The Evolution of Communal Nest-Weaving in Ants: Steps That May Have Led to a Complicated Form of Cooperation in Weaver Ants Can be Inferred From Less Advanced Behavior in Other Species

Bert Hölldobler (left) and E.O. Wilson (right) examining an ant nest (what else?) in Bavaria in German in May 1983. Photograph: Friederike Hölldobler.

For those living in the tropics in Africa, Asia and Australia, the arboreal nests of weaver ants are iconic. For sociobiologists, their method of nest construction makes them even more special. As Bert Hölldobler and Edward O. Wilson note in this classic paper, “One of the most remarkable social phenomena among animals is the use of larval silk by weaver ants of the genus Oecophylla to construct nests”.

The genus Oecophylla belongs to the large subfamily of ants, the Formicinae, named after their unique habit of using formic acid for prey capture and defence. In nearly all ants in the Formicinae, larvae produce silk and spin protective cocoons around themselves before becoming pupae.
However, while ants in the genus *Oecophylla* produce silk they do not spin cocoons for themselves. Instead, they remain naked and donate all their silk to the communal nests of their colonies. Much of what we know today about the evolution of their remarkable nest-building behaviour comes from the extensive studies of the Harvard biologists Bert Hölldobler and Edward O. Wilson of *O. longinoda* in Africa and *O. smaragdina* in Australia described in this classic paper.

As Hölldobler and Wilson have documented in impressive detail, the nest-building behaviour of the weaver ants is “complicated, precise and distinctive”, involving several adaptations of the adult ants as well as the larvae. There are at least three questions of interest. How do the ants build their nests and enlist the help of the larvae? How did the ants attain this level of perfection through evolutionary time? And why do the larvae donate their silk?

Hölldobler and Wilson answer these questions with their extensive study of nest building in many different ant species, painstakingly unearthing evidence of a gradual process of perfection in nest-building behaviour through natural selection. They have also conducted remarkably simple laboratory experiments to show that female larvae are more altruistic in donating silk for their communal nest than male larvae, as described in this classic paper.


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The Evolution of Communal Nest-Weaving in Ants

Steps that may have led to a complicated form of cooperation in weaver ants can be inferred from less advanced behavior in other species.

It would seem that close attention to the exceptional properties of Oecophylla nest-weaving could shed new light on how cooperation and altruism operate in ant colonies, and especially on how larvae can function as an auxiliary caste. In addition, a second, equally interesting question is presented by the Oecophylla case: How could such extreme behavior have evolved in the first place? As is the case with the insect wing, the vertebrate eye, and other biological prodigies, it is hard to conceive how something so complicated and efficient in performance might be built from preexisting structures and processes. Fortunately, other phyletic lines of ants have evolved communal nest-weaving independently and to variably lesser degrees than Oecophylla, raising the prospect of reconstructing the intermediate steps leading to the extreme behavior of weaver ants. These lines are all within the Formicinae, the subfamily to which Oecophylla belongs. They include all the members of the small Neotropical genus Dendromyrmex, the two Neotropical species Camponotus (Myrmotherus) semen and C. (M.) formiciformis, which are aberrant members of a large cosmopolitan genus, and various members of the large and diverse Old World tropical genus Polyrhachis.

Two additional but doubtful cases have been reported outside the Formicinae. According to Baroni Urbani (1978), silk is used in the earthen nests of some Cuban species of Leptothorax, a genus of the subfamily Myrmicinae. However, the author was uncertain whether the material is obtained from larvae or from an extraneous source such as spider webs. Since no other myrmicine is known to produce silk under any circumstances, the latter alternative seems the more probable.
Similarly, the use of silk to build nests was postulated for the Javan ant Technomyrmex bicolor textor, a member of the subfamily Dolichoderinae, in an early paper by Jacobson and Forel (1899). But again, the evidence is from casual field observations only, and the conclusion is rendered unlikely by the fact that no other dolichoderines are known to produce silk.

During the past ten years we have studied the behavior of both living species of Oecophylla in much greater detail than earlier entomologists, and have extended our investigations to two of the other, poorly known nest-weaving genera, Dendromyrmex and Polyrhachis. This article brings together the new information that resulted from this research and some parallel findings of other authors, in a preliminary characterization of the stages through which the separate evolving lines appear to have passed.

In piecing together our data, we have utilized a now-standard concept in organismic and evolutionary biology, the phylegetic grade. The four genera of formicine ants we have considered are sufficiently distinct from each other on anatomical evidence as to make it almost certain that the communal nest-weaving displayed was in each case independently evolved. Thus it is proper to speak of the varying degrees of cooperative behavior and larval involvement not as the actual steps that led to the behavior of Oecophylla but as grades, or successively more advanced combinations of traits, through which autonomous evolving lines are likely to pass. Other combinations are possible, even though not now found in living species, and they might be the ones that were actually traversed by extreme forms such as Oecophylla. However, by examining the behavior of as many species and phyletic lines as possible, biologists are sometimes able to expose consistent trends and patterns that lend convincing weight to particular evolutionary reconstructions. This technique is especially promising in the case of insects, with several million living species to sample. Within this vast array there are more than 10,000 species of ants, most of which have never been studied, making patterns of ant behavior exceptionally susceptible to the kind of analysis we have undertaken and are continuing to pursue on communal nest-building.

The highest grade of cooperation

The studies conducted on Oecophylla prior to our own were reviewed by Wilson (1971) and Hemmingsen (1973). In essence, nest-weaving with larval silk was discovered in O. smaragdina independently by H. N. Ridley in India and W. Saville-Kent in Australia, and was subsequently described at greater length in a famous paper by Dolfin (1905). Increasingly detailed accounts of the behavior of O. longinoda, essentially similar to that of O. smaragdina, were provided by Lodous (1950), Chauvin (1952), Sudd (1963), and Hölldobler and Wilson (1977a).

The sequence of behaviors by which the nests are constructed can be summarized as follows. Individual workers explore promising sites within the colony's territory, pulling at the edges and tips of leaves. When

Figure 1. To make a nest out of leaves and larval silk, worker ants of the species Oecophylla smaragdina, the Australian green tree ant, first choose a pliable leaf. They then form a row and pull in unison, as shown in the photograph, until they force two leaves to touch or one leaf to curl up on itself. (All photographs are by Bert Hölldobler unless otherwise indicated.)

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a worker succeeds in turning a portion of a leaf back on itself, or in drawing one leaf edge toward another, other workers in the vicinity join the effort. They line up in a row and pull together (Fig. 1), or, in cases where a gap longer than an ant’s body remains to be closed, they form a living chain by seizing one another’s petiole (or “waist”) and pulling as a single unit. Often rows of chains are aligned so as to exert a powerful combined force (Fig. 2). The formation of such chains of ants to move objects requires intricate maneuvering and a high degree of coordination. So far as is known, it is unique to Oecophylla among the social insects.

When the leaves have been maneuvered into a tentlike configuration, workers carry larvae out from the interior of the existing nests and use them as sources of silk to bind the leaves together (Figs. 3, 4). Our previous studies (Wilson and Hölldobler 1980) showed that the O. longinoda larvae recruited for this purpose are all in the final of at least three instars, and have heads in excess of 0.5 mm wide. However, their bodies (exclusive of the rigid head capsule) are smaller than those of the larva at the very end of the final instar, which are almost ready to turn into prepupae and commence adult development. Thus the larvae used in nest-weaving are well along in development and possess large silk glands, but they have not yet reached full size and hence are more easily carried and manipulated by the workers.

In O. longinoda, all the workers we observed with spinning larvae have been majors, the larger adults that possess heads between 1.3 and 1.8 mm in width. Hemmingsen (1973) reported that majors of O. smaragdina perform the weaving toward the exterior, while minor workers—those with heads 1–1.2 mm wide—wove on the inner surfaces of the leaf cavities. We have observed only major workers performing the task in O. longinoda, but admittedly our studies of interior activity have been limited. Hemmingsen also recorded that exterior weaving is rare during the daytime but increases sharply at night, at least in the case of O. smaragdina working outdoors in Thailand. We have seen frequent exterior weaving by O.
ginoda during the day in a well-lit laboratory, as well as by O. smaragdina outdoors in Queensland.

In recent studies reported here for the first time, we followed the spinning process of O. longinoda through a frame-by-frame analysis of 16-mm motion pictures taken at 25 frames per second. The most distinctive feature of the larval behavior, other than the release of the silk itself, is the rigidity with which the larva holds its body. There is no sign of the elaborate bending and stretching of the body or of the upward thrusting and side-to-side movements of the head that characterize cocoon-spinning in other formicine ant larvae, particularly in Formica (Wallis 1966; Schmidt and Görsch 1971). Rather, the larva keeps its body stiff, forming a straight line when viewed from above but a slightly curved, \$\text{-}\$ shaped line when seen from the side, with its head pointing obliquely downward as shown in Figure 4. Occasionally the larva extends its head for a very short distance when it is brought near the leaf surface, giving the impression that it is orienting itself more precisely at the instant before it releases the silk. The worker holds the larva in its mandibles between one-fourth and one-third of the way down the larva's body from the head, so that the head projects well out in front of the worker's mandibles.

The antennae of the adult workers are of an unusual conformation that facilitates tactile orientation along the edges of leaves and other vegetation. The last four segments are shorter relative to the eighth segments closest to the body than in other ants we have examined, including even communal silk-spinning formicines such as Camponotus sericeus and Polyrhachis acuta. They are also unusually flexible and can be actively moved in various directions in a fashion seen in many solitary wasps.

As the worker approaches the edge of a leaf with a larva in its mandibles, the tips of the antennae are brought down to converge on the surface in front of the ant. For 0.2 \pm 0.1 sec (X \pm SD, n = 26, involving a total of 4 workers), the antennae play along the surface, much in the manner of a blindfolded person feeling the edge of a table with his hands. Then the larva's head is touched to the surface and held in contact with the leaf for 1 sec (0.9 \pm 0.2 sec, n = 26). During this time, the tips of the worker's antennae are vibrated around the larva's head, stroking the leaf surface and touching the larva's head about 10 times (9.2 \pm 3.6, n = 26). At some point the larva releases a minute quantity of silk, which attaches to the leaf surface.

About 0.2 sec before the larva is lifted up again, the worker spreads and raises its antennae. Then it carries the larva directly to the edge of the other leaf, causing the silk to be drawn out as a thread. While moving between leaves, the worker holds its antennae well away from the head of the larva. When it reaches the other leaf, it repeats the entire procedure exactly, except that the larva's head is held to the surface for only 0.5 sec (0.4 \pm 0.01 sec, n = 26), during which time the worker's antennae touch the larva about 5 times (5.2 \pm 2.4, n = 26). In other words, the workers alternate between a longer time spent at one leaf surface and a shorter time at the opposing surface.

To summarize, the weaving behavior of the Oecophylla worker is even more complicated, precise, and distinctive than realized by earlier investigators. The movements are rigidly stereotyped in form and sequence. The antennal tips are used for exact tactile orientation, a "topotaxis" somewhat similar to that employed by honeybee workers to assess the thickness of the waxen walls of the cells in the comb (Lindauer and Martin 1969). The worker ant also appears to use its flexible antennal tips to communicate with the larva, presumably to induce it to release the silk at the right moment. Although we have no direct experimental proof of this effect, we can report an incidental observation consistent with it. One worker we filmed held the larva upside down, so that the front of the larva's head and its silk-gland openings could not touch the surface or be stroked by the antennal tips. The worker went through the entire sequence correctly, but the larva did not release any silk.

For its part, the larva has evolved distinctive traits and behaviors that serve communal weaving. It releases some signal, probably chemical, that identifies it as being in the correct phase of the final instar. When a worker picks it up, it assumes an unusual \$\text{-}\$ shaped posture. And when it is held against the surface of a leaf and touched by a worker's antennae, it releases silk, in a context and under circumstances quite out of the ordinary for most immature insects.
Intermediate steps

The existence of communal nest-weaving in *Polyrhachis* was discovered in the Asiatic species *Polyrhachis myrmoepla* (Myrmoepla) dives by Jacobson (Jacobson and Wasmann 1905). However, few details of the behavior of these ants have been available until a recent study by Hölldobler, reported here for the first time.

A species of *Polyrhachis* (Caryotermes), tentatively classified as *doddii*, was observed in the vicinity of Port Douglas, Queensland, where its colonies are relatively abundant. The ants construct nests among the leaves and twigs of a wide variety of bushes and trees (Fig. 5). Most of the units are built between two opposing leaves, but often only one leaf serves as a base or else the unit is entirely constructed of silk and is well apart from the nearest leaves.

*Polyrhachis* ants have never been observed to make chains of their own bodies or to line up in rows in the manner routine for *Oecophylla*. Occasionally a single *Polyrhachis* worker pulls and slightly bends the tip or edge of a leaf, but ordinarily the leaves are left in their natural position and walls of silk and debris are built between them.

The weaving of *Polyrhachis* differs markedly from that of *Oecophylla*. The spinning larvae are considerably larger and appear to be at or near the end of the terminal instar (Fig. 4). The workers hold them gently from above, somewhere along the forward half of their body, and allow the larvae to perform all of the spinning movements. In laying silk on the nest wall, the larvae use a version of the cocoon-spinning movements previously observed in the larvae of *Formica* and other formicine ants. Like these more “typical” species, which do not engage in communal nest-building, *Polyrhachis* larvae begin by protruding and retracting the head relative to the body segments while bending the forward part of the body downward. Approximately this much movement is also seen in *Oecophylla* larvae prior to their being touched to the surface of a leaf.

The *Polyrhachis* larvae are much more active, however, executing most of the spinning cycle in a sequence very similar to that displayed by cocoon-spinning formicines. Each larva begins with a period of bending...
and stretching, then returns to its original position through a series of arcs directed alternately to the left and right; in sum, its head traces a rough figure eight. Because the larvae are held by the workers, the movements of their bodies are restricted. They cannot complete the "looping-the-loop" and axial rotary movements described by Wallis (1960), by which larvae of other formicine ants move around inside the cocoon to complete its construction. In fact, the Polythachis larvae do not build cocoons. They pupate in the naked state, having contributed all their expelled silk to the communal nest. In this regard they fall closer to the advanced Oecophylla grade than to the primitive Dendromyrmex one, discussed below.

Polythachis ants are also intermediate between Oecophylla and Dendromyrmex in another important respect. The Polythachis workers do not move the larvae constantly like living shuttles as in Oecophylla, nor do they hold the larvae in one position for long periods of time or leave them to spin on their own as in Dendromyrmex. Rather, each spinning larva is held by a worker in one spot or moved slowly forward or to the side for a variable period of time (range 1–26 sec; mean 8 sec; SD 7.1 sec, n = 29). After each such brief episode the larva is lifted up and carried to another spot inside the nest, where it is permitted to repeat the stereotyped spinning movements. While the larva is engaged in spinning, the worker touches the substrates, the silk, and the front half of the larva's body with its antennae. However, these antennal movements are less stereotyped than in Oecophylla.

The product of this coordinated activity is an irregular, wide-meshed network of silk extending throughout the nest. The construction usually begins with the attachment of the silk to the edge of a leaf or stem. As the spinning proceeds, some workers bring up small particles of soil and bark, wood chips, or dried leaf material that the ants have gathered on the ground below. They attach the detritus to the silk, often pushing particles into place with the front of their heads, and then make the larvae spin additional silk around the particles to secure them more tightly to the wall of the nest. In this way a sturdy outside shell is built, consist-

![Image: Nest of Polythachis ant](image)

Figure 5. The nest of the Australian Polythachis species (top) is at an intermediate level of complexity, consisting of sheets of silk woven between leaves and twigs and reinforced by soil and dead vegetable particles. The interior of this type of nest (bottom) has a layer of silk tightly molded to the supporting leaf surfaces.

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America. It is one of only two representatives of the very large and cosmopolitan genus Camponotus known to incorporate larval silk in nest construction (although admittedly very little information is available about most species of this genus), and in this respect must be regarded as an evolutionarily advanced form. The most complete account of the biology of C. senex to date is that of Schreinem (1972, 1979a, b).

Unlike the other weaver ants, C. senex constructs its nest almost entirely of larval silk. The interior of the nest is a complex three-dimensional maze of many small chambers and connecting passageways. Leaves are often covered by the silken sheets, but they then die and shrivel, and thereafter serve as no more than internal supports. Like the Australian Polyrhachis, C. senex workers add small fragments of dead wood and dried leaves to the sheets of silk along the outer surface. The detritus is especially thick on the roof, where it serves to protect the nest from direct sunlight and rain.

As Schreinem stressed, chains of worker ants and other cooperative maneuver among workers of the kind that characterize Oecophylla do not occur in C. senex. The larvae employed in spinning are relatively large and most likely are near the end of the final instar. Although they consume substantial amounts of silk collectively, they still spin individual cocoons—in contrast to both Oecophylla and the Australian Polyrhachis. Workers carrying spinning larvae can be most readily seen on the lower surfaces of the nest, where walls are thin and nest-building unusually active. During Schreinem’s observations they were limited to the interior surface of the wall and consequently could be viewed only through the nascent sheets of silk. Although numerous workers were deployed on the outer surface of the same area at the same time, and were more or less evenly distributed and walked slowly about, they did not carry larvae and had no visible effect on the workers inside. Their function remains a mystery. They could in fact be serving simply as guards.

Although Schreinem himself chose not to analyze the weaving behavior of C. senex in any depth, we have been able to make out some important details from a frame-by-frame analysis of his excellent film (Schreinem 1972). In essence, C. senex appears to be very similar to the Australian Polyrhachis in this aspect of their behavior. Workers carry the larvae about slowly, pausing to hold them at strategic spots for extended periods. They do not contribute much to the contact between the heads of the larvae and the surface of the nest. Instead, again as in Polyrhachis, the larvae perform strong stretching and bending movements with some lateral turning as well. When held over a promising bit of substrate, larvae appear to bring the head down repeatedly while expelling silk. We saw one larva perform six “figure eight” movements in succession, each time touching its head to the same spot in what appeared to be typical weaving movements. The duration of the contact between its head and the substrate was measured in five of these cycles; the range was 0.4–1.5 sec and averaged 0.8 sec. During the spinning movement the workers play their antennae widely over the front part of the body of the larva and the adjacent substrate.

The weaving of C. senex, then, is the same as that of the Australian Polyrhachis. The only relevant difference is that C. senex larvae construct individual cocoons and Polyrhachis larvae do not.

The simplest type of weaving

A recent study of the tree ants Dendromyrmex chartifex and D. fabricii has revealed a form of communal silk-weaving that is the most elementary conceivable (Wilson 1981). The seven species of Dendromyrmex are concentrated in Brazil, but at least two species (chartifex and fabricii) range into Central America. The small colonies of these ants build oblong carton nests on the leaves of a variety of tree species in the rain forest (Weber 1944).

The structure of the nests is reinforced with continuous sheets of larval silk (Fig. 6). When the nest’s walls are deliberately torn to test their strength, it can be seen that the silk helps hold the carton together securely. Unlike Oecophylla larvae, those of Dendromyrmex construct silk only at the end of the final instar, when they are fully grown and ready to pupate. Moreover, only part of the silk is used to make the nest. Although a few larvae become naked pupae, most enclose their own bodies with cocoons of variable thickness. Workers holding spinning larvae remain still while the larvae perform the weaving movements; in Oecophylla, the larvae are still and the workers move. Often the larvae add silk to the nest when lying on the surface unattended by workers. Overall, their nest-building movements differ from those of cocoon-spinning only by a relatively small change in orientation. And, not surprisingly, this facultative communal spinning results in a smaller contribution to the structure of the nest than is the case in Oecophylla and other advanced weaver ants.

Figure 6. Dendromyrmex chartifex, of Central and South America, makes the simplest type of woven nest, a carton-like structure of chewed vegetable fibers reinforced with larval silk. (Photograph from Wilson 1981.)

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Anatomical changes

The behavior of communally spinning ant larvae is clearly cooperative and altruistic in nature. If general notions about the process of evolution are correct, we should expect to find some anatomical changes correlated with the behavioral modifications that produce this cooperation. Also, the degree of change in the two kinds of traits should be correlated to some extent. And finally, the alterations should be most marked in the labial glands, which produce the silk, and in the external spinning apparatus of the larva.

These predictions have generally been confirmed. Oecophylla, which has the most advanced cooperative behavior, also has the most modified external spinning apparatus. The labial glands of the spinning larvae of Oecophylla and Polyrhachis are in fact much larger in proportion to the size of the larva’s body than in the case in other formicine ant species whose larvae spin only individual cocoons (Karawajew 1929; Wilson and Hölldobler 1980). On the other hand, C. senex larvae do not have larger labial glands than those of other Camponotus larvae. Schrem-

Figure 7. Scanning electron micrographs reveal adaptations in the spinning apparatus of ant larvae in Oecophylla. At the left, the head of an O. longinoda larva is shown from the side (top) and front (middle); the arrows indicate the slit-shaped opening of the silk glands, which is modified substantially from the more primitive forms at the right. The reduced lateral nozzles in O. longinoda and the larger central nozzle are clearly visible at the bottom left. In Notomyrmecia macrops, a living Australian ant thought to be similar to the earliest formicines, there is no central nozzle and the lateral nozzles are much more prominent; the arrow at the top right points to the area enlarged at the middle right. The silk-gland opening of the Australian weaver ant, a species of Polyrhachis (bottom right), is similar in structure to that in Notomyrmecia. (Micrographs by Ed Selig.)
The uncertain climb toward cooperation

In order to summarize existing information on the evolution of communal spinning, the grades in Table 1 are defined according to the presence or absence of particular traits associated with communal nest-weaving. We believe that it is both realistic and useful to recognize three such stages. It is also realistic to suppose that the most advanced weaver ants, those of the genus *Ocophylla*, are derived from lines that passed through lower grades similar to, if not identical with, those exemplified by *Dendromyrmex*, *Polyrhachis*, and *Camponotus sexdens*.

On the other hand, we find it surprising that communal nest-weaving has arisen only four or so times during the one hundred million years of ant evolution. Even if new cases of this behavior are discovered in the future, the percentage of ant species that weave their nests communally will remain very small. It is equally puzzling that the most advanced grade was attained only once. The separate traits of *Ocophylla* nest-weaving provide seemingly clear advantages that should predispose arboreal ants to evolve them. The remarkable cooperative maneuvers of the workers allow the colony to arrange the substrate in the best positions for the addition of the silk bonds and sheets. By taking over control of the spinning movements from the larvae, the workers enormously increase the speed and efficiency with which the silk can be applied to critical sites. For their part the larvae have benefited the colony by moving the time when they produce silk forward in the final instar, thus surrendering once and for all the ability to construct personal cocoons but allowing workers to carry and maneuver them more effectively because of their smaller size.

The case of *Dendromyrmex* is especially helpful in envisioning the first steps of the evolution in behavior that culminated in the communal nest-weaving of *Ocophylla*. Although the contribution of the larvae to the structure of the nest is quite substantial, the only apparent change in their behavior is a relatively slight addition to their normal spinning cycle, so that the larva releases some silk onto the floor of the nest while weaving its individual cocoon. It is easy to imagine such a change occurring with the alteration of a single gene affecting the weaving program. Thus, starting the evolution of a population toward communal weaving does not require a giant or otherwise improbable step.

There is another line of evidence indicating the general advantage of communal nest-weaving and hence a relative ease of progression. We discovered that both male and female larvae contribute silk to the nest in the case of *Ocophylla* (Wilson and Hölldobler 1980) and *Dendromyrmex* (Wilson 1981); male contribution has not yet been investigated in *Polyrhachis* and *Camponotus*. Because cooperation and altruism on the part of male ants is rare, it is always worthy of close examination. Bartz (1985) has recently shown that in social Hymenoptera, natural selection will favor the evolution of either male workers or female workers, but not both, and the restrictive conditions imposed by the haplodiploid mode of sex determination—used by all Hymenoptera—favor all-female worker castes. In fact, the sterile workers of hymenopterous societies are always female.

<table>
<thead>
<tr>
<th>Grade</th>
<th>Larvae contribute silk to nest</th>
<th>Workers always hold spinning larvae</th>
<th>Larvae no longer make individual cocoons</th>
<th>Workers repeatedly move larva</th>
<th>Workers cooperate in adjusting substrate</th>
<th>Workers perform most spinning movements</th>
<th>Silk is produced before end of final instar</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>Dendromyrmex spp.</td>
<td>+</td>
<td>-</td>
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<tr>
<td>2</td>
<td>Polyrhachis <em>Techo</em></td>
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<tr>
<td></td>
<td>Camponotus sexdens</td>
<td>+</td>
<td>-</td>
<td>+</td>
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</tr>
<tr>
<td>3</td>
<td>Ocophylla spp.</td>
<td>+</td>
<td>+</td>
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Table 1. Grades of communal nest-weaving

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(Oster and Wilson 1978). In boreal carpenter ants of the genus Camponotus, where the males do contribute some labor to the colony, it is in the form of food-sharing, an apparent adaptation to the lengthy development cycle of Camponotus. The males are kept in the colonies from late summer or fall to the following spring, and it benefits both the colony and the individual males to exchange liquid food (Hölldobler 1966).

The contribution of silk by male wasp larvae is a coprophagous case. When the queens of Oecophylla and Dendromyrmex die, some of the workers lay eggs, which produce males exclusively (Hölldobler and Wilson 1983). Such queenless colonies can last for many months, until the last of the workers have died. During this period it is clearly advantageous for male larvae to add silk to the nest, for their own survival as well as that of the colony as a whole.

In summary, then, weaver ants exhibit a very important problem of evolutionary theory: why so many intermediate species possess what appear to be "imperfect" adaptations at least mechanically less efficient adaptations. Two hypotheses can be posed to explain the phenomenon that are fully consistent with the manifest operation of natural selection in such cases. The first is that some species remain in the lower grades because counterpressures of selection come to balance the pressures that favor the further evolution of the trait. In particular, the tendency for larvae to collaborate in the construction of nests could be halted or even reversed in evolution if surrendering the ability to make cocoons reduces the larvae's chance of survival. In other words, the lower grade might represent the optimum compromise between different pressures.

The second, quite different hypothesis is that the communal weavers are continuing to evolve—and will eventually attain or even surpass the level of Oecophylla—but species become extinct at a sufficiently high rate that most such evolutionary trends are curtailed before they are consummated. Even a moderate frequency of extinction can result in a constant number of species dispersed across the various evolutionary grades.

At present we see no means of choosing between these two hypotheses or of originating still other, less conventional evolutionary explanations. The greatest importance of phenomena such as communal nest-weaving may lie in the prospects they offer for a deeper understanding of arrested evolution, the reasons why not all social creatures have attained what from our peculiar human viewpoint we have chosen to regard as the peninsules of altruistic cooperation.

References