. 3). While the colonies of other species occupy nests that remain stationary and may continue to be expanded for several generations (e.g. Vollrath, 1982; Seibt & Wickler, 1988; Lubin, 1991; L. Avilés, pers. obs.), the colonies of $A. \text{binotata}$ relocate themselves at least once a generation. These relocations may either involve short distance displacements, usually of colonies in intermediate stages of their life cycle, or long distance relocation events occurring during mating and prior to egg-laying (Table 3). Laboratory and field observations suggest that the long distance relocation events may last several weeks and lead to the displacement of the colonies dozens of meters away from their natal site, thus representing a true nomadic phase. In contrast, nest relocations in species such as *Stegodyphus sarasinorum* or *Anelosimus eximius* appear to occur only in response to nest damage and to involve less than a couple of meters of displacement (e.g. Subrahmanyam, 1952; Vollrath, 1982). Coordinated group migration has been reported during the establishment of daughter colonies by budding or swarming in *Achaearanea wau* and *A. eximius*. Observed events, however, involved only fractions of a colony and just a few meters of group migration (e.g. Lubin & Robinson, 1982; Vollrath, 1982; Avilés, 1992). Among the cooperative spiders, therefore, a nomadic phase is apparently unique to $A. \text{binotata}$. Colony fission, as well, sets *A. binotata* apart from other cooperative spiders with known modes of colony proliferation. In these other species colony proliferation usually involves the production of several to numerous daughter groups which are relatively small subsets of the maternal colony (reviewed in Avilés, 1997).

The contrasting life cycles and modes of colony reproduction in the cooperative spiders are reminiscent of the alternative life history strategies that characterize individual organisms (e.g. Stearns, 1992). By drawing analogies across levels, we may hypothesize that trade-offs between size and number of offspring and age and size at maturity may have influenced the evolution of diverse colony life histories in these spiders. Since this is an area that has not been previously considered for spiders, and has received little attention even for social insects (see Bourke & Franks, 1995), I will introduce the problem here by briefly speculating about the factors
that might be responsible for the particular traits that characterize \textit{A. binotata} colonies.

The two-dimensional nature of \textit{A. binotata}'s nests (Fig. 3)—which contrasts with the three-dimensionality of the nests of other cooperative spiders (see Fig. 1, Avilés, 1997)—could be responsible for the occurrence of fission as its primary mode of colony proliferation. \textit{A. binotata}'s nests may be limited by the size of individual leaves or by the number of leaves that can be maintained interconnected in the forest understory. As a result, parts of an expanding colony may become separated and drift away from each other as relocation events take place. Once fission becomes established as a mode of colony proliferation, other aspects of the life history of colonies could evolve in response to its advantages and disadvantages.

A potential advantage of colony fission is the production of large daughter groups that may have an edge in survival probability and reproductive success over small groups. In \textit{A. eximius}, for instance, the survival probability of newly-founded colonies increases dramatically with the number of females they contain (Vollrath, 1982; Avilés, 1992). Average female lifetime reproductive success in this species also increases from small to intermediate-sized colonies (Avilés & Tufiño, 1998). Data collected during the course of this study suggests that \textit{A. binotata} females may also have the greatest success in intermediate-sized colonies (Fig. 2a), which, interestingly, are of about the median size of colonies that are starting a new generation cycle (see ‘Colony fission’). A potential disadvantage of fission is the limited bet-hedging opportunities arising when only two or a few daughter groups are produced. Also, in species with limited group-migration capabilities, large daughter groups may be less able to disperse far from the maternal nest. In \textit{A. eximius}, for instance, nests produced by budding or swarming are established within a few meters of the maternal nest, while nests containing single females may become established several dozen meters away (Vollrath, 1982; Avilés, 1992).

A nomadic phase in a colony’s life cycle may have arisen partly as a means of overcoming some of the disadvantages of fission. By separating the products of fission by potentially hundreds of meters, for instance, a nomadic phase would eliminate the possibility for competition among them. Also, because migrating groups establish temporary nests during their relocation trip, nomadism would provide an opportunity to sample the environment for better foraging sites. Finally, by limiting the time that a colony remains at any one site, a nomadic phase may help prevent the accumulation of parasites. It is noteworthy that, while commensals and parasites are a common problem in various cooperative spiders (Griswold & Meikle-Griswold, 1987; Seibt & Wickler, 1988; Wickler & Seibt, 1988; Cangialosi, 1990a,b; Avilés & Tufiño, 1998), none of the nests or egg sacs of \textit{A. binotata} examined in this study contained any visible parasites.

Why has not a nomadic phase evolved in the life cycle of other cooperative spiders? The explanation may reflect both constraints and absence of a selective pressure. On the one hand, a nomadic phase may not be necessary in species whose colonies produce numerous small propagules that disperse some distance away from the maternal colony. On the other hand, as suggested by the fact that \textit{A. binotata}'s colonies containing egg sacs and small spiderlings do not relocate, a nomadic life style may require strict synchronization of individual life cycle stages within colonies. Such strict synchronization may not be easily accomplished in these other species. The strict synchronization of individual life cycle stages within \textit{A. binotata} colonies may have co-evolved with and may be actively maintained by nomadism. Strict life cycle synchronization, in turn, could have influenced other aspects of the biology
of this species. A potential side-effect, for instance, is the documented absence of reproductive skew within *A. binotata* colonies (Avilés, 1993a) as similar-sized individuals may be less able to dominate each other. In sum, we may hypothesize that through processes of self-organization, amplification, and natural selection the peculiar life cycle of *A. binotata* could be traced back to the two-dimensional architecture of its nests.

*A. binotata*’s colony life cycle (Fig. 3) has astounding parallels with the fixed pattern of nomadism and reproduction by colony fission that is characteristic of army ants (Franks & Fletcher, 1983; Franks, 1989). As in *A. binotata*, sedentary and nomadic phases in army ants are associated with the internal demography of their colonies. Colonies that contain eggs and pupae remain stationary, while those containing larvae and newly eclosed workers undergo a nomadic phase. Sedentary and nomadic phases alternate throughout the lives of the colonies and are, as in *A. binotata*, asynchronous among colonies (Franks & Fletcher, 1983). Curiously, as in *A. binotata*, such a nomadic life style is also associated with fission as a mode of colony reproduction. An association between frequent nest relocations and colony fission has also been described for the obligately thelytokous ant *Pristomyrmex punges* (Tsuji, 1988) and among fugitive and opportunistic ants (Holldobler & Wilson, 1977; Smallwood, 1982).

The fact that the colonies of *A. binotata* are not founded and potentially controlled by a single reproductive female makes its level of behavioral coordination that much more remarkable. This opens up the question of the extent to which *A. binotata*’s level of integration may be an epiphenomenon of individually adaptive behaviors and the extent to which selection on whole colonies may be involved. As discussed below, the presence of highly-female biased sex ratios in the colonies of this species does suggest that—in addition to any self-organizing properties of the colonies—intercolony selection may have played a role in shaping *A. binotata*’s colony-level life history patterns.

As shown here, despite its unusual features, *A. binotata* has converged with other cooperative spiders in developing highly female-biased sex ratios (Table 2). It has been hypothesized that an overproduction of females in these other species is the result of intercolony selection for higher rates of colony proliferation (Avilés, 1986, 1993b, 1997). Because, according to the usual Fisherian argument (Fisher, 1930), selection within colony lineages is expected to favor equal investment in males and females, the results reported here suggest that *A. binotata* may also have met the conditions considered necessary for selection among groups to override counteracting selection within them (reviewed in Avilés, 1993b; see also Leigh, 1983). These conditions—isaolation of the colony lineages, relatively high rates of colony turnover, relatively small founding groups—have been shown or are suspected to be present in other cooperative spider species with biased sex ratios (Lubin & Crozier, 1985; Riechert & Roelofs, 1993, Smith & Engel, 1994; Smith & Hagen, 1996). Whether *A. binotata* actually fulfills these conditions, however, still requires formal verification.

Several lines of evidence do suggest that *A. binotata* colonies may also be isolated from one another: (a) barring colony fission, colony members remain together during their development, relocate as a group, and, as in the laboratory colony, may mate with each other; (b) different colonies are undergoing different stages in their life cycle, a situation that could not be maintained under the homogenizing effects of migration; and (c) the relatively short lifespan of males, combined with the lack of synchronization in life cycle stage among colonies, suggest that wandering individuals
would have a difficult time finding mates outside their nest. Further studies using genetic markers, however, are needed to confirm these observations.

The presence of biased sex ratios in a species whose colonies reproduce by fission is of great theoretical interest. Some authors have argued that fission cannot create sufficient between-group variation to allow selection among perpetually inbreeding population lineages to overcome counteracting selection within them (Hamilton, 1975; Pollock, 1983; Wilson, Pollock & Dugatkin, 1992; but see Haldane, cited in Hamilton, 1975). In contrast, a stochastic simulation model (Avilés, 1993b) demonstrated that differential group fission may be effective at counteracting selection within isolated colony lineages if the size of the fissioning groups is relatively small (<1000) and the rate of group turnover is relatively high (>10%). Within this context, it is interesting that the colonies of *A. binotata* are small relative to those of other cooperative spiders with biased sex ratios but relatively small propagules (reviewed in Avilés, 1997). In *A. binotata*, colony fission followed by relocation of the parts may provide an escape from local population regulation and give an edge to faster growing, more female-biased colony lineages.

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