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Trails of the Leafcutters

These industrious ants transport vast amounts of vegetation to their subterranean gardens. They establish and maintain their impressively long roadways by laying down chemical road signs

BY JOHN C. MOSER

The trails of leaf-cutting ants are among the most conspicuous and long-lived of all ant roadways. In tropical America, where such ants are abundant, paths leading from underground nests are often a foot wide and extend for 100 yards or more to trees or other plants whose leaves the ants gather. The ants commonly carry their forage above their heads, and when the trails are in full use, parades of busy worker ants resemble running streams of chlorophyll. The ants form permanent colonies underground where they cultivate extensive fungus gardens (NATURAL HISTORY, January, 1962). They use their trails constantly, for months at a time, and transport hundreds of pounds of green vegetation to their subterranean stores, thereby providing the "soil" to feed the fungus, which, in turn, feeds the ants.

The odor-trail substance, which enables the leaf-cutting ants to establish and maintain such gigantic trails, is a chemical that belongs to a group of biological agents known as "pheromones." A pheromone, according to E. O. Wilson of Harvard, is a substance that, when produced by an individual, excites behavioral or physiological changes, or both, in another member of the same species. Dr. Wilson considers that "unlike true hormones, which are secreted internally to regulate the organism's own physiology, or internal environment, pheromones are secreted externally, and help to regulate the organism's external environment. Moreover, pheromones may affect members of other species, but here the term can be applied only if such agents *first* affect members of the species from where the chemicals originate."

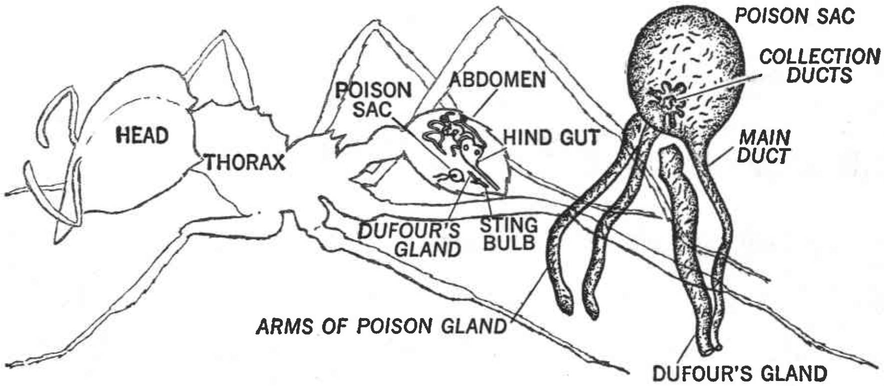
The method of chemical trail marking can be illustrated by the behavior of a laboratory colony of the town ant, *Atta texana*, at Alexandria, Louisiana, where I have been making ecological studies of this insect for the U.S. Forest Service. When a supply of green leaves is placed near a nest, scouting workers locate and examine it, and as they return to the nest they touch their abdomens to the ground and deposit the pheromone substance at regular intervals of two or three millimeters. Presently other workers follow the trail to the food supply, where they cut leaves and then carry the pieces back to the nest. The ants detect the trail by tapping the ground with their antennae, and they reinforce it by marking it frequently while carrying the forage nestward. Marking is sporadic on the outbound trip. Once a trail is well established, foragers cease touching their abdomens to the ground.

The odor substance is insoluble in water, and in the field, foraging activity continues even on wet trails and during light rains. The splashing action of a thundershower, however, temporarily disrupts the ants' efforts. At the beginning of a shower, workers moving to the foraging area quickly reverse direction and start back toward the nest. If the rain continues to be heavy, the ants simply drop their leaf sections and move to the side of the trail, there to mill about in the grass until the storm subsides to a drizzle. Then they pick up the leaves and resume one-way travel to the nest, taking alternate routes around puddles. Immediately after the rain stops, movement toward forage areas resumes.

Leaf-cutting ants, which belong to the tribe Attini, occur only in the New World and range from New Jersey to California and south to Argentina. They number about 250 species, of which about thirteen are in the United States. All Attini presumably possess the same basic odor-trail substance. In the laboratory, for example, specialized species, such as those of the genus *Atta*, readily follow trails marked by substances from the tribe's less complex genera —and vice versa. In the field, however, although the trails of various species cross, the workers generally find their own trails easily. Indeed, when I placed ants of one species on the trail of another, they wandered about until they encountered their own trail. Possibly each species produces some other chemical, in addition to the basic odor-trail substance, that attracts only members of its own species. Members of different tribes do not follow attine trail substances.

The main odor-trail pheromone is secreted by the gland that produces poisonous substances in other ant species. It is deposited by a modified stinger; that is, the mechanism probably once used by the Attini for defense or attack has evolved into a device whose sole function is communication. Most other ants of the subfamily Myrmecinae (to which the Attini belong), such as the fire ant, have retained functional stings, but these species are either scavengers or predators, and Attini are vegetarians.

The structure of the attine poison apparatus is almost identical in four representative genera that I have examined, and is evidence of a close relationship among species of the group. The odor-substance is formed in the true poison gland and is stored in the poison sac, a bladder-like structure with a crinkly surface. A tube connects this sac to the stinger; a large Dufour's gland also connects to the stinger. The Dufour's gland supplies the basic odor-substance of



In the leaf-cutting ants, the odor-trail substance is a pheromone that is produced in the poison gland and stored in the poison sac. It is deposited on the trails by a modified sting apparatus located at the tip of the abdomen.

fire ants and perhaps for attines furnishes a secondary substance that distinguishes their trails. The latter point is speculative, however, and if the secondary substance exists, it may be an anal emission.

The substance that attines lay on trails is a clear liquid that forms a milky-white suspension in acetone, alcohol, or water. When exposed to the air on a glass slide it quickly solidifies into a hard, shiny, amorphous material resembling clear fingernail polish. Only a fraction of the poison sac contents may actually constitute the odor-trail pheromone.

To test the potency of this substance, I extracted poison sacs from attines of several species, crushed each sac in one milliliter of carbon tetrachloride, and then progressively diluted the resulting solution. Smaller-sized workers—large workers are simply too excitable for tests of this kind—readily followed a circular line scribed on paper with a 1/100 dilution of the original solution, and a few of the workers could detect a 1/10,000 dilution. Sacs of large workers were obviously bigger and hence contained more odor-substance than the sacs of small workers, but the potency did not vary significantly per unit of volume. The substance is remarkably stable and persistent. Contents of *Atta texana* poison sacs crushed in carbon tetrachloride and kept at room temperature, for example, retained high potency for several months.

In the town ant, poison sacs first appear in pupae. They are empty at that stage, and when macerated in carbon tetrachloride do not attract workers on artificial trails. Sacs in young adult workers are only partially full and the contents have limited potency, but by the time the insect achieves the full red color of an adult, the sacs are full. Queens, both virgin and fertile, have a complete poison apparatus, but the sacs are always empty. Males, on the other hand, have no poison apparatus. Males and queens, however, avidly follow odor trails in the laboratory.

The genus *Atta* is the most specialized group of attines and forms the largest colonies. Main trails, a foot and sometimes more in breadth, radiate from the nest, usually branching as they approach foraging sites. In the large nests of some *Atta* species, the trails originate from "feeder holes" that form entrances to tunnels perhaps 100 yards from the central part of the colony. Thus, part of the trail is underground, usually at a depth of 1 to 1½ feet, which could help to prevent leaves from desiccating as they are carried to the fungus gardens. The tunnel-and-trail combination greatly extends the foraging range of the workers and permits the development of huge nests having 1,000 or more underground cavities, covering perhaps a half-acre on the surface and penetrating to a depth of at least 15 feet. Some one million ants may occupy a single large nest.

The foraging trails are not always busy and are not used by all ants in a nest. For example, workers of *Atta texana* in Louisiana leave their nests only when trail temperatures (not air temperatures) are between 52° and 85° F. Thus, foraging usually occurs during the day in winter and at night in summer. Species of *Atta*, unlike other attines, produce polymorphic workers—workers that vary greatly in size. The smaller workers, from two to three millimeters in length, rarely appear aboveground, as they are primarily occupied in tending the fungus gardens. Similarly, the large workers, eight to sixteen millimeters long, which seem to be the nest protectors, rarely appear on the trail. Thus the trail-making and foraging *Atta* are the medium-sized workers.

The leaf-cutting attines show preferences for certain plants as forage material. Workers in laboratory colonies of *Atta texana* like wild geranium, hackberry, sweet clover, beech, and mushrooms, and they sometimes carry pine, dock, white ash, and redbud to the nests. However, they refuse lettuce, Persian clover, sycamore, and rye grass. Certain types of breakfast food—corn flakes, for example—are highly favored, even though they are dry and crisp. The ants can carry the leaflike cereal flakes easily, and they readily add them to fungus gardens—which solves the problem of providing winter forage in the laboratory if the supply of frozen leaves becomes exhausted.

In the wild the primary foraging material in winter is *Geranium carolinianum* and certain other forbs; in summer, oak, hickory, and sweet gum are gathered. Pine needles, although not favored, are harvested extensively during January and February when they form the only abundant source of green forage. On warm winter days the ants may strip the needles from pine seedlings and saplings (hence the interest of the Forest Service in this insect). Workers always cut forage at the tops of trees and work down; this habit is most evident on pines twenty to thirty feet high, the tops of which may be clipped while the lower parts are left intact. Pines over thirty feet tall are rarely attacked, even though their branches may touch the nest.

Strictly speaking, many genera of Attini are not "leaf-cutting" ants. Less specialized members of the group, such as *Cyphomyrmex*, forage only for insect feces—caterpillar droppings, for example. In rare instances, workers of *Atta texana* will forage almost anything. They will cut and carry aluminum foil from discarded lunch wrappings and will even take small stones when the trails are near gravel roads. If a cow, fox, or some other animal dies on or near a nest, workers may cut and

:y bits of the flesh into their nests. laboratory colonies workers will ıetimes dismember small frogs or :cts and add them to the gardens. pical species of *Atta* use trails the removal of leafy matter that been depleted of nutrients by the gus in nest gardens, piling the ıse in heaps a short distance away n nests. Colonies of *Atta texana* y their refuse underground and their trails only for foraging.

ʌn unexpected discovery in the ıisiana research was that a comısal—a "guest" insect living with *a texana*—readily followed the s' artificial odor trails. This was small roach, *Attaphila fungicola*, ich inhabits fungus gardens only the nests of *Atta texana* and preıably behaves in the same way as ches do in human habitation.

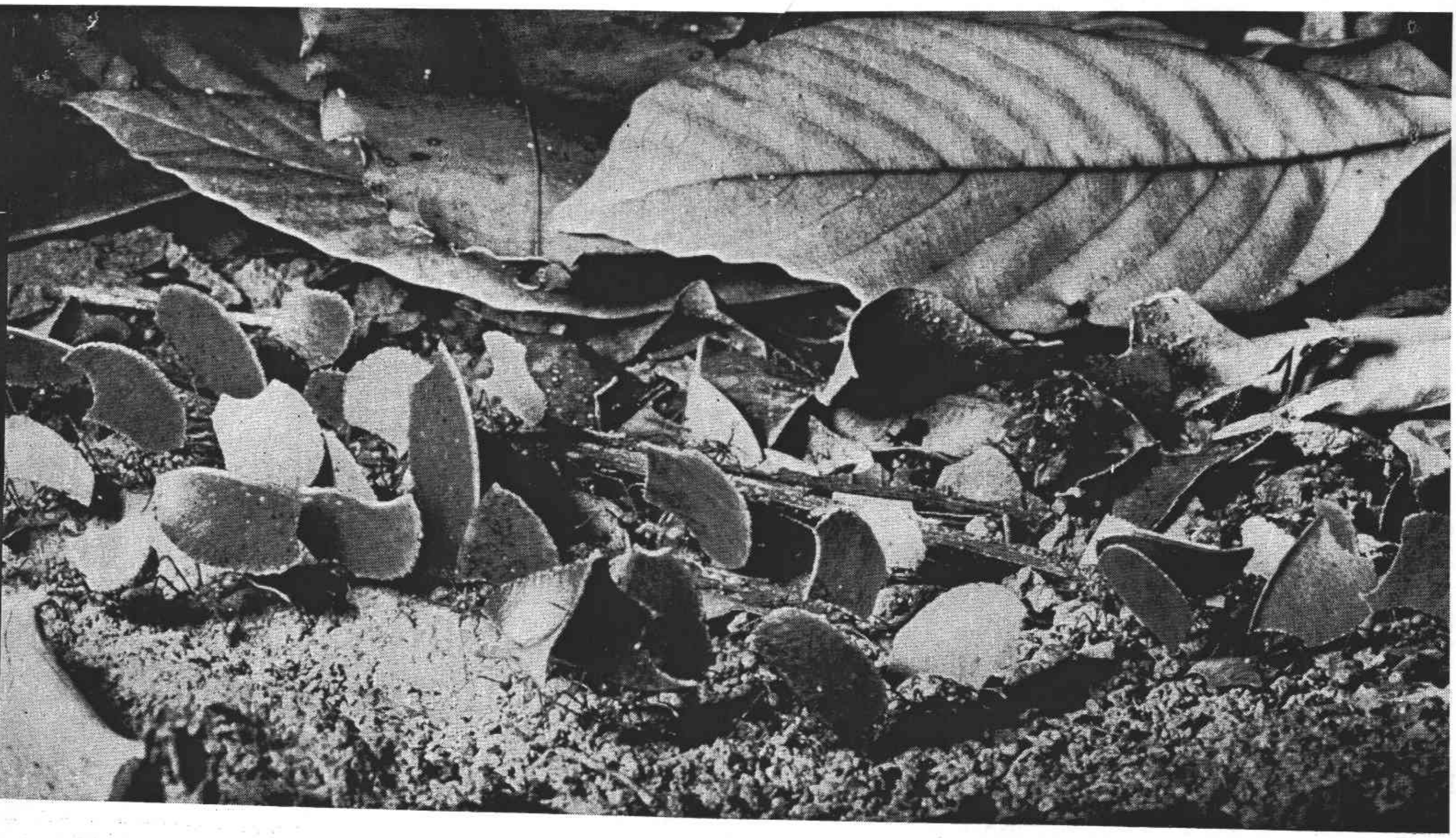
ʌlthough the roach follows artifil trails almost as readily as do the s, this behavior has been observed y once on a field trail. In this innce, three female roaches were n about 100 yards from an ant t, traveling toward the nest on a il heavily occupied by foraging rkers. Since this roach species is ıgless, it may use the odor-trail ıstance as a means of getting from one ant nest to another. More effective dispersal, however, occurs during the ant mating flights in spring, when numerous roaches attach themselves physically to queens and ride to the new nests.

Roaches are only distantly related to ants, but the ability of *Attaphila* to follow the odor-trail substance attests to its close associations with the ant, and is an excellent demonstration of how the evolution of the behavior of one animal can parallel that of another. The relationship also shows how one animal can use the pheromone of another to regulate its own behavior. It is interesting that the roach also follows artificial trails of at least one other leaf-cutting ant, *Trachymyrmex septentrionalis*, although it does not live in the nests, which are often superimposed on the larger nests of *Atta texana*. Other species of *Attaphila* do live in the nests of some South American species of *Acromyrmex*. Curiously, however, they have not been reported from nests of South American *Atta*.

Perhaps the next step in research on the attines will identify their pheromone chemically. This is a task for a biochemist, but perhaps not an extremely difficult one. Sacs from large workers of *Atta* are only slightly bigger in diameter than the period at the end of this sentence and a skilled technician can remove them from ants at the rate of one per minute. The contents of the sac probably are a mixture of compounds and although the amount of actual pheromone may be small, there are now models for such "eliminative" research—one of them being the successful identification of the sex-attractant pheromone of *Ips confusus*, a bark beetle found on ponderosa pine.

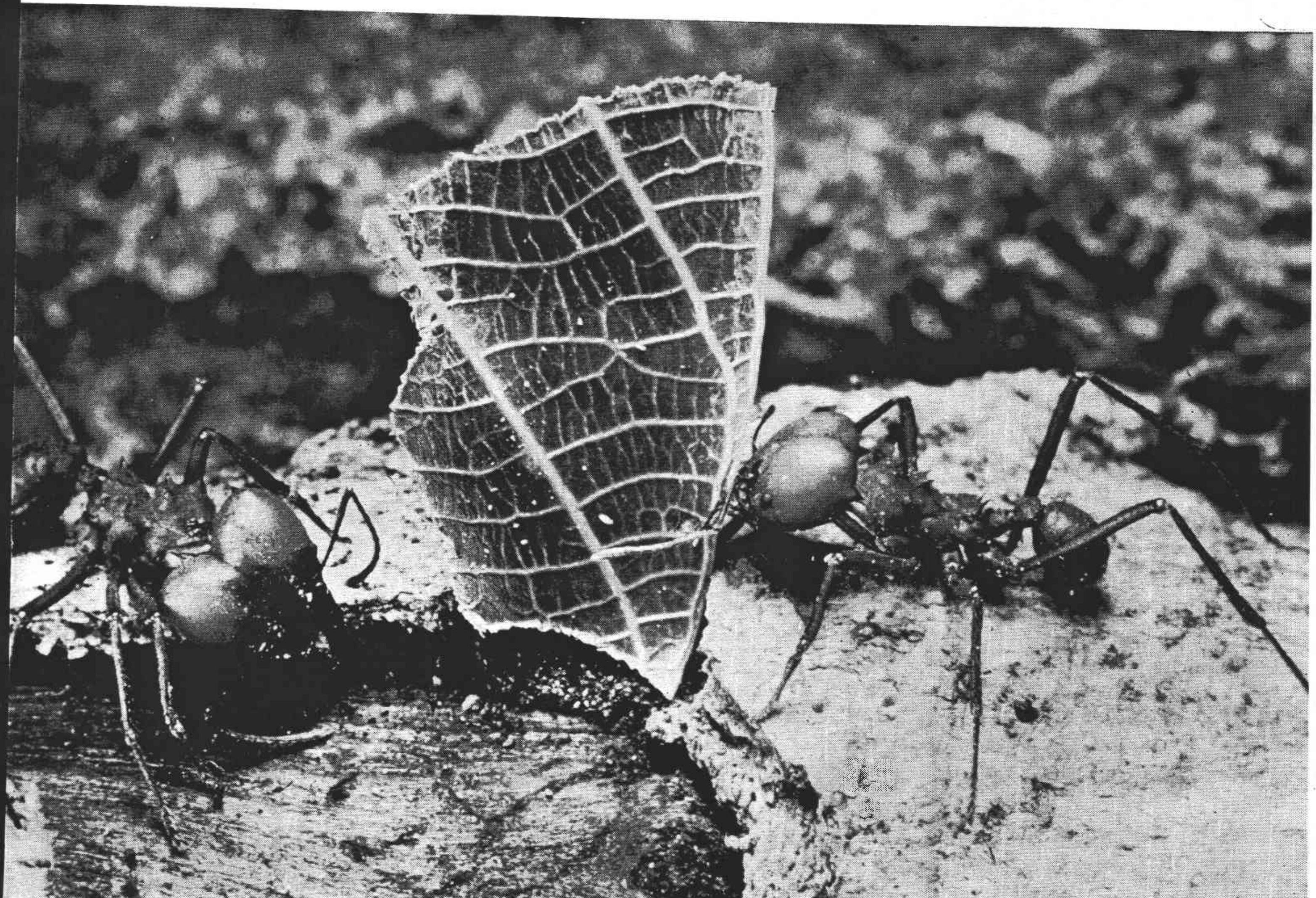
Leaf-cutting ants of the genera *Atta* and *Acromyrmex* are serious pests in some areas of the New World. In fact, in parts of Louisiana and Texas, *Atta texana* is responsible for killing more pine seedlings than are forest fires. In South America *Atta sexdens* must be locally exterminated before coffee and citrus crops can be grown; in Paraguay this ant has been cited as the primary reason for the poverty of many farmers. Perhaps the addition of the odor-trail pheromone to a lethal bait will aid in effectively controlling these ants where they compete economically with man.

Town ant, perhaps under the illusion that the pebble it carries is a leaf, detects the odor-trail substance by touching the trail with its antennae



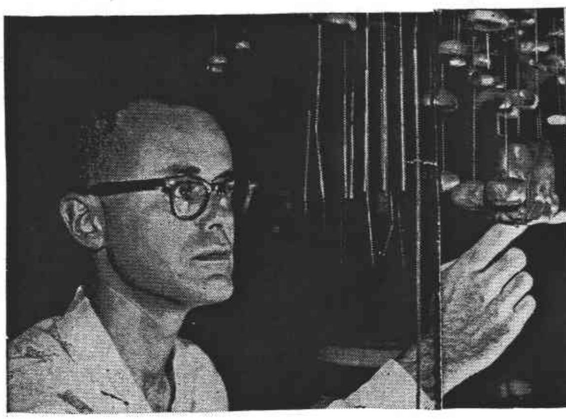
The heavy traffic of worker ants on a trail in Brazil resembles a rushing stream of liquid chlorophyll. The ants, Atta cephlotes, *transport leaf sections to their underground gardens.*

*Below, wielding in its mandibles a leaf section much larger than itself, a worker ant of another species—*Atta texana, *the town ant—moves toward its nest. Worker at left is outbound.*

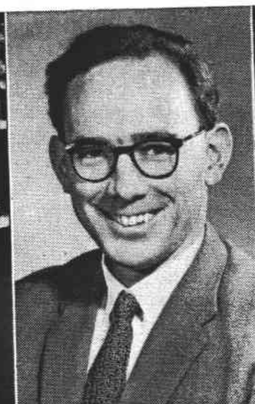


Marston Bates

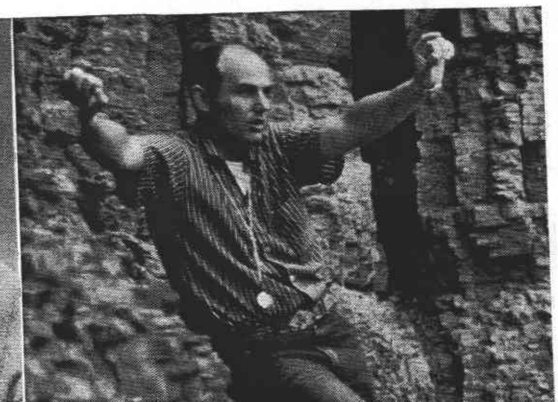
ABOUT THE AUTHORS



John Moser



David Dineley



Christopher Schuberth

One hardly need introduce MARSTON BATES, naturalist and author, whose article on human drug use marks a significant appearance in NATURAL HISTORY. Next month Professor Bates will begin a regular column for the magazine, to be called "A Naturalist at Large." Before assuming a professorship in zoology at the University of Michigan in 1952, he had served in the international health division of the Rockefeller Foundation for 15 years. His research in the tropics on diseases such as malaria and yellow fever led to several well-known books, including *The Natural History of Mosquitoes* and *The Forest and the Sea.*

NAPOLEON A. CHAGNON spent more than a year in Venezuela among the Yanomamö, studying their demography, kinship, social organization, warfare, and population genetics. From his work came his article, "Yanomamö—The Fierce People," and a Ph.D. in anthropology from the University of Michigan, from which he also received his undergraduate degrees and where he has been a teaching fellow. He will continue to study South American Indians, specifically the Yanomamö who he feels are "the most significant remaining large populations of undisturbed American Indians in either continent."

JOHN C. MOSER is seen above with a clay model of an ant nest used in the study on which his article, "Trails of the Leafcutters," is based. His finger touches a scaled representation of a cavity that was actually large enough for him to crawl into. Dr. Moser is a research entomologist for the Forest Insect Research Project of the U.S. Forest Service in Alexandria, Louisiana. He received a doctorate in insect ecology from Cornell University and is the author of numerous papers.

DAVID L. DINELEY, author of "Ancient Fishes of Escuminac Bay," is Chairman of the Geology Department of the University of Ottawa and has done extensive work on the rocks and fossils of Devonian times. Born in England, Dr. Dineley received his Ph.D. in geology from the University of Birmingham. He has written more than thirty articles for scientific journals in Europe and North America and has recently returned from a field session on Somerset Island, Northwest Territories, where he studied fossil fish hitherto unknown in the Canadian north. His particular interest is Arctic geology, geography, and wildlife.

CHRISTOPHER J. SCHUBERTH is a senior instructor in the Department of Education at The American Museum of Natural History and is on the geology faculty at Hunter College and Fairleigh Dickinson University. Author of "The Hudson's Six Geologies," he has done extensive field research in New York and New Jersey. He also conducted a four-year field study near The American Museum's Southwestern Research Station in Arizona. Mr. Schuberth, who holds an M.S. in geology from New York University, is presently working on three books on geology to be published by the Natural History Press.

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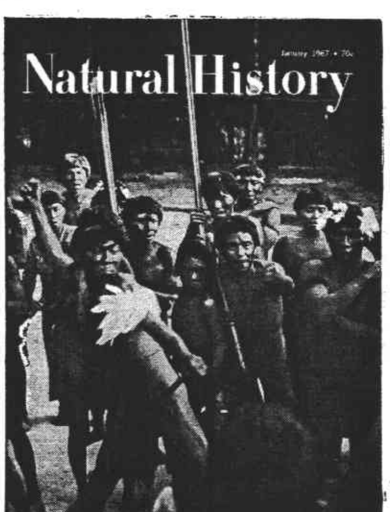
DEPARTMENTS



COVER: Recorded here by Napoleon A. Chagnon is the chest-pounding duel, a way of adjudicating grievances among the chronically violent Yanomamö Indians of southern Venezuela. The antagonists take turns delivering the hardest blows they can. Anthropologist Chagnon explains in his article (*page 22*) that Yanomamö practice a "graded form of violence"—a formal type of escalation. Chest pounding is more brutal than side slapping but much less so than the revenge raid or the "trick" (an ambush). While living with the jungle people, Chagnon met photographer Karl Weidmann, who helped with illustrating this article.

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