some detail (*23*), and in the adult, the frequency and duration of spontaneous swimming episodes is directly related to the level of serotonin bathing the nervous system (*13*). When juveniles with ablations were subjected to conditions that provoke swimming in normal juveniles (*24*), they responded with uncoordinated wriggling or dorsal or ventral flexions of the whole body that alternate at the approximate frequency (1 to 3 Hz) of the swimming body wave. None of the juveniles with ablations developed the ability to swim for as long as 10 weeks after treatment. However, the ability to swim could be instated by injecting serotonin into the coelom of a treated juvenile (three animals tested) or by immersing the juvenile in water containing $10^{-5}M$ serotonin (15 animals tested). Within 10 minutes after exposure to serotonin, the juveniles with ablations exhibit normal swimming. Furthermore, their other behavioral abnormalities of general inactivity and hypersensitivity disappear. When these embryos are returned to serotonin-free water, the behavioral abnormalities return, with swimming movements gradually deteriorating over a 15- to 20-minute period. The ability to swim is not obtained by immersing juveniles with ablations in water containing other monoamines, such as dopamine, octopamine, or histamine in concentrations of up to $10^{-4}M$ (four animals tested with each monoamine).

Because the swimming incapacity of juveniles lacking serotonin-containing neurons is eliminated by exogenous serotonin, that incapacity must be a consequence of depletion of serotonin in the nervous system or body wall, rather than being attributable to deterioration or altered development of swim generator neurons or muscles. Moreover, although at least some serotonin-containing neurons are essential for the expression of the normal swimming movement, this serotonin-mediated expression of swimming is of minor importance during genesis of the swim generator circuit because a functional circuit develops without it. These results resemble findings made with amphibians (*25*) and arthropods (*26*), in which execution of a locomotory behavior during embryogenesis is unnecessary for development of the pattern generator of that behavior.

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Dispersal by Swarming in a Social Spider

Abstract. *Groups of* Achaearanea wau *(Theridiidae) disperse and found new colonies by means of synchronized emigrations of adult and subadult females. Emigrations involve the construction of silk highways from parent colonies to new web sites, synchronized migrations along the highways, and the establishment of daughter colonies. Emigrations of* Achaearanea wau *are similar in timing, group composition, and in some behavior components to swarming of social bees and wasps.*

Some social bees and wasps disperse and found new colonies by swarming, a process which has been described in wasps as "movements between old and new nest sites effected by coordinated, synchronous migration of large numbers of individuals including both workers and queens" (*1*). Swarming of this sort was considered unique to apid bees and some polybiine wasps. As a means of dispersal, swarming may have profound effects on the structure and dynamics of populations (*2*). We found a similar phenomenon, involving the formation of new colonies by synchronized, group emigration, in a social theridiid spider, *Achaearanea wau* Levi (*3*), in Papua New Guinea.

Achaearanea wau was studied near Wau, Morobe Province, Papua New Guinea (7°19′S, 146°44′E). Colonies of these spiders, often containing several hundred individuals, occurred in discrete populations in treefall gaps and along edges of montane forest. One population of 13 to 35 colonies on Mount Kaindi (at

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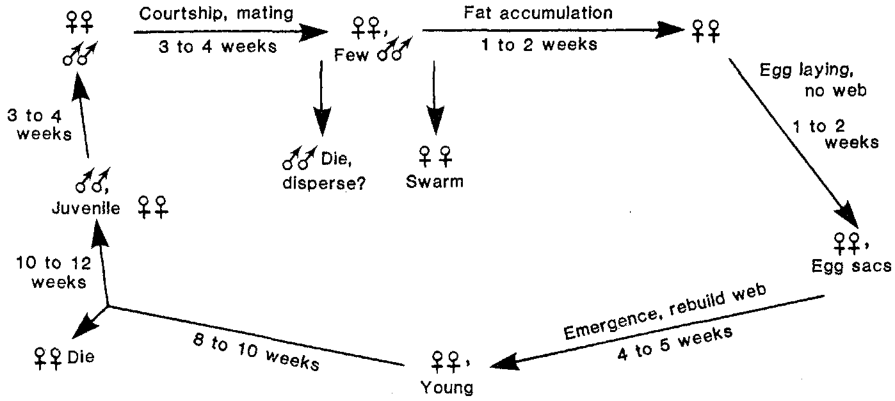

Fig. 1. Life cycle of an *Achaearanea wau* colony.

1600 m) and three on Mount Missim (at 1520, 1530, and 1600 m) with 6 to 11, 7 to 18, and 6 to 30 colonies, respectively, were examined weekly from April 1979 to October 1980 and sporadically from December 1980 to February 1981. In addition, experimental colonies were established on the grounds of the Wau Ecology Institute at 1200 m and were examined at least three times a week (*4*).

The communal web consists of a horizontal sheet of tightly woven silk with a loose tangle of vertical threads above it. Flying insects which strike the vertical barrier threads drop onto the sheet, where they are attacked by the spiders. Web construction and prey capture are group activities, occurring primarily at night; during the day the spiders sit in groups inside curled-leaf retreats suspended in the barrier web by strong guy threads. Within a colony, most individuals of a given sex mature at about the same time (Fig. 1). Generations are discrete, lasting approximately 7 months, with an overlap of about 3 months between adult females and offspring. Egg sacs are suspended within the communal leaf retreats and the emerging young remain in the parent colony. Young and juvenile spiders do not disperse.

Three stages could be distinguished in dispersal and foundation of new colonies: (i) construction of a silk highway from the old (parent) web to a new web site or web sites, (ii) synchronized group emigrations along the highway, and (iii) establishment of a new colony or colonies (*5*). One or two nights before emigration there was a sharp increase in building activity during which time females appeared at first to extend the sheet in one direction. After several hours, a single broad highway was produced, often a meter wide and several meters long, generally following substrate contours and conserving a single compass direction. Unlike the dense mesh construction of the communal sheet, the highway consisted of loose threads oriented parallel to its long axis. Males also traveled short distances on the highway, rarely moving more than 50 cm from the parent colony. There was little interaction between spiders of either sex during highway construction, although occasionally females tapped one another with the legs as they passed on the same thread.

Table 1. Composition and size (number of individuals) of parent colonies at swarming and composition of daughter colonies. Numbers in parentheses are number of colonies when different from *N*. Experimental daughter colonies contained an average of 13 females (range, 1 to 132) and were an average of 8.5 m (range, 1 to 25.5 m) from the parent colony. Daughter colonies in the field contained an average of 19.1 females (range, 1 to 44) and were on the average 5.4 m (range, 1.1 to 14.4 m) from the parent colony.

	Number of colonies (*N*)	Composition (number of colonies)				Colony size	
		Females			Males	100 to 500	500
		Adult	Subadult	Immature*			
			Parent colonies				
Experimental	11	11	6 (9)	1	8 (10)	6	5
Field	11	11	5	0	6	6	4
			Daughter colonies				
Experimental	39	39	6 (34)†	1	3		
Field	21	21	7 (17)†	0	7		

*Immatures are earlier than fifth instar. †Subadults include fifth and sixth instars; these were not distinguished from adults in some daughter colonies.

During emigration, which took place over a period of one, or more rarely, two nights, females traveled together along the highway away from the parent colony, forming temporary clusters en route under leaves and at branch tips. The next day, one or more clusters were found at or near the end of the highway. These groups were easily disturbed, and movements between clusters sometimes occurred on the night after emigration. New capture webs were built by the third day, and although the highway remained intact for several days, there was no further movement of females between parent and daughter colonies on the nights after emigration.

Emigrations took place at a particular stage in the colony life cycle—namely after courtship and mating and before egg laying (Fig. 1). In eight experimental colonies, migrations occurred 10 to 62 days (mean ± standard deviation, 35.8 ± 15.4) after the onset of courtship, and egg-sac production in four parent colonies and six daughter colonies took place 12 to 60 days (mean, 33.5 ± 14.2) after migration. Synchronized migrations differed from short-range relocation or splintering of colonies, which occurred when the communal web supports broke as a result of treefalls or other disturbances. In such relocations, new webs were built near the previous web sites, without the construction of extensive highways.

Migrating groups consisted of adult and occasionally fifth- and sixth-instar (subadult) females and, more rarely, adult males (Table 1) (*6*). Since males were generally absent from daughter colonies, it must be assumed that most migrating females had mated in the parent colony. Indeed, 64.7 percent of 34 adult females examined in the field from three migrating groups derived from a single parent colony had sperm in one or both spermathecae (*7*), and eight of ten adult females from an experimental colony were fertilized at least 22 days before emigration. Nonetheless, some mating may take place in daughter colonies, as evidenced by observations of courtship in one experimental colony, in which males migrated with females only 10 days after the onset of courtship, and by the fact that males of unknown origin occasionally joined daughter colonies after the migration.

Not all females migrated, and in most instances the parent colony remained intact. It was not clear how spiders chose between emigrating and remaining in the original colony. In two out of three experimental colonies, females that emigrated were significantly larger than ones that remained behind, but in the third colony the opposite was true (*8*). Migrating females that were marked and returned to the parent colony tended to reemigrate the following night (*9*).

Only large colonies of 100 or more spiders produced emigrations, though not all large colonies did so. Lack of space for colony expansion (*10*) or the presence of kleptoparasites (*11*), or both, may influence whether or not a colony produces an emigration. Colonies of *A. wau* often hosted kleptoparasitic spiders (*Argyrodes* spp., Theridiidae), which stole prey from the hosts and sometimes attacked egg sacs, young, and host adults as well. Spiders in colonies with numerous kleptoparasites ceased to repair the capture web or removed it entirely and withdrew into the leaf retreats for several days, during which time many *Argyrodes* abandoned the colony (*12*). Seven of the 11 experimental colonies that produced emigrations had old and torn capture webs or no web at all prior to constructing the highway, suggesting that conditions within the colony were not optimal.

In most solitary spiders, dispersal is characteristic of early juvenile stages. Recently emerged spiderlings and, more rarely, juveniles or adults balloon or walk out on bridge threads which are released from the spinnerets and allowed to float until they attach to a nearby substrate (*13*). In certain noncooperative, group-living spiders, young disperse in groups rather than individually, but it is not known if individuals share bridge threads (*14*). Even in species with prolonged maternal care, older juveniles leave the maternal web or burrow before they reach maturity (*15*). Other solitary and subsocial species of *Achaearanea* disperse as recently emerged young or as juveniles, but in *A. wau* dispersal occurs only in the adult stage and, significantly, involves fertilized females.

Comparisons can be made between synchronized emigrations in *A. wau* and swarming in social wasps and bees (*1, 2*). (i) Highway construction and increased activity in *A. wau* before emigration parallel the increased activity of scouts and the laying of odor trails in polybiine wasps. (ii) Temporary clusters of migrating individuals form along migration paths of social wasps and highways of *A. wau*. (iii) Swarms are produced by large colonies of *A. wau* that contain numerous adult females; likewise, polybiine wasps and honey bees swarm only when there are large numbers of workers and queens in the nests. (iv) In *A. wau* and in the social wasps and honey bees, males rarely swarm with the females. These similarities in behavior and timing of synchronized group emigrations in *A. wau* and in social bees and wasps justify the use of the term "swarming" to describe the phenomenon in social spiders.

Two other species of social spiders, *Agelena consociata* Denis (Agelenidae) and *Anelosimus eximius* (Keyserling) (Theridiidae) may also disperse by swarming, although in the latter species this may be a rare event (*16*). In the former, new colonies were found to contain only adult and juvenile females, suggesting that groups of females disperse from established colonies (*17*).

Swarming, as it occurs in *A. wau*, may have several advantages over solitary dispersal mechanisms. First, the highway matrix protects emigrating females during dispersal off the web, when the risk of predation is high. Second, synchronization of dispersal enables the establishment of new colonies by groups of females, and there is evidence that large colonies have higher rates of success than colonies containing few individuals (*16, 18*). Third, foundresses are fertilized females capable of laying eggs shortly after dispersal, thereby ensuring rapid growth of the new colony. Finally, each new colony is founded by females that came from a single parent colony and had mated in the parent colony. The offspring of these females are closely related, a fact which undoubtedly influences selection for cooperative behaviors in these spiders (*19*).

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5. Emigration highways were seen in 11 experimental and nine field colonies and inferred in two additional field colonies. Descriptions of highway building and emigrations are based on observations of experimental colonies.
6. Females matured after six molts (five molts outside the egg sac) and males after four molts (based on data from two experimental colonies).
7. Spiders were killed by freezing and dissected immediately in saline. Ovaries were exposed and stained with neutral red (1 percent) solution. The diameter of the largest ovariole was estimated with an ocular micrometer calibrated at 0.025-mm intervals. Spermathecae were removed from 34 adult females and six fifth- and sixth-instar juveniles from three daughter colonies from Mount Missim (1530 m; collected 1 October 1981), squashed on a glass slide, stained with Giemsa R66, and examined (magnification, ×900) for the presence of motile sperm. Immature females had no sperm, and their spermathecae were not fully developed. In the three groups, 13 out of 15, 8 of 9, and 1 of 10 adult females had sperm in at least one spermatheca. Maximum ovariole size varied little (0.08 to 0.1875 mm) as did total ovary length (1.0 to 1.125 mm) and appeared unrelated to spider size. Usually only a fraction of the ovarioles present were developed, suggesting that females are potentially capable of producing more than one clutch.
8. Migrating and nonmigrating females were weighed from three experimental colonies (mean ± standard deviation, in milligrams; sample size in parentheses) and compared by *t*-tests (migrants to nonmigrants): (i) colony KCl, migrants 11.3 ± 2.7 (25), nonmigrants 7.8 ± 1.9 (25), $P < .001$; (ii) colony 1/2-1, migrants 12.4 ± 1.7 (7), nonmigrants 9.8 ± 3.0 (10), $P < .05$; (iii) colony 1/2-2, migrants 10.8 ± 1.7 (25), nonmigrants 9.6 ± 1.3 (10), $P < .025$. Also, nonmigrants and migrants were compared: colony N2/3, migrants 11.4 ± 1.8 (20), nonmigrants 14.0 ± 3.1 (16), $P < .001$.
9. Seven females that emigrated from colony 1/2 on the night of 24 January 1981 were marked on the next day with dots of white paint and returned to the parent colony. A day later, 35 emigrant females were found, two of which had white dots. The 35 migrants were marked with green dots and again returned to the parent colony. When checked 2 days later, colony 1/2 contained two white, six green, and one green and white marked spiders. Thus of the total of 42 marked females (including those marked twice), 78.5 percent had reemigrated and one female reemigrated twice.
10. A connection between colony expansion and emigration is suggested by observations of an experimental colony which had a 3-m long highway that was destroyed by rains and rebuilt on two successive nights. On the third night, the entire colony shifted 1 m from its original web site and enlarged the capture web in the direction of the former highway.
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