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ANIMAL BEHAVIOR

Ants & the Art of War

Battles among ants can be startlingly similar to human military operations *By Mark W. Moffett*

THE RAGING COMBATANTS FORM A BLUR ON ALL SIDES. THE SCALE OF THE violence is almost incomprehensible, the battle stretching beyond my field of view. Tens of thousands sweep ahead with a suicidal single-mindedness. Utterly devoted to duty, the fighters never retreat from a confrontation—even in the face of certain death. The engagements are brief and brutal. Suddenly, three foot soldiers grab an enemy and hold it in place until one of the bigger warriors advances and cleaves the captive's body, leaving it smashed and oozing.



Marauder ants

from one colony attack a member of rival marauder colony, slowly tearing it limb from limb.

I back off with my camera, gasping in the humid air of the Malaysian rain forest, and remind myself that the rivals are ants, not humans. I have spent months documenting such deaths through a field camera that I use as a microscope, yet I still find it easy to forget that I am watching tiny insects—in this case, a species known as *Pheidologeton diversus*, the marauder ant.

Scientists have long known that certain kinds of ants (and termites) form tight-knit societies with members numbering in the millions and that these insects engage in complex behaviors. Such practices include traffic control, public health efforts, crop domestication and, perhaps most intriguingly, warfare—the concentrated engagement of group against group in which both sides risk wholesale destruction. Indeed, in these respects and others, we modern humans more closely resemble ants than our closest living relatives, the apes, which live in far smaller societies. Only recently, however, have researchers begun to appreciate just how closely the war strategies of ants mirror our own. It turns out that for ants, as for humans, warfare involves an astonishing array of tactical choices about methods of attack and strategic decisions about when or where to wage war.

SHOCK AND AWE

REMARKABLY, these similarities in warfare exist despite sharp differences between ants and humans in both biology and societal structure. Ant colonies consist mostly of sterile females that function as workers or soldiers, occasionally a few short-lived males that serve as drones, and one or more fertile queens. Members operate without a power hierarchy or permanent leader. Although queens are the center of colony life because they reproduce, they do not lead troops or organize labor. Rather colonies are decentralized, with workers that individually know little making combat decisions that nonetheless prove effective at the group level without oversight—a process called swarm intelligence. But although ants and humans have divergent lifestyles, they fight their foes for many of the same reasons, including access to dwelling spaces, territory, food and even labor—certain ant species kidnap enemies to serve as slaves.

The tactics ants use in war depend on what is at stake. Some ants succeed in battle by being on the constant offensive, calling to mind Chinese military general Sun Tzu's assertion in his sixth-century B.C. book *The Art of War* that "rapidity is the essence of war." Among army ants, species of which inhabit warm regions around the world, and a few other groups, such as Asia's marauder ant, hundreds or even millions of individuals proceed blindly in a tight phalanx, attacking prey and enemies as they come across them. In Ghana I witnessed a seething carpet of workers of the army ant species *Dorylus nigricans* searching together across an area 100 feet wide. These African army ants—which, in species such as *D. nigricans* that move in broad swathes, are called driver ants—slice the flesh of their enemy or quarry with bladelike jaws and can make short work of victims thousands of times their size: although vertebrate creatures can



usually outrun ants, in Gabon I once saw an antelope, caught in a snare, eaten alive by a colony of driver ants. Both army ants and marauder ants will drive rival ants from food—the sheer number of troops is sufficient to overrun any rivals and control their food supply thereafter. But army ants almost always hunt en masse with a more malicious aim, storming other ant societies to seize the colony's larvae and pupae as food.

The advancing phalanxes of army and marauder ants are reminiscent of the fighting formations that humans have used from ancient Sumerian times to the regimented fronts of the American Civil War. Marching en masse in this way without a specific target, as humans sometimes did, every raid is a gamble: the ants might proceed over barren ground and find nothing. Other ant species send a far smaller number of workers called scouts out from the nest to search separately for food. By fanning out across a larger area while the rest of the colony stays home, they encounter more prey and enemies.

Yet colonies that rely on scouts may kill fewer adversaries in total because a scout must return to its nest to assemble a fighting force—usually by depositing a chemical called a pheromone for the reserve troops to follow. In the time it takes a scout to assemble troops for battle, the enemy might have regrouped or retreated. In contrast, the workers of the army ants or marauder ants can immediately summon any help they require because a slew of assistants are marching directly behind them. The result is maximal shock and awe.

ALLOCATING THE TROOPS

IT IS NOT just the huge number of fighters that makes the army and marauder ants so deadly. My research on marauder ants has shown that troops are deployed in ways that increase efficiency and reduce the cost to a colony. How an individual is deployed depends on the female's size. Marauder ant workers vary in size more than workers of any other ant species. The tiny "minor"

IN BRIEF

Some kinds of ants live in tight-knit colonies containing thousands or millions of individuals that go to war with

other colonies over resources such as territory or food. **The diverse tactics** these insects use in

combat can be remarkably similar to human war strategies, varying according to what is at stake.

The ants' capacity for warfare is enhanced by their extreme allegiance to their colony.



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On the battlefield: Highly territorial weaver ants spread-eagle a much stronger army ant, eventually tearing it to pieces (1). Smaller honeypot ant stands on a pebble to look larger, a tactical deception that scares its larger foe away (2). Minor worker of the marauder species rides on the head of a major worker of the same species; minors catch enemies, whereas majors kill them (3). Reddish suicide bomber ant ruptures its own body to spray a toxic yellow glue on its enemy, killing both instantly (4).



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workers (the foot soldiers of my opening description) move quickly to the front lines—the danger zone where competing ant colonies or prey are first encountered. A single minor has no more chance against the enemy than would an equally small scout of a lone-hunting species. But their sheer numbers at the front of a raid present a commanding barricade. Although some may die along the way, the minors slow or incapacitate the enemy until the larger workers, known as the medias and the majors, arrive to deliver the deathblow. The medias and the majors are much scarcer than the minors but far more lethal, with some individuals weighing 500 times as much as one minor.

The minors' sacrifices on the front lines assure a low mortality for the medias and the majors, which require far more resources for the colony to raise and maintain. Putting the easily replaced fighters at greatest risk is a time-honored battle technique. Ancient societies did the same thing with conscripted farmers, cheaply obtained and available in droves, who absorbed the worst of the warfare. Meanwhile elite soldiers, who received the best training and finest weapons and armor, remained relatively safe within the hordes. And just as human armies may defeat their enemies by attrition, destroying

unit by unit rather than attacking a whole force at once—a tactic known to military strategists as “defeat in detail”—so, too, do marauder ants mow down enemies a few at a time as a raid advances instead of engaging the enemy's entire strength.

In addition to killing other enemy species and prey, marauder ants intensely defend the areas around their nests and food from other colonies of their own kind. The medias and majors hang back while each minor grabs an opponent's limb. These confrontations last for hours and are deadlier than in the jostles that occur between the marauder and its other competitors. Hundreds of little ants become interlocked over a few square feet as they slowly tear one another asunder.

This insect variant of hand-to-hand combat represents the common mode of killing among ants. Mortality is nearly certain, reflecting the cheapness of labor in a large colony. Ants that are less cavalier about loss of troops employ long-range weapons that allow them to hurt or impede the enemy from afar; for example, stunning their enemy with a Mace-like spray, as *Formica* wood ants from Europe and North America do, or dropping small stones onto enemy heads as *Dorymyrmex bicolor* ants from Arizona do.

Research conducted by Nigel Franks, now at the University of Bristol in England, and his colleagues has demonstrated that the organized violence practiced among army ants and marauders is consistent with Lanchester's square law, one of the equations developed in World War I by engineer Frederick Lanchester to un-

derstand potential strategies and tactics of opposing forces. His math showed that when many fights occur simultaneously and within one arena, greater numbers trump individual fighting power. Only when dangers become extreme do the larger marauder ants put themselves at risk—for example, workers of all sizes will rush an entomologist foolish enough to dig up their nest, with the majors inflicting the most savage bites.

Still, just as Lanchester's square law does not apply in all situations for warring humans, neither does it describe all the behaviors of warring ants. Slave-making ants offer a fascinating exception. Certain slave makers steal the brood of their target colony to raise as slaves in the slave maker nest. The slave makers' tough armor, or cuticle, as it is termed, and daggerlike jaws give them superior fighting abilities. Yet they are greatly outnumbered by the ants in the colonies they raid for slaves. To avoid being massacred, some slave makers release a "propaganda" chemical that throws the raided colony in disarray and keeps its workers from ganging up on them. In so doing, as Franks and his then University of Bath graduate student Lucas Partridge have shown, they are following another Lanchester strategy that at times ap-

TERRITORIAL CONTROL

OTHER HUMANLIKE military strategies emerge from observations of weaver ants. Weaver ants occupy much of the canopy of tropical forests in Africa, Asia and Australia, where colonies may span several trees and contain 500,000 individuals—comparable to the enormous populations of some army ants. Weavers also resemble army ants in being highly aggressive. Yet the two have entirely different *modi operandi*. Whereas army ants do not defend territories because they stay packed together while roaming in search of other ant species to attack for food, weaver colonies are entrenched at one site, spreading their workers wide within it to keep competitors out of every inch of their turf.

They handily control huge spaces within the trees by defending a few choke points such as the spot at which the tree trunk meets the ground. Leafy "barrack nests" placed strategically in the crowns distribute the troops where they are most needed.

Weaver ant workers are also more independent than army ant workers. Army ant raids function by stripping away the workers' autonomy. Because the army ant troops confine themselves to the close quarters of their advancing pack, they require



Shut the front door: Door-making ant of the genus *Stenamma* (middle) uses a pebble to block an army ant (left) from entering its nest.

plies also for humans. This so-called linear law holds that when battles are waged as one-on-one engagements—which is what the propaganda substance allows—victory is assured for the superior fighters even when they are outnumbered. In fact, a colony besieged by slave makers will often allow the invaders to do this plundering without any fighting or killing.

Among ants, a fighter's value to its colony bears on the risks the ant takes: the more expendable she is, the more likely she is to end up in harm's way. The guards lining marauder foraging trails, for instance, are commonly elderly or maimed workers that often struggle to stay upright while lunging at intruders. As Deby Cassill of the University of South Florida reported in *Naturwissenschaften* in 2008, only older (months-old) fire ants engage in fights, whereas weeks-old workers run off and days-old individuals feign death by lying motionless when under attack. Viewed from the ant perspective, the human practice of conscripting healthy youngsters might seem senseless. But anthropologists have found some evidence that, at least in a few cultures, successful human warriors tend to have more offspring. A reproductive edge might make combat worth the personal risk for people in their prime—an advantage unattainable by ant workers, which do not reproduce.

relatively few communication signals. They respond to enemies and prey in a highly regimented way. Weavers, in contrast, wander more freely and are more versatile in their response to opportunities and threats. The differences in style call to mind the contrasts between the rigidity of Frederick the Great's armies and the flexibility and mobility of Napoleon Bonaparte's troops.

Like army ants, weaver ants take similar tacks in dealing with prey and destroying an enemy: in both cases, a weaver deploys a short-range recruitment pheromone from its sternal gland to summon nearby reinforcements to make the kill. Other weaver ant communiqués are specific to warfare. When a worker returns from a fight with another colony, it jerks its body at passing ants to alert them to the ongoing combat. At the same time, it deposits a different scent along its path, a pheromone released from the rectal gland that its colony mates follow to the battlefield. Moreover, to claim a previously unoccupied space, workers will use yet another signal, defecating in the spot, much as canines mark their territory by urinating on it.

A MATTER OF SIZE

FOR BOTH ANTS AND HUMANS, the propensity to engage in true warfare is related at least in a rough way to the size of a society.

Small colonies seldom conduct protracted battles except in defense. Like human hunter-gatherers, who are often nomadic and tend to live hand to mouth, the tiniest ant societies, which contain just a few dozen individuals, do not build a fixed infrastructure of trails, food stashes or dwelling places worth dying for. At times of intense conflict between groups, these ants, like their human counterparts, will often choose flight over fight.

Modestly sized societies will likely have more resources to defend but are still small enough to be judicious about jeopardizing their troops. Honeypot ants of the southwestern U.S., which live in medium-size colonies containing a few thousand individuals, provide an example of danger mitigation by these insects. To harvest nearby prey unchallenged, a honeypot colony may stage a preemptive tournament near a neighboring nest to keep the enemy busy rather than risking deadly battles outright. During the tournament the rivals stand high on their six legs and circle one another. This “stilting” behavior mirrors the mostly bloodless, ceremonial displays of strength commonplace in small human clans, as biologists Bert Hölldobler of Arizona State University and E. O. Wilson of Harvard University have remarked. With luck, the colony with the smaller stilting ants—typically from the weaker colony—can retreat without loss of life, but the winning side will wreak havoc on their enemies given the opportunity, devouring the loser’s brood and abducting workers called repletes that are swollen with food they regurgitate on request for hungry nest mates. The honeypot victors will drag the repletes back to their nest and keep these living larders as slaves. To avoid this fate, reconnaissance workers survey the tournament to assess whether their side is outnumbered and, if necessary, organize a retreat.

Full-bore conflicts appear to be most common for ant species with mature colonies composed of hundreds of thousands of individuals or more. Scientists have tended to consider these large social insect societies inefficient because they produce fewer new queens and males per capita than smaller groups do. But I see them as being so productive that they have the option to invest not only in reproduction but in a workforce that exceeds the usual labor requirements—much like our bodies invest in fatty tissue we can draw on in hard times. Writing in *Behavioral Ecology and Sociobiology* in 2007, Raphaël Jeanson of Paul Sabatier University in Toulouse, France, and his colleagues predicted that individual ants have less work to do as colonies grow larger. This growth would amplify the expansion of a dedicated army reserve that can take full advantage of Lanchester’s square law in its encounters with enemies. Similarly, most anthropologists see human warfare as having emerged only after our societies underwent a population explosion fueled by the invention of agriculture.

SUPERORGANISMS AND SUPERCOLONIES

ULTIMATELY THE CAPACITY for extreme forms of warfare in ants arises from a social unity that parallels the unity of cells in an organism. Cells recognize one another by means of chemical cues on their surface; a healthy immune system attacks any cell with different cues. In most colonies, ants, too, recognize one another by means of chemical cues on their body surface, and they attack or avoid foreigners with a different scent. Ants wear this scent like a national flag tattooed on their bodies. The permanence of the scent means ant warfare can never end with one colony usurping another. Midstream switches in allegiance are

impossible for adult ants. With perhaps a few rare exceptions, each worker is a part of her natal society until it dies. (Not that the interests of ant and colony always coincide. Workers of some species can attempt to reproduce—and be thwarted—much as conflicts of interest between genes can occur within an organism.) This identification with their colony is all ants have because they form anonymous societies: beyond distinguishing castes such as soldiers from queens, ant workers do not recognize one another as individuals. Their absolute social commitment is the fundamental feature of living as part of a superorganism, in which the death of a worker is of no more consequence than cutting a finger. The bigger the colony, the less a small cut is felt.

The most breathtaking example of colony allegiance in the ant world is that of the *Linepithema humile* ant. Though native to Argentina, it has spread to many other parts of the world by hitching rides in human cargo. In California the biggest of these “supercolonies” ranges from San Francisco to the Mexican border and may contain a trillion individuals, united throughout by the same “national” identity. Each month millions of Argentine ants die along battlefronts that extend for miles around San Diego, where clashes occur with three other colonies in wars that have may have been going on since the species arrived in the state a century ago. The Lanchester square law applies with a vengeance in these battles. Cheap, tiny and constantly being replaced by an inexhaustible supply of reinforcements as they fall, Argentine workers reach densities of a few million in the average suburban yard. By vastly outnumbering whatever native species they encounter, the supercolonies control absolute territories, killing every competitor they contact.

What gives these Argentines their relentless fighting ability? Many ant species, as well as some other creatures, including humans, exhibit a “dear enemy effect,” in which, after a period of conflict, death rates sharply decline as the two sides settle on a boundary—often with an unoccupied, no-man’s-land between them. In the floodplains where Argentine ants originated, however, warring colonies must stop fighting each time the waters rise, forcing them to higher ground. The conflict is never settled; the battle never ends. Thus, their wars continue unabated, decade after decade.

The violent expansions of ant supercolonies bring to mind how human colonial superpowers once eradicated smaller groups, from Native Americans to Australian Aborigines. Luckily, humans do not form superorganisms in the sense I have described: our allegiances can shift over time to let immigrants in, to permit nations to merge. Although warfare might be inescapable among many ants, it is, for us, avoidable. ■

MORE TO EXPLORE

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More ant photos are available at ScientificAmerican.com/dec2011/ants