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NEWLY-DISCOVERED SOCIALITY IN THE NEOTROPICAL SPIDER *AEBUTINA BINOTATA* SIMON (DICTYNIDAE?)

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ABSTRACT. The neotropical spider *Aebutina binotata* Simon (Dictynidae?), previously known from a few museum specimens, was discovered to live in colonies and to exhibit highly cooperative behaviors that would classify it as non-territorial, permanently social. Colonies of this species, that contained from 14–106 adult females plus their offspring, were observed in a tropical rainforest site in Eastern Ecuador. The spiders occupied communal nests in which they cooperated in prey capture and fed communally on the prey. Large prey items were moved to the feeding site by the coordinated effort of two or three individuals. The spiders periodically carried out web maintenance activities; but when widespread damage to the nest occurred, they moved as a group to a new location. Care of the brood appeared to be communal since the offspring from different mothers intermixed in the colonies and were all cared for by a decreasing number of surviving females. Adult females participated most heavily in all the activities of the colonies, with no apparent division of labor among them. In particular, no reproductive division of labor was observed: all adult females in colonies observed throughout the egg-laying period apparently laid a single egg sac each.

The most advanced form of social behavior known for spiders involves cooperation among members of a colony in building and maintaining a communal nest, capturing prey on which to feed communally, and taking care of the offspring (Buskirk 1981; D'Andrea 1987). These tasks are performed by members of the same generation without any apparent division of labor among them (Darchen & Delange-Darchen 1986). In particular, unlike what occurs in the most highly social insects (Wilson 1971), no specialized reproductive castes are present in social spiders: most, if not all (Vollrath 1986), individuals in a social spider colony apparently bear offspring. This form of social behavior, labeled as non-territorial permanently social (D'Andrea 1987) or quasisocial (Wilson 1971), has arisen independently in at least six spider families. To date, a total of 14 species in eight genera have been described as possessing the traits that would define them as having attained this level of sociality (for partial lists see Buskirk 1981; and D'Andrea 1987; for species not included in these partial lists, see Main 1988, Rypstra & Tirey 1989; Avilés in press 1, in press 2). Ten of these species have been described or their sociality discovered in the last 30 years, indicating that highly cooperative behavior in spiders, although rare relative to the total number of spider species (about 40,000 described species), is perhaps more widespread than previously believed.

Here, I report on newly discovered sociality in the neotropical cribellate spider *Aebutina binotata* Simon (Simon 1892). This species was described by Simon at the end of the last century from a few female specimens collected in the Brazilian Amazonas Province (Simon 1892). From a systematic point of view, *Aebutina binotata* has proven to be an enigmatic species whose placement in any of the currently described spider families is not fully resolved (Lehtinen 1967). The genus *Aebutina*, of which *A. binotata* is the type species, is temporarily assigned to the Dictynidae (Petrunkevitch 1928; Millot 1933), after having been originally placed by Simon (1892) in the Uloboridae. Previous to the present study, no information on the life history or behavior of *A. binotata* was available. The observations that I report here indicate that this species is colonial and that it exhibits the strongly cooperative behaviors common to non-territorial permanently social spiders.

In this paper I describe the structure of the nests and colonies and report on behavioral aspects of the sociality of this species: observations involving cooperation on web maintenance and repair, colony relocation, prey capture and transport, food sharing, communal brood care, and

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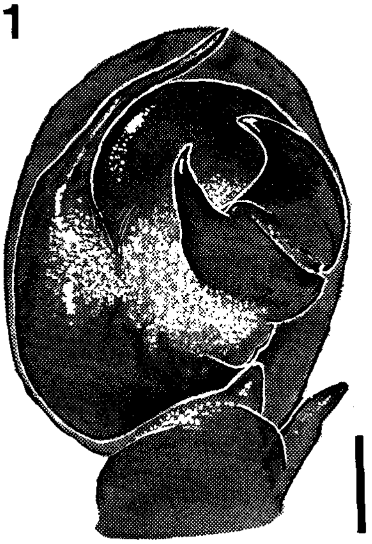
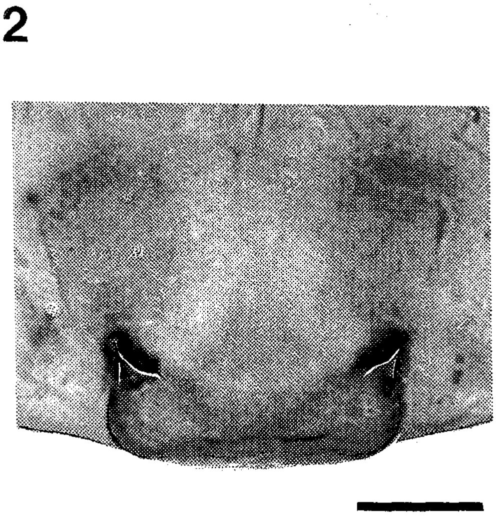




Figures 1, 2.—*Aebutina binotata* genitalia: 1. Male; 2. Female. Drawings from computer digitized images by W. Maddison. Scale bars correspond to 0.1 mm.

tolerance to members of other colonies. Even though not directly related to sociality, I also present observations on courtship and mating.

METHODS

The spider.—Live adult females of *A. binotata*, which measure about 5 mm in length ($\bar{x}$ = 4.7, n = 7), have a diamond-shaped, bright yellow abdomen with a black spot on each side (therefrom the name *binotata*). The males (3.4 mm when adult, n = 2) and early-instar individuals are also yellow, of less intense coloration and with somewhat less clearly marked spots. Males are adult in the 7th instar while females are adult in the 8th instar (Avilês 1992). The egg sacs are spherical and measure around 3.5 mm in diameter. They consist of a mesh of white silk that surrounds the yellow-colored embryos.

One of the reasons for the uncertainty in the systematic placement of *A. binotata* has been the lack of male specimens (Lehtinen 1967). In connection with the present study I collected males which have been deposited in the collections of the Museum of Comparative Zoology, Harvard University. In this study I do not address the systematic placement of *A. binotata*. However, I provide drawings of male and female genitalia for future reference (Figs. 1, 2). Initial determination of the female specimens was done by J. Hunter of the MCZ and later confirmed by comparison with the types by H. W. Levi.

The observations.—I studied colonies of *A. binotata* in a tropical rainforest site by the Tarapuy River in Eastern Ecuador, Sucumbios (formerly Napo) Province (0° 08′ S, 76° 16′ W, 210 m above sea level). I first discovered two colonies in January 1983 and then an additional one in February 1984. From this date to September 1984, I visited the area on six occasions and identified a total of 44 colonies (24 up to a July visit and 20, either new or previously recorded colonies that had relocated themselves, in the September visit).

For each colony observed, I recorded its position, distance from the ground, and structure of the nest, including the size of the leaf (or leaves) supporting the colony and the percent of the leaf (or leaves) occupied. I counted the total number of adult females, egg sacs, and males present in the colonies, and estimated the number of juveniles of different size classes (i.e., instars).

I conducted behavioral observations on an opportunistic basis. Observations were conducted during the day, usually between 900 and 1800 h, on one occasion from 700 h. Activities involving nest maintenance and repair were observed regularly in the colonies. I observed one complete short-distance colony relocation event, a portion of another, and a 13-hour period (1200–1800 h and 700–1400 h of the day after) of one long-distance relocation event. I also obtained indirect evidence of six other relocation events. I recorded complete sequences of prey capture, including prey transportation and initiation of feeding, on 13 occasions, and on five others after feeding had been initiated. Four cases of prey rejection were observed. Other prey capture or feeding events were observed on a more casual basis. I observed courtship and mating for a period of 100 min (1215–1400, August 4, 1984) in one colony containing four adult males and 106 females. I observed a total of four copulations and 16 unsuccessful mounting attempts. One additional copulation was observed at an earlier date in a different colony (colony 5, May 20, 1155 h). A pilot test of tolerance to conspecifics involved the introduction of one adult female into a foreign nest. Additionally, for ten weeks I maintained in the laboratory two colonies on which I conducted casual behavioral observations.

RESULTS

The nest and colonies.—The nests of *A. binotata* are basically two-dimensional structures consisting of one or a few contiguous leaves and their connecting branches covered on both surfaces by a continuous layer of silk (Fig. 3). The outer surface of the web is covered by cribellate silk that cause insects to get entangled when landing on it. The sheet of silk on the underside of the leaves (the lower web) is not attached to the leaf blade, but separated by an open space that is used by the spiders as refuge. Egg sacs and spiderlings occupy this space, sitting on the inner surface of this lower web and congregated towards the center. Openings allow spiders to move freely from one surface of the web to the other. Adult spiders sit on the outer surface of the lower web, lined up along the edges of the leaf (Fig. 4) in a position that allows them rapid access to the top of the leaf where insects usually get entangled. Major perturbations to the nest, such as experimental shaking, cause the larger individuals in a colony to drop to the ground on silk draglines along which they return once the disturbance has stopped.

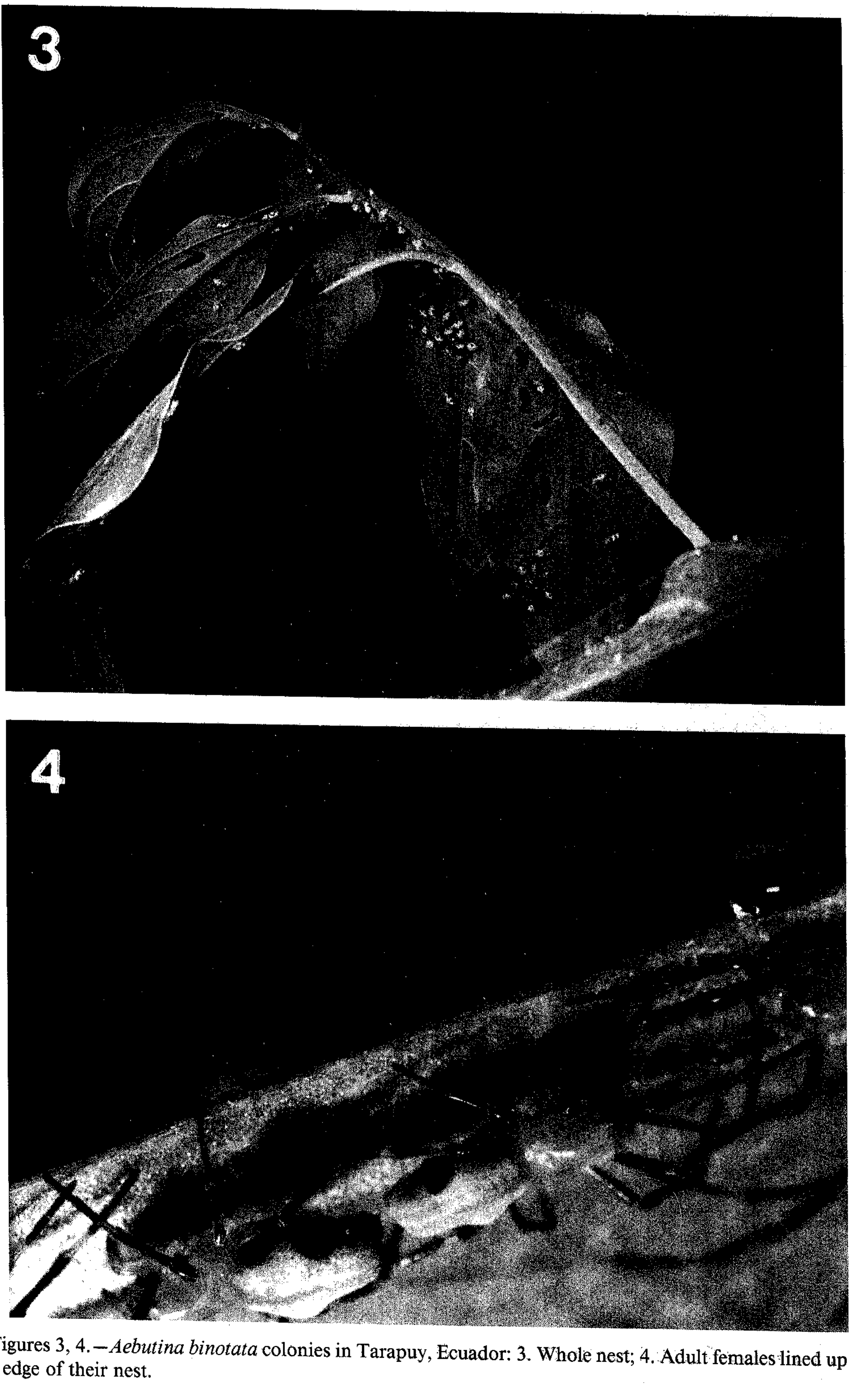
The size of the colonies, measured as the number of adult females present in a colony around the time the eggs were being laid, ranged from 14–106 (n = 19, median = 40, mean = 46.7 ± 11.8, 95% conf. int., Fig. 5). Colonies with young spiderlings could contain up to eight hundred individuals; but, because of the smaller size of the young, the total biomass was probably within a similar range. The area occupied by a nest was found to be proportional to the number of adult females present (Fig. 6); it ranged from 74–200 cm^2 and included either a portion of a large leaf or several small leaves. Nests were found between 0.5 m and 4.5 m from the ground, although nests occurring higher than this would have probably been missed. The nests appeared invisible when seen from above and could only be located by looking for the spiders underneath leaves. From below, the appearance of the colonies was striking because of the bright yellow coloration of the adult females and spiderlings and the whiteness of the egg sacs.

Web construction and repair.—The nests were constructed and maintained cooperatively. Web maintenance activities involved: (a) periodically adding cribellate silk to maintain the stickiness of the web, (b) removing and replacing damaged web following destruction by the rain, (c) repairing holes left by ensnared prey, and (d) throwing out debris. All these activities could be simultaneously performed by several individuals in different areas of the nest. For instance, in a nest of 13 adults and around 190 juveniles, web repair after a rain storm required about two hours during which 16–26 spiders working at a time removed the damaged silk, added new silk lines across the surface of the leaves, and added a final layer of cribellate silk.

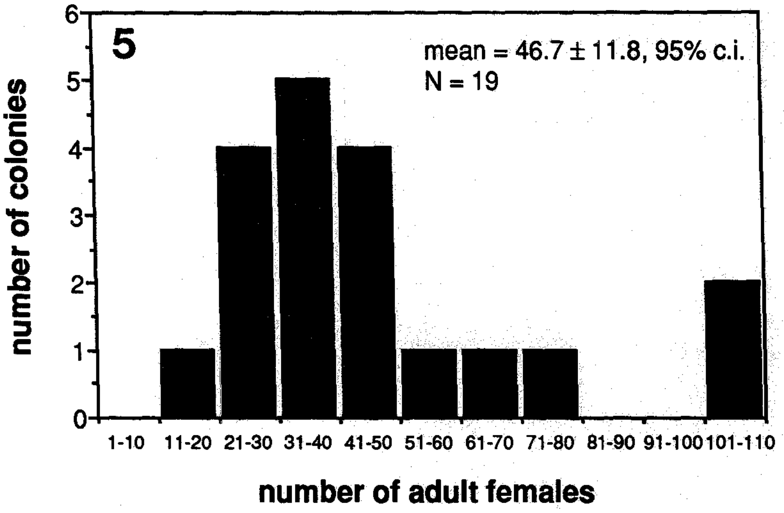
Unlike other social spiders where regular web reinforcement activities take place exclusively at sunset (e. g., in *Anelosimus eximius*, Tapia & De Vries 1980), *A. binotata* spiders added cribellate silk periodically throughout the day. The spiders were inactive in colonies seen early in the morning (around 700–730 h) and all activity seemed to have ceased in two colonies observed at 1800 h. At this time the spiders retreated to the underside of the leaves and presumably carried out only prey capture activities until the following day.

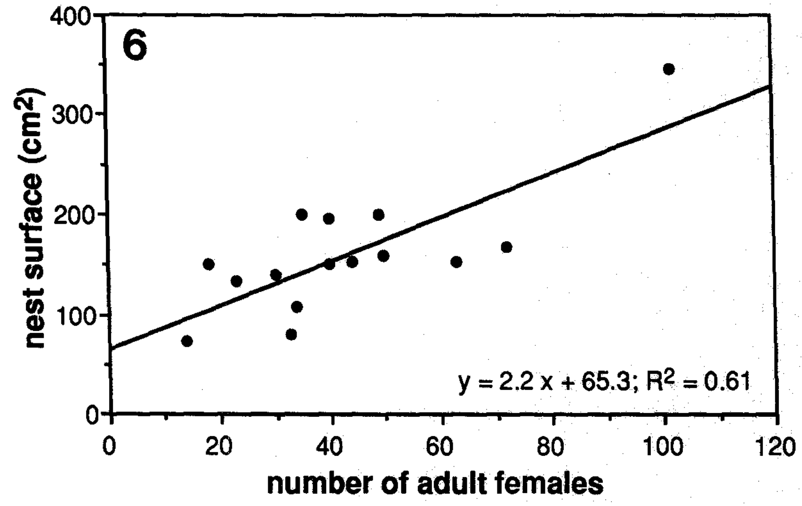
Colony relocation.—Extensive destruction of the web resulted in colonies abandoning their original nest. One of the colonies, for instance, moved to a leaf 12 cm from its original location after the leaf that supported its nest dried out. At later dates, this and three other colonies moved from 0.3–4.5 m after a heavy rain destroyed their nests. Colony relocation involving much greater distances (> > 5 m), independent of web destruction, apparently took place prior to mating and egg laying (Avilés 1992).

Just prior to colony relocation, a fraction of the spiders in a colony could be seen initiating the production of airborne silk lines by hanging down 2–5 cm from their nest (see Eberhard 1987



Figures 3, 4.—*Aebutina binotata* colonies in Tarapuy, Ecuador: 3. Whole nest; 4. Adult females lined up along the edge of their nest.





Figures 5, 6.—5. Number of adult females (and/or egg sacs, whichever is larger) present in *Aebutina binotata* colonies seen sometime immediately before or during the egg laying period; 6. Correlation between the number of adult females in a colony and the surface occupied by their nest (measured in cm^2).

for method of airborne line production). Once a dragline became attached to the nearby vegetation it was first followed by the spider that originated it and then by other spiders. Even if there were draglines attaching in different directions, all spiders eventually moved along a single dragline since the spiders following an isolated route returned to join the majority. This method was repeated from one stop to the next until the eventual settlement of the colony. In the cases observed, all individuals in a nest moved to the new location.

The relocation of a colony could be completed in a few hours or in consecutive days. For instance, a colony with eight adult females and more than 200 juveniles (mostly 4th-instar) moved to a location 30 cm away in the span of 5–6 hours. Another colony that contained eight adult females and approximately 350 3rd–5th instar juveniles moved first to an intermediate stop 1.8 m from its original location, remained there for a period of a day and then continued on for an additional meter. Colonies migrating previous to mating and egg laying appear to migrate for longer periods. For instance, a colony with adult males and females that I followed for

13 hours had not settled when I stopped the observations after a day and a half and 50 m of group migration (Avilés 1992).

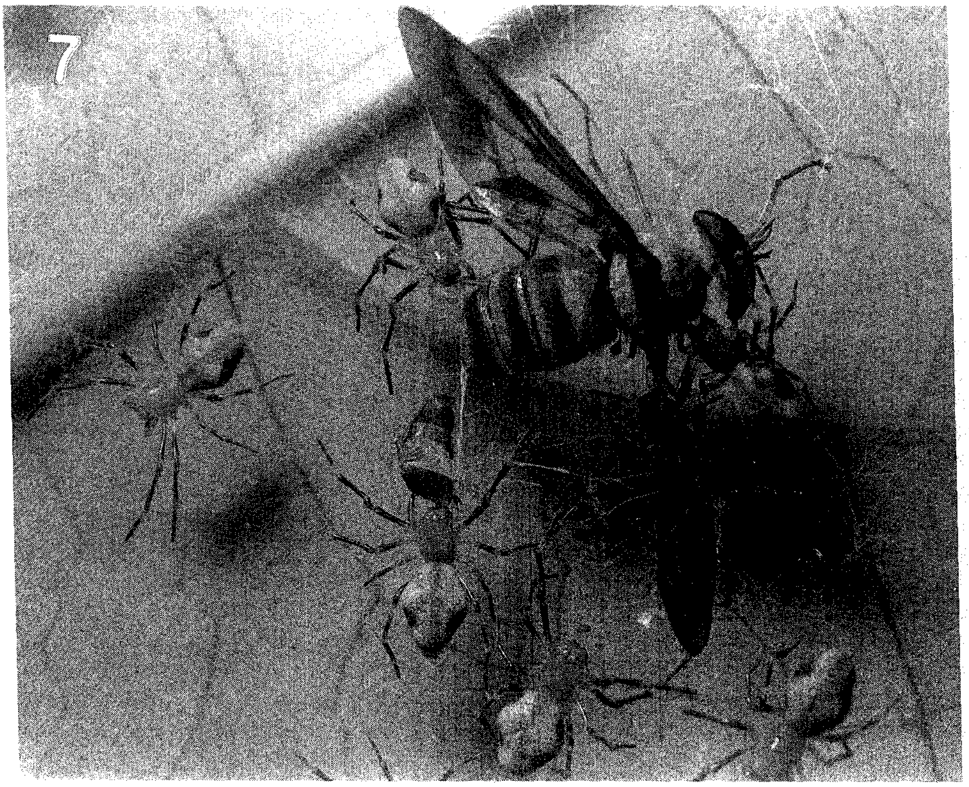
Prey capture and feeding.—Prey capture involved the simultaneous participation of 1–6 individuals, apparently depending on the size of the prey and the efforts it made to free itself. If present in sufficient numbers, only the adult females participated in prey capture, though later-instar spiderlings would participate when there were relatively few adult females in the nest or the prey were small. The females placed along the edge of the nest closest to an struggling insect would rush towards it and attack it by first biting its appendages and then other parts of the body. Once completely overcome, prey items were moved to the underside of the leaves where feeding took place. Adult spiders initiated prey digestion (Fig. 7) and later left the prey to the juveniles. Prey trapped and consumed included wasps, mosquitoes, cockroaches, one large ant, some beetles. A small coccinelid and another small beetle were rejected. Very large insects, such as a 4 cm long moth and a 2 cm cetonine beetle, were ignored.

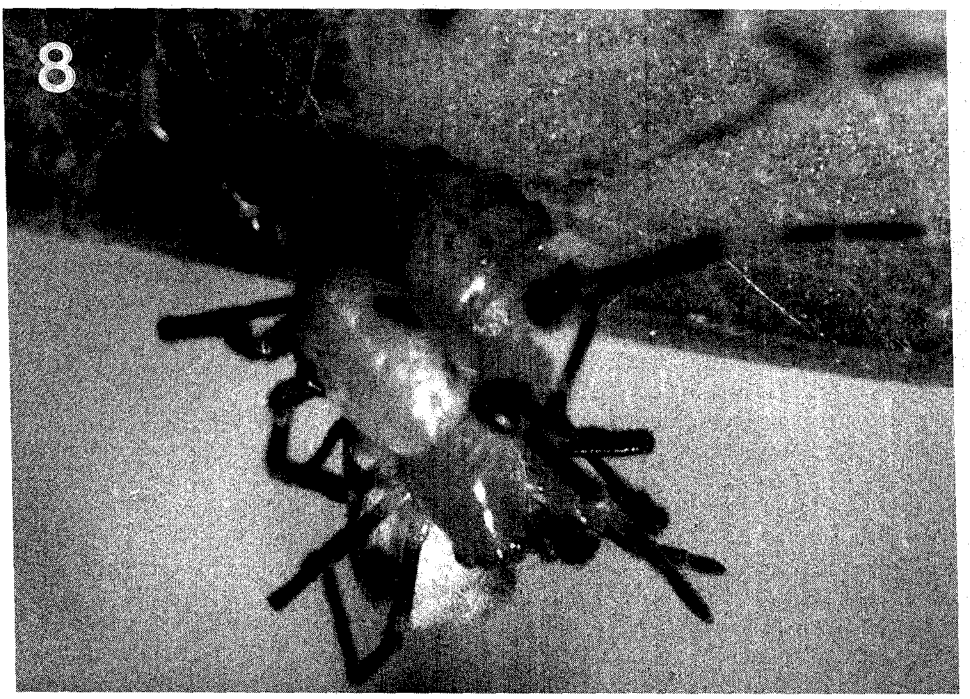
Group transport.—Transportation of items around the nest, either prey to be consumed or debris to be thrown out, were also among the activities regularly carried out by the spiders. Small items were handled by individual spiders. The transportation of large objects, on the other hand, required a group effort that was particularly challenging given the sticky nature of the entire surface of the web. Complete group transport events were observed on three occasions. A large ant moved from the upper to the lower surface of the nest, for instance, involved the participation of three individuals. While one individual cut pieces of web to release the ant, the second one pulled and the third pushed the ant in a given direction. Once released, the ant was transported toward the edge of the nest. One individual lifted the ant from below so as to maintain it at a distance from the surface of the web. As this individual walked towards the edge, the other two individuals, one in front and one in the back, helped by pulling and pushing in the required direction. Once at the edge, the ant was successfully moved to the other side by having one spider hold it from above as it walked towards the edge while the other two supported the item and pulled it from below. It took the spiders four minutes to disentangle and bring the ant to the edge, three more minutes to bring it over the edge and onto the other side of the nest, and another three minutes to move it one cm into its final position where feeding was initiated. Two other group transport events observed required two and three individuals to transport an homopteran and a fly, respectively.

Communal brood care.—While most of the adult females lined up along the edges of the nest ready to participate in prey capture, a number of them mounted guard by the egg sacs and spiderlings. Besides sac guarding, parental care included catching prey for the spiderlings and initiating the enzymatic digestion of the prey. Regurgitation feeding was not observed during the study period, though specific studies would be required to confirm its absence.

Two lines of evidence suggest that parental care is communal: (1) the spiderlings in a nest intermix freely, in a way that it does not seem possible for a mother to discriminate between her own and other mother's offspring; and, (2) the number of adult females present in the colonies drops continuously (most likely due to mortality) during the incubation and emergence periods, while all the egg sacs and offspring present in the colonies continue to be cared for. For instance, half the adult females of one of the colonies observed throughout most of its life cycle were already gone by the time their offspring had only reached their third or fourth instar. All the offspring, however, continued to be cared for by the remaining females whose number continued to decrease until none were left by the time the offspring had reached their sixth instar. This indicates that a large majority of the offspring were raised by females other than their mother.

Division of labor.—Adult females tended to participate disproportionately in all the activities of the colony, though later-instar juveniles participated to varying degrees. Later instar juveniles, for instance, handled small prey or participated in group efforts when the relative number of adults in the nest was low. Juveniles were relatively more active in web maintenance activities, particularly in laying down cribellate silk, though the numbers in which they participated were not representative of the proportion in which they occurred in the colonies. For instance, after a storm had destroyed the upper web of one of the colonies under study, all adult females (a total of eight) and 20% of the juveniles (out of a total of 200) were seen removing the damaged web and laying down new strands of silk. In a different colony, which contained 13 adult females and





Figures 7, 8.—*Aebutina binotata*. 7. Group of adult females feeding on a prey; 8. Mating couple in Tarapuy, Ecuador.

around 190 juveniles, 30–100% of the females were active at different times during a two-hour period following a storm, while only 4–7% of the juveniles were. The youngest juveniles that appeared able to participate in activities such as laying cribellate silk belonged to the 4th-instar. Immature males in the colonies kept in the laboratory were seen laying silk during web reinforcement, while it was not possible to determine whether adult males participate in this or any other activity since they were seen in the colonies for only a short period of time.

There was no evidence of division of labor among spiders of a given age group: a task started by one individual was often completed by another and the same individual could be seen carrying out different tasks. Marking experiments, however, are needed to confirm these observations. Regarding reproductive division of labor, in all the colonies observed throughout the egg laying period the total number of eggs cases present was the same as the number of adult females in the nest (Table 1). Since all the egg sacs in a colony were laid within a short time span (Avilés 1992); and thus it is unlikely that some females may have laid more than one case, it follows that all females in the colonies observed reproduced. Reproductive division of labor, therefore, appears absent in *Aebutina binotata*.

Social interactions and tolerance to conspecifics.—The 14 adults and 74 juveniles kept in the laboratory in a 40 × 30 × 30 cm terrarium remained aggregated throughout a 10-week observation period. When they relocated their nest within the terrarium, all the spiders moved together. Encounters between spiders, which were common during the course of their daily activities, involved touching each other with the legs and pedipalps.

Spiders in the field did not appear to discriminate against members of other colonies. One spider experimentally introduced into a foreign nest was initially approached by other spiders, probably in response to the vibrations produced, but was soon treated as a member of the colony. After its introduction, the spider resumed the activity (adding cribellate silk) it had been performing when removed from its native nest. A month later, the spider was still in the colony, and, aside from the experimental mark, was indistinguishable from other spiders in the nest.

Table 1.—Number of females and egg sacs laid in *A. binotata* colonies periodically observed throughout the egg laying period. In addition to the 45 egg sacs shown, colony 14 contained newly eclosed juveniles from around four egg sacs.

	Colony				
	9	22	23	14	25
Adult females	102	44	30	48–49	52
Egg sacs present	102	44	29	45+	54

Courtship and mating.—I observed courtship and mating in a colony that contained 106 females, 4 males, and 1 egg sac. During the 100 min of observations, three of the males attempted insistently to mount females. Most of the attempts observed (16 out of 18) were rejected by the females who either moved away or resisted. Two resulted in copulations. Two additional copulations had already been initiated when the observations started. Copulations took place with the male over the back of the female and both facing in opposite directions (fig. 8; position "c" in Foelix 1982, p. 195). In one of the matings observed the female remained motionless all through the mounting. In a second mating observed, the male seemed to exert force over the female. The two complete copulations observed lasted around 4 min. Given the disparity in the numbers of males and females, and the observation that most or all the females in a colony lay eggs (see above), it follows that each male is able to fertilize a large number of females.

DISCUSSION

The social behavior here described for *A. binotata* has strong similarities with that of other non-territorial permanently social spiders present in the genera *Achaearanea* (Theridiidae), *Agelena* (Agelenidae), *Anelosimus* (Theridiidae), *Diaea* (Thomisidae), *Mallos* (Dictynidae), *Stegodyphus* (Eresidae), *Tapinillus* (Oxyopidae), and *Theridion* (Theridiidae) (Buskirk 1981; D'Andrea 1987; Avilés pers. obs.). These similarities, which include cooperative web building and maintenance, cooperative prey capture, communal feeding, communal brood care, tolerance to members of other colonies, and a lack of castes, are particularly striking given the phylogenetically diverse set of species in which they have evolved.

One feature common to this diverse set of species, which might be to a large extent responsible for these similarities is an irregular type of web, present in all but the social thomisid (Main 1988; Evans & Main 1993), but absent in other colonial but non-cooperative species such as *Metabus* *gravidus* or *Philoponella republicana* (Buskirk 1981; D'Andrea 1987). An irregular web is thought to constitute a preadaptation for cooperative behavior in spiders because it allows communal habitation and the simultaneous involvement of more than one individual in web construction and repair as well as in prey capture (Buskirk 1981). Cooperative web building, because it allows the construction of a relatively large area or volume of entangling web, leads to the capture of relatively large prey items, which, in turn, require the concurrence of several individuals for their subjugation. Large prey items can then be shared by several individuals in a nest, leading to communal feeding, a trait common again to the non-territorial permanently-social species studied (Buskirk 1981; see also Main 1988; Rypstra & Tirey 1989), but absent in the colonial orb weavers. A communal nest also facilitates communal care of the brood because it renders discrimination among spiderlings intermixed in a common space impractical.

A. binotata is typical among the non-territorial permanently social spiders in having an irregular type of web and in having developed cooperative prey capture, communal feeding, and communal brood care. As in these other species (Buskirk 1981), cooperation allows *A. binotata* spiders the capture of prey items larger than those single individuals could handle and facilitates the sharing of prey among a larger proportion of colony members than those participating in their capture. The advantages of cooperation in the care of the brood become specially evident in *A. binotata*, where the survival of orphaned offspring is only possible because surviving females indiscriminately care for all the young in a nest (see also Christenson 1984; D'Andrea 1987).

The ways in which the architecture of the nests of *A. binotata* differs from that of other non-territorial permanently social species may be responsible for some of the features that appear unique to this species. One such feature is the cooperative transport of prey items from the site of their capture to their consumption site, a trait that in this species is developed to a greater extent than in any other social spider. Three aspects of the structure of the nests of *A. binotata* pose a special challenge to prey transport in this species: (1) the sticky nature of the web surface; (2) the relatively small capture area; and, (3) the fact that prey items need to be brought over the edge of the leaf with the consequent danger of accidentally dropping them out of the nest. In other cooperative spiders, webbing usually surrounds the prey in all directions during its transport and the nests are considerably larger than the prey being transported, so that their overall efficiency is not critically affected by damage to a portion of the web caused by dragging a prey item.

The instances of group transport that I observed in *A. binotata* required a degree of coordination among the individuals involved that can only be explained if some sort of communication was taking place among them. Prey transport in other species usually involves a number of individuals pulling in the same general direction or some form of, apparently uncoordinated, relay activity (e.g., Ward & Enders 1985). In the genus *Agelena* the prey is either carried by a single individual (Krafft 1971) or eaten on the site of its capture when it is too large for individual transport (Darchen 1967; Krafft 1971). In *Achaearanea disparata* (Darchen 1967) some individuals pull while others aid in cutting the threads that hinder the movement of the item, suggesting, in this case, some degree of coordination. It must be noted that group transport is an extraordinary task to be performed by an invertebrate. Even among vertebrates, group transport is only known among humans, dolphins, whales, and some canids (Moffett in press). Among invertebrates, the only other reported case of group transport is represented by the ants (Moffett in press).

Another feature apparently unique to *A. binotata* which may also result from the special architecture of its nests is its nomadic habit that leads to the periodic relocation of its colonies. The nests of other non-territorial permanently social species, which are usually expanded and occupied by more than one generation of spiders, are three-dimensional structures that are probably expensive to build and whose prey capture efficiency does not appear to depend on their invisibility. The two-dimensional nests of *A. binotata*, on the other hand, may be less expensive to rebuild and, most importantly, they appear to critically depend on their invisibility to trap prey. Such invisibility can best be achieved by rebuilding the nest in a new and debris-free locality.

The observation that egg laying is universal in *A. binotata* (Table 1) illustrates perhaps to an extreme a feature common to non-territorial, permanently social spiders which critically differentiates them from the most highly social insects: a lack of reproductive castes (Buskirk 1981; Darchen & Delange-Darchen 1986). Even though competition over resources leading to differences in reproductive success are not entirely absent in social spiders (Riechert 1985; Seibt & Wickler 1988; Vollrath 1986; Rypstra in press), social spider colonies critically contain multiple reproductives of both sexes that can mate among themselves to produce subsequent generations. This leads to mating within colonies and to the highly subdivided population structure that characterize non-territorial permanently social species (Lubin & Crozier 1985; Smith 1986; Main 1988; Roeloffs & Riechert 1988; Avilés 1992). In contrast, perpetual inbreeding is rare or absent among the eusocial insects in which nuptial flights result in the crossing of individuals from different nests (Wilson 1971). Evidence that *A. binotata* has followed the route of other non-territorial permanently social spiders in developing strong population subdivision leading to intercolony selection and female-biased sex ratios will appear elsewhere.

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