Weaver Ants

These social insects use their own larvae as shuttles to weave leaves into large nests in the rain forests of Africa and Asia. Their behavior is coordinated by complex chemical stimuli

by Berthold K. Hölldobler and Edward O. Wilson

Some insect species live in advanced social orders characterized by cooperation, caste specialization and individual altruism. Among the thousands of species of social insects a few deserve to be called classic, because certain remarkable features in their behavior have prompted unusually careful and thorough studies. The honeybees, the bumblebees, the driver ants, the army ants, the leafcutter ants, the slave-maker ants and the fungus-growing termites are all examples of classic social insects. The latest candidates for this select group are the weaver ants of the genus *Oecophylla* of Africa and tropical Asia. These ants devote a large part of their behavioral repertory to communication. The communication is further enriched by variations based on the weaver ants' caste system. As a result a weaver ant colony can perform feats far beyond the capabilities of single ants.

Weaver ants are extremely abundant, aggressive and territorial. They have achieved a position of exceptional ecological importance in the rain forests, cacao plantations and similar wooded environments they inhabit. For this reason the weaver ants have been the object of an increasing number of field studies. Over the past two years, however, we have succeeded in cultivating colonies of the African species *Oecophylla longinoda* in the laboratory. We induced the ants to live in potted trees and glass tubes. Under these conditions it has been possible for the first time to study the full range of the social life of the weaver ant.

These slender yellow insects are exquisitely adapted for life in the leafy canopies of tropical forests. Their main social unit is the colony, which consists of as many as 500,000 female workers, the progeny of a single enormous queen. The caste system within each colony consists of three forms of adult female: the heavy-bodied queen, a large population of "major" workers and a smaller population of "minor" workers. The weaver ant males, like those of other ant species, participate relatively little in the social life of the colony. They leave soon after maturing to participate in wedding flights with the virgin queens, after which they die without returning to the nest.

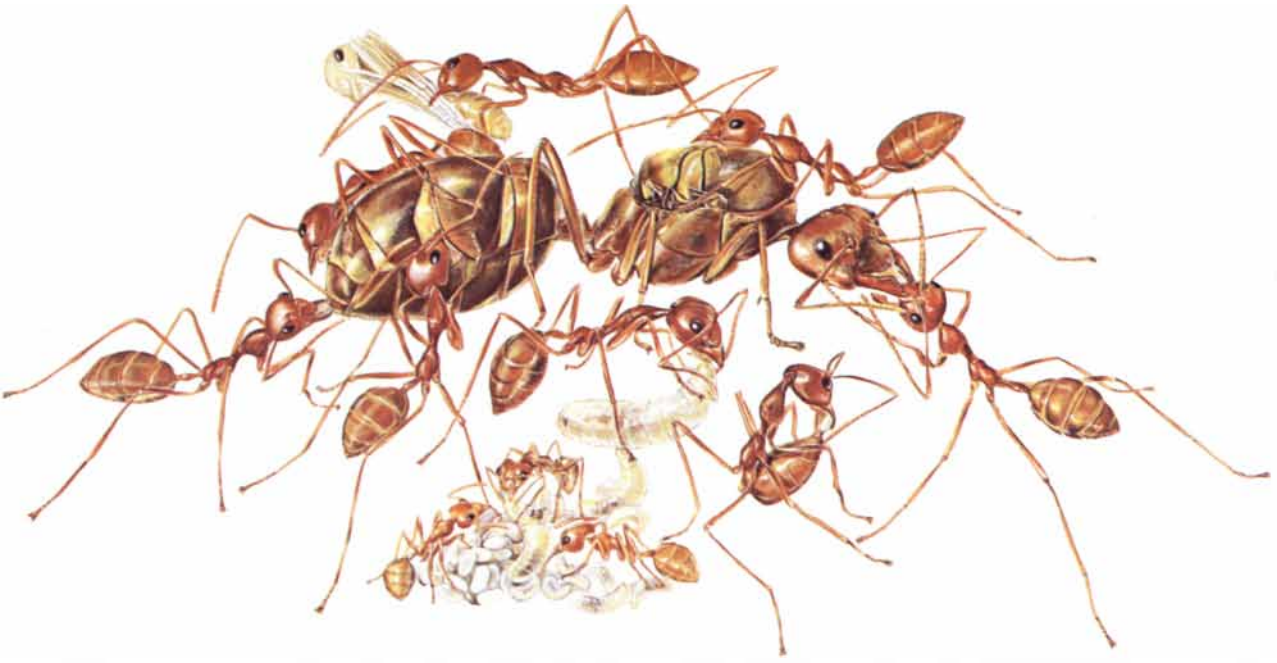
The major workers are fairly large, averaging six millimeters (about a quarter of an inch) in length. They are the general laborers, responsible for most of the foraging and nest construction. The more aggressive of the two worker castes, they rush from the nest at the slightest disturbance to bite an intruder and release formic acid from their poison gland. Major workers also form a dense retinue around the queen. They grasp her with their powerful legs so tightly that at times she is held in midair in the center of the nest cavity. About once a minute one of the major workers regurgitates a liquid meal into the mouth of the queen. At somewhat less frequent intervals a member of the queen's retinue lays a special trophic egg—a flaccid object without the ability to survive—that is immediately fed to the queen. This virtually continuous flow of nutrients enables the queen to manufacture hundreds of eggs a day. As the eggs are extruded from the queen's oviduct major workers carry them to special brood piles. There the smaller minor workers care for the eggs and feed and wash the tiny larvae that hatch from them. When the larvae are close to their maximum size, the major workers and minor workers share about equally in their care.

Weaver ants are named for their method of nest construction. The nests are made of leaves folded or fastened together to form tight, tentlike compartments. The leaves are held in place by seams of silk spun by the larvae, which the major workers employ like shuttles for weaving the nests. This nest building is one of the most remarkable instances of social cooperation among lower animals.

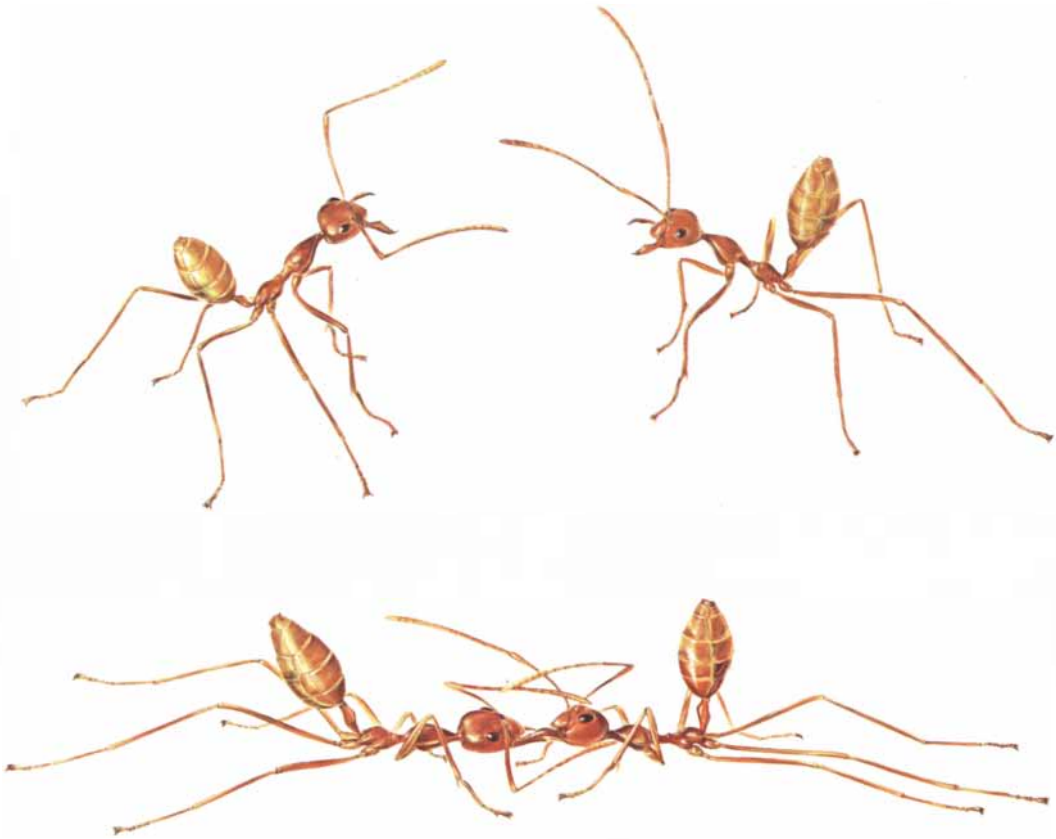
Once the weaver ants have chosen a tree branch suitable for a nest they spread out on the leaves of the branch and begin to pull on the tips and edges. When an ant succeeds in turning up a segment of a leaf, nearby workers are attracted to that part of the leaf, and soon there is a small group of ants pulling in unison. When a leaf is broader than the length of an ant's body, or when two leaves must be pulled together across a wide space, the workers form living bridges between the points to be joined. Then some of the ants in the chain climb onto the backs of their neighbors and pull backward, thus shortening the chain and bringing the leaf edges together. When the leaves have been maneuvered into shape, some of the ants remain on them, employing their legs and mandibles to hold the leaves in place. Other ants go back to already established nests and return to the new site carrying partly grown larvae. The workers wave the larvae back and forth across the leaf seams. This causes the larvae to release threads of silk from gland openings located just below their mouth. Thousands of these threads woven into sheets are strong enough to hold the leaves in place. Sheets of silk are also spun to make circular entrances and outer galleries leading to the interior of the new nest.

A single weaver ant colony can occupy a substantial volume in the canopy of a forest. The colony can fill an entire tree or even several adjacent trees without breaking the lines of communication that are vital to social insects. From the leaves of the trees the weaver ants construct hundreds of nests to serve as retreats, nurseries and outposts. During the day foragers patrol every square centimeter of leaf and bark within their territory. They rout enemies, capture insect prey and gather the sweet "honeydew" excrement of the swarms of scale insects and other sap-feeding homopterous insects that the ants guard as though they were dairy cattle.

The species of *Oecophylla* are not the only insects that weave. A few other



CASTE SYSTEM of the African weaver ant consists of three forms of adult female: a single queen, a population of "major" (large) workers that forage for food and perform a variety of other tasks, and a lesser number of "minor" (small) workers that care for the eggs and younger larvae. The queen (*center*) is occupied solely with receiving food from the major workers, chiefly by regurgitation, and laying eggs. In the foreground one major worker regurgitates to a larva; a second lays a "trophic" egg that lacks survival ability and will be fed to the queen. Minor workers are clustered around a brood pile. Scene was painted by Turid Hölldobler. Ants are enlarged about six times.



TERRITORIAL COMBAT of two weaver ants is initiated by a dance-like maneuver in which the combatants raise themselves by extending their legs and circle each other with stiff, jerky movements (*top*). Then one ant attempts to seize the other with its mandibles (*bottom*).

tropical species use larval silk to construct nests in trees and shrubs. The weaver ants are distinguished, however, by their close control of their environment. Indeed, man has employed weaver ants to control the arboreal environment for him.

Records from the Canton area of China show that weaver ant nests were gathered, sold and placed in selected citrus trees to combat insect pests in about A.D. 300. The same technique was noted in the 12th century and was still practiced in southern China well into the 20th century. The weaver ant used for this purpose is the Asian species *Oecophylla smaragdina*. This utilization of weaver ants is the oldest-known instance of the biological control of insects in the history of agriculture. Recently Dennis Leston, formerly of the University of Ghana, and other entomologists have recommended employing the African species of weaver ant to control pests of tree crops such as cacao. Studies in Ghana have shown that the presence of weaver ants reduces the incidence of two of the most serious diseases of cacao, one caused by a virus and the other by a fungus. In both cases the pathogen is transmitted by mirid leaf bugs. The weaver ants evidently combat the diseases by attacking the bugs. The *Oecophylla* workers are also particularly effective in hunting insects that feed on the tissue and sap of trees.

The weaver ants' exceptional control of their environment has been achieved through the evolution of advanced forms of social behavior. The communication system we have observed in our studies of the African species of weaver ant is one of the most complex and advanced systems known among the social insects. The great strength of the weaver ants lies in their ability, demonstrated in their nest building, to cooperate in group activities. They employ five different recruitment systems, consisting of distinct combinations of chemical and tactile signals, to initiate other group endeavors. These recruitment systems are employed in the main occupations of the weaver ants outside the nest: penetrating new territory, defending it and extracting food from it.

Weaver ants have an impressive sense of place that helps them to secure new territory. Their large eyes give them vision that is unusually acute for ants. Moreover, they are able to remember the appearance of many details of the nest area. If an object is simply shifted from one side of a nest tree to the other, workers come out of the nest to explore the object as if it were fresh terrain. In fact, when a conspicuous object such as a potted plant or a box is moved close to a weaver ant nest, the alert workers crawl out over the branches and leaves of their own tree in an effort to reach it. If the ants fail to get onto the new surface by reaching with their legs, they begin to climb on top of one another, constructing pyramids or chains with their bodies until the chasm is bridged. Then workers rush onto the new territory and begin to explore it.

The first explorers return to the nest to recruit other workers to help in securing the new territory. They mark the route from the territory to the nest with odor trails, that is, trails of a pheromone, or message-bearing chemical, that will guide their nestmates to the new area. The odor trails are created in an unusual way. The ants extrude a glandular segment of the hindgut through the anus. This organ, which we call the rectal gland and which is known only in weaver ants, is used in four of the recruitment systems. When the gland is extruded, it rests on a tiny sled consisting of two bristles that project from the tip of the ant's abdomen. As an ant runs back to the nest a secretion from the rectal gland is brushed on the ground, thereby creating the odor trail. When an ant laying one of these trails encounters nestmates, it jerks its body in their direction while touching them on the head with its antennae. The greeting stimulates the nestmates, with the result that they follow the trail to the new territory and begin to explore it. We call this process the system of recruitment to new terrain.

LIVING CHAIN of weaver ants folds over the tip of a leaf during the construction of the arboreal nest, a remarkable example of cooperative behavior. The workers shorten the chains by climbing up on the backs of nestmates while hauling edge of the leaf behind them.

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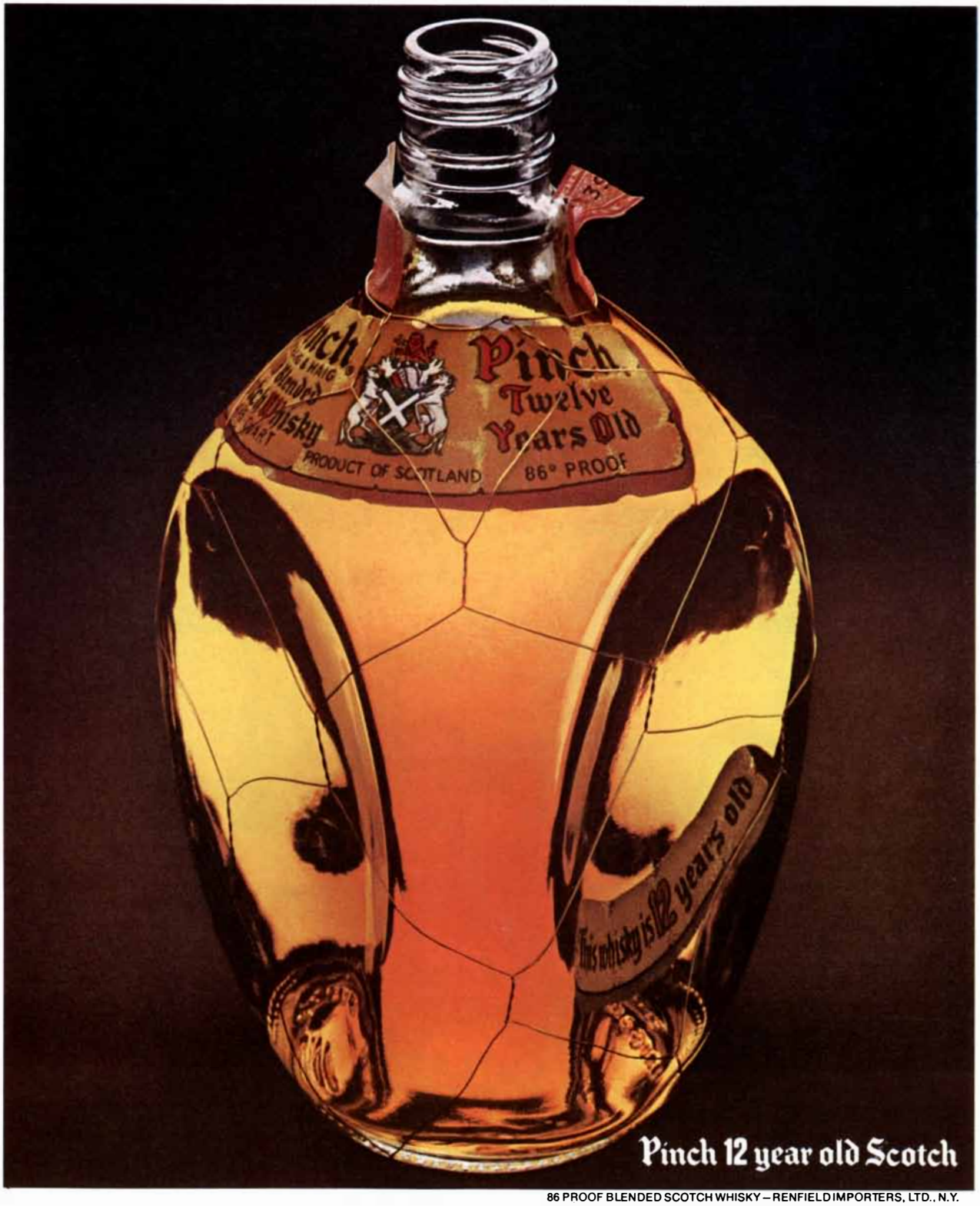

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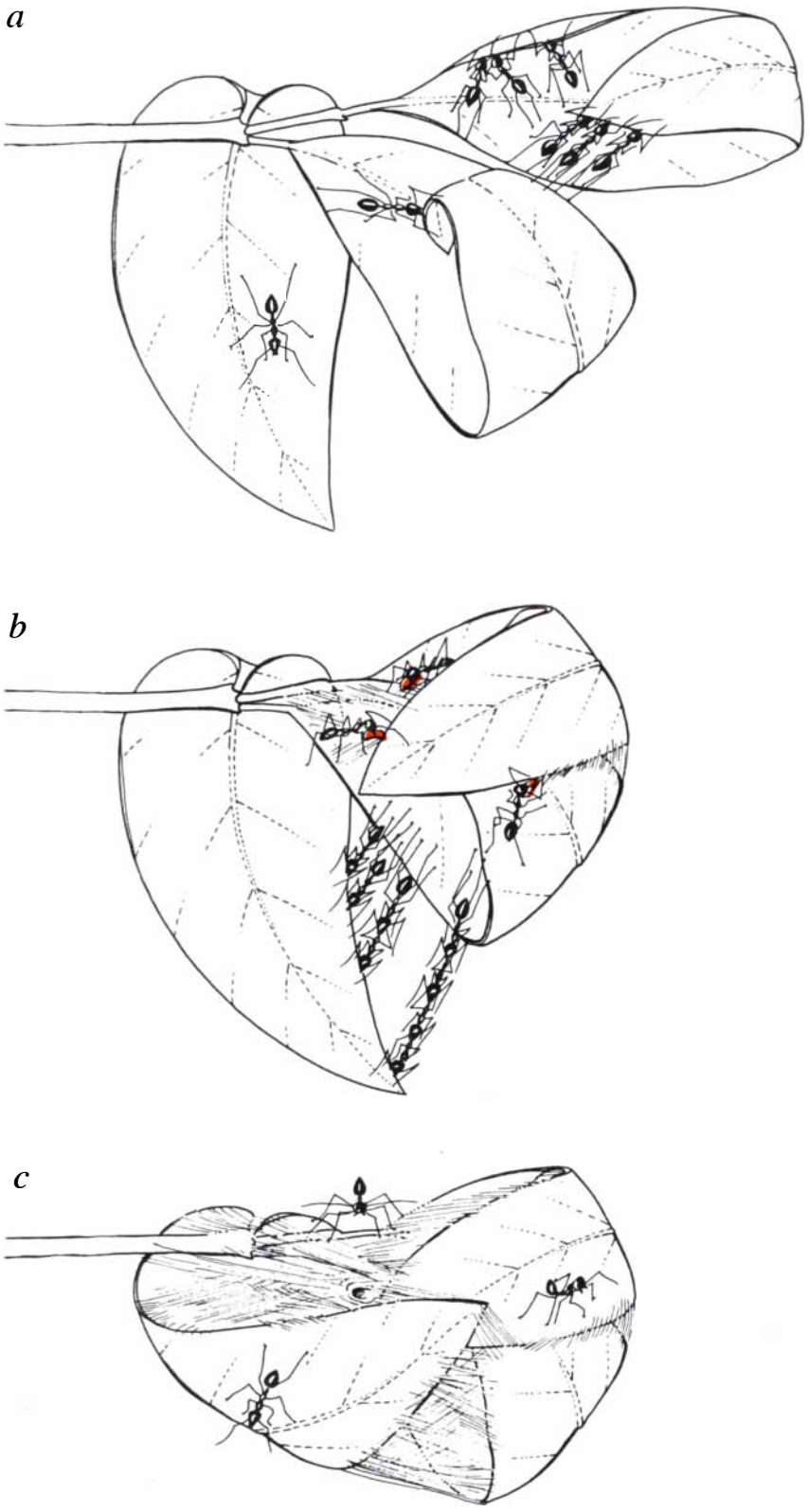
After an extension of a weaver ant colony's territory has been secured, the workers sweep back and forth across it in search of food. When a worker encounters a sugary secretion (usually from scale insects), it returns to the nest to recruit nestmates. Once again the rectal gland is employed to lay an odor trail. In this recruitment system the worker stimulates its nestmates by stroking them with its antennae while offering them regurgitated food from the find. Emigration to nests built in the new territory is effected by still another recruitment system, one that includes a rectal-gland odor trail, stroking with antennae and the physical transport of nestmates.

Two more recruitment systems are employed in defending the colony's territory. Weaver ants are particularly aggressive toward members of other weaver ant colonies. In fact, Leston has found that the territories of different colonies are separated by "no-ant's-lands," that is, narrow zones into which few ants venture. A contact between colonies of weaver ants usually results in immediate, spectacular warfare, numerous casualties and eventually the retreat of one of the colonies from part or all of its territory. In the natural habitat of the African species such battles can last for days as the massed opponents struggle along slowly shifting lines of defense.

Foraging workers that encounter enemy weaver ants react with a series of swift, precise movements. Individual combat is initiated with a dancelike maneuver in which the combatants raise themselves on extended legs and circle each other with stiff, jerky movements. Then they thrust and snap at each other with their mandibles. A defeated ant is pinned spread-eagled to the ground. Its legs and antennae are then clipped off and scattered, and its abdomen is often sliced open as well. Throughout the melee ants crumple dead and dying. Some of the workers rush back to the nest laying rectal-gland odor trails. When the trail layers encounter nestmates, they jerk their bodies in what appears to be a ritualized version of the preliminary combat dance. The nestmates respond, however, not by fighting but by running out along the trail to the battle site.

At the same time the fighting workers employ a shorter-range recruitment system to organize group attacks. When a forager encounters an enemy ant but fails to engage it in combat, the forager often runs short looping patterns while dragging its abdomen over the ground. In this recruitment system the ant rotates the terminal segment of its abdomen to expose its sternal gland. This newly discovered organ is also known only in weaver ants. The ants are attract-



COOPERATIVE NEST BUILDING in the weaver ant is illustrated in this sequence. At first the workers labor independently in their attempts to pull down or roll up leaves. When success is achieved by one or more of them at any part of the leaf, other workers in the vicinity abandon their own efforts and join in (*a*). When the leaves have finally been shaped into tentlike configurations, some of the ants continue to hold them in place with their legs and mandibles while others carry partially grown larvae (*color*) from preexisting nests and bind leaves together with sticky larval silk (*b*). Sheets of silk are then added to create circular entrances and galleries (*c*).

SILK TO BIND NESTS is spun by partially grown larvae, which the adult workers hold in their mandibles and move back and forth over the leaf seam like shuttles. The threads of silk, released from gland openings just below the larva's mouth, are woven into sheets.

COMPLETED NEST was constructed by a colony of the African weaver ant (*Oecophylla longinoda*) in a potted grapefruit tree grown in authors' laboratory at Harvard University. In the wild a colony of some half-million workers (the progeny of a single queen) may construct hundreds of nests from the leaves of one or more trees. The ants patrol this domain by day and withdraw into the nests at night.

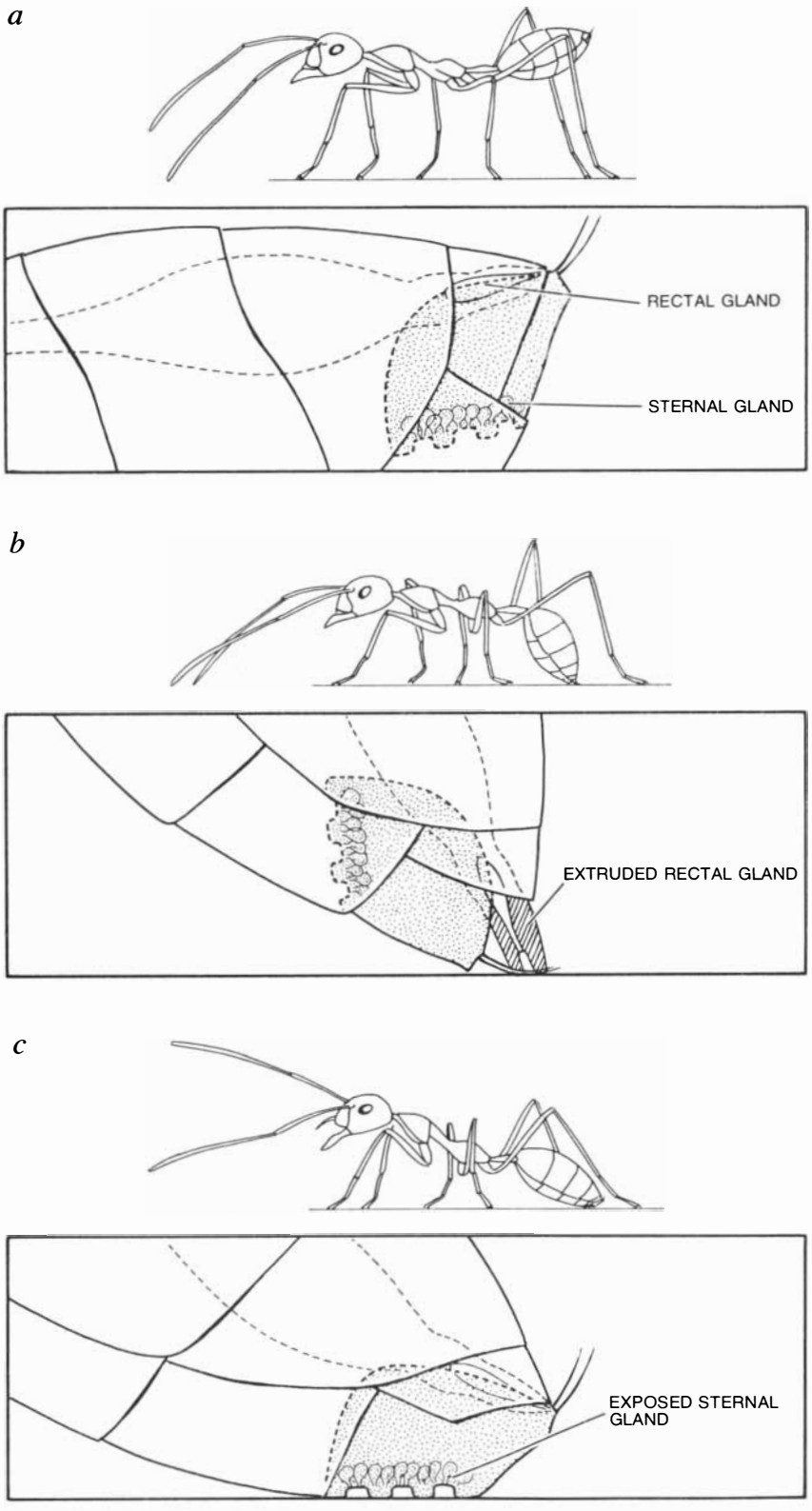
ed by the scent of the sternal-gland secretion from as far away as 10 centimeters. As a result small clusters of ants gather at the places where the enemy was first encountered.

J. W. S. Bradshaw and his colleagues at the University of Southampton have shown that this effect is enhanced by the release of various alarm substances from glands located at the base of the weaver ant's mandibles. Some of these substances attract nestmates to the scene. Others increase the ants' level of excitement and aggressiveness. We have observed repeatedly that these groups of recruited ants are far more effective in combat than individual ants. For example, workers of the large black tree ant *Polyrhachis militaris* can easily knock aside single weaver ants. When three or more weaver ants form a tight group, however, they can seize a tree ant in concert and pin it to the ground. Other workers quickly converge on the spot and assist in the kill.

The weaver ant is a sophisticated judge of odor cues. We noticed that after foragers occupied a new territory in the laboratory they began to deposit large droplets of fecal matter over the surface of the territory. This behavior differs from that displayed by most kinds of ants, which concentrate their excrement in refuse areas and other restricted locations. When the weaver ants patrol their territory, they inspect the fecal droplets. If a weaver ant encounters a droplet left by a member of another colony, it reacts momentarily with aversion, assumes a hostile posture and then inspects the droplet more closely. We have been able to induce the same set of reactions with fluid taken from the hindgut of alien ants.

The fecal substances give weaver ants an advantage when they are the defenders in territorial combat. We arranged a series of eight "wars" between colonies in areas previously marked out with fecal droplets by one or another of the colonies. In each case the members of the colony that had deposited the droplets were less hesitant to forage over the terrain and quicker to recruit nestmates when they encountered alien ants. As a result they gained the initial advantage and secured more ground during the initial fighting.

It appears that the distinguishing characteristics of the weaver ants evolved a long time ago. The African and Asian species are survivors of one of the most distinctive and ancient lineages of ants. Many insect fossils from over the past 100 million years are preserved in amber, which is fossilized resin. Fossils of two extinct species of weaver ant, *Oecophylla brevinodis* and *Oecophylla brischkei,* are found in amber that was deposited in the area of the Baltic Sea some 30



ODOR TRAILS are laid down by weaver ants to coordinate social activity. Normally the foraging worker ant walks with its abdomen elevated (*a*). When the ant encounters a new terrain or food source, it lowers its abdomen, extrudes the rectal gland through the anus and deposits a pheromone, or message-bearing substance, in a line along the ground (*b*). While the rectal gland is extruded it rests on a tiny sled consisting of two bristles. Nestmates that have been tactilely stimulated by the trail-laying ant will follow the trail to a new terrain. Short-range recruitment of major workers to fight invading ants and other intruders is achieved by exposing the sternal gland of the abdomen and dragging it over the ground to deposit a short, looping odor trail (*c*).

million years ago in the Oligocene epoch. During that period northern Europe contained both tropical and Temperate Zone forests. The fossil record shows that many of the insects of those forests resembled the insects of similar environments in the Europe and tropical Asia of today. In particular the extinct species of *Oecophylla* are related more closely to the modern Asian species than to any ants that are now found in Europe.

Some 15 years ago a first glimpse was obtained of the social organization of the extinct *Oecophylla*. In 1963 Mary Leakey was searching for fossils on Mfwangano Island in Lake Victoria in Kenya. She uncovered an assemblage of ant fossils: 366 tiny crystalline ants clustered in a single spot. The ants apparently had been living in a leaf nest that had fallen into a freshwater pool, where the nest and its inhabitants were quickly covered with sediment. Under those conditions an unusual amount of surface detail was preserved. One of us (Wilson) identified the assemblage as a portion of a colony of extinct weaver ants. It is the first and so far the only insect society that has been found in the fossil state. The assemblage includes clusters of larvae and pupae. Some of the fossil ants are still attached to fragments of leaves. Since there was a small population rather than the usual single fossil specimens, it was possible to make a statistical study of the caste system of the fossil species. The anatomical characteristics of these ants and the relative abundances of the two worker castes turned out to be quite similar to those that, among modern ants, are unique to the *Oecophylla* species.

The most distinctive element of the caste system of modern weaver ants is the minor worker: the caste of smaller and less numerous ants specializing in the care of eggs and small larvae. In most ant species that have more than one caste it is the major workers that are anatomically deviant and less numerous. The fossil population discovered by Mary Leakey was in a lower Miocene deposit and is therefore at least 15 million years old. The unusual anatomy and size distribution shared by the Miocene and modern weaver ants suggest that the peculiar division of labor among the living species of *Oecophylla* is of great age.

As the evidence from the fossil weaver ants implies, advanced social organization confers an evolutionary stability on the insect societies. This stability has advantages and disadvantages. On the one hand our studies suggest that individual workers perform no more than 50 distinct behavioral acts, most of which are for the purpose of communication. The result of this almost exclusively social orientation is that the weaver ant colony is an extremely successful working unit. On the other hand, the effectiveness of the colony is obtained by the rigid programming of the relatively simple components of individual behavior, which secures a complex but lockstep pattern of cooperation during group activities. It appears that the colony can flourish only at the expense of any semblance of independent action on the part of the individual. In other words, the weaver ants, like the honeybees, seem to have reached the extreme of one spoke of adaptive radiation among the social insects.

SYSTEM	FUNCTION	CHEMICAL SIGNALS	TACTILE SIGNALS	PATTERN OF MOVEMENT
Recruitment to food	Recruitment of major workers to immobile food source, particularly sugary materials	Odor trail from rectal gland and regurgitation of liquid from crop	Touching with antennae, head-waving and mandible-opening associated with the offering of food	Looping trails laid around food source, with main trail leading directly to nest
Recruitment to new terrain	Recruitment of major workers to new terrain	Odor trail from rectal gland	Touching with antennae and occasionally jerking body back and forth	Broad, looping trails laid around new terrain with deposition of hindgut material containing territorial pheremone; main trail leads directly to nest
Recruitment during emigration	Emigration of members of colony to a new nest site	Odor trail from rectal gland	By touching with antennae, one ant indicates its readiness to carry another to new nest site	Main trail leads directly to nest site without additional looping trails. Workers carry first mostly larvae and pupae, then other workers to nest site
Short-range recruitment to enemies	Short-range recruitment of nestmates for assembly and more rapid capture of invaders and prey	Short, looping odor trails from sternal gland; exposure of gland surface when abdomen is lifted in air	None	Short, looping trails limited to the vicinity of contact with enemy
Long-range recruitment to enemies	Long-range recruitment of major workers to fight invaders. Particularly intense during territorial wars with members of same species	Odor trail from rectal gland	Touching with antennae. During periods of greater excitement, body is jerked back and forth	Main trail leads directly to nest

RECRUITMENT SYSTEMS of the weaver ant are summarized in this table. The two pheromones secreted by the rectal gland and the sternal gland, when combined with tactile signals and the spatial configuration of the odor trail, can communicate five different messages.

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