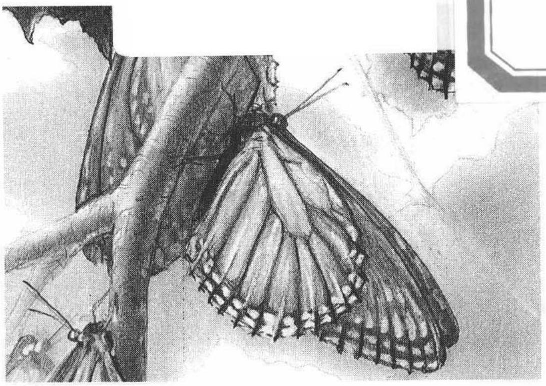
Gilbert Waldbauer

Millions of Monarchs

Bunches of Beetles

HOW BUGS FIND STRENGTH IN NUMBERS

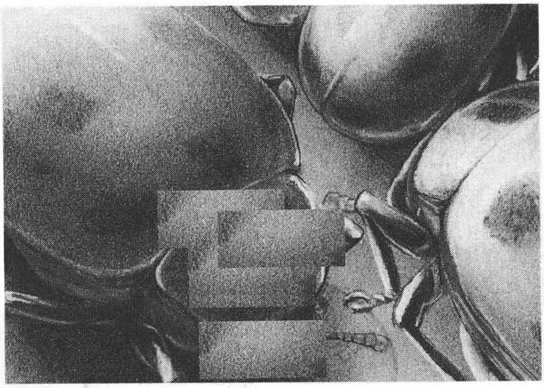
GILBERT WALDBAUER



Millions of Monarchs

HOW BUGS FIND STRENGTH IN NUMBERS

Bunches of Beetles



HARVARD UNIVERSITY PRESS

CAMBRIDGE, MASSACHUSETTS, AND LONDON, ENGLAND

Printed in the United States of America
Third printing, 2001

First Harvard University Press paperback edition, 2001

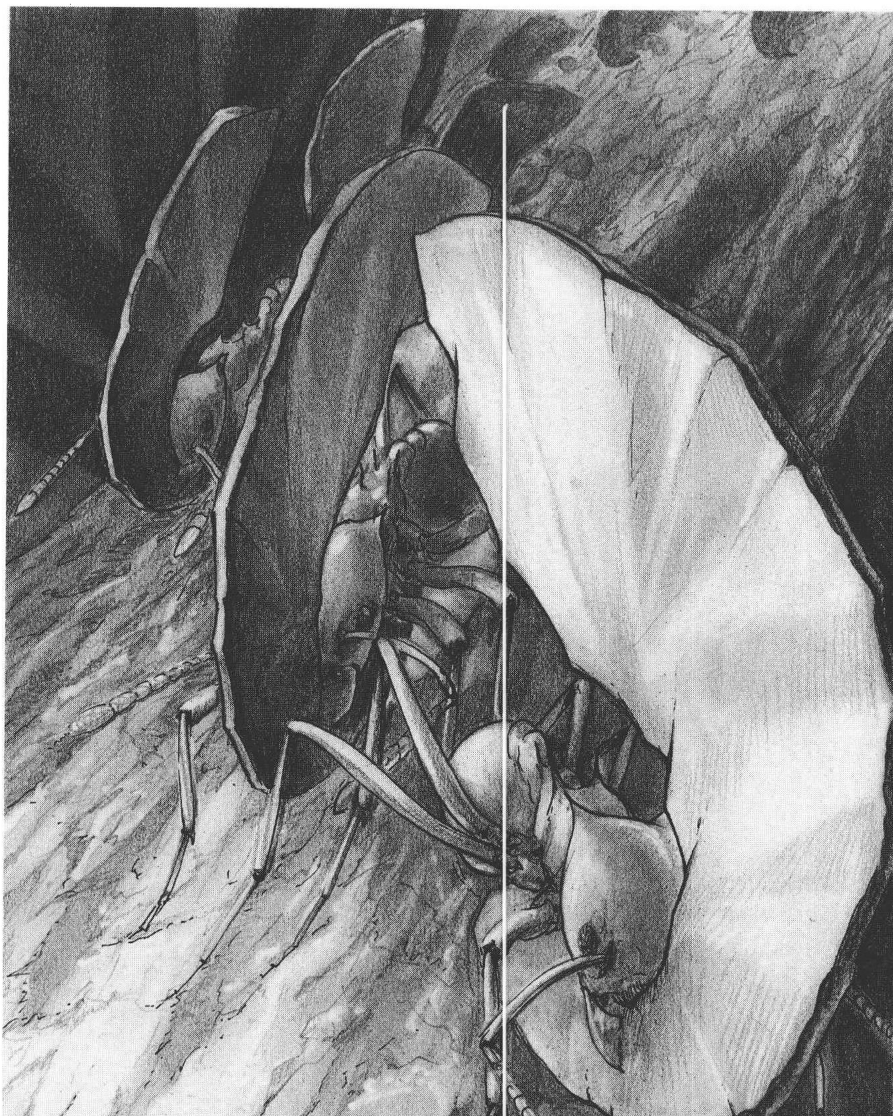
Illustrations by Katherine Brown-Wing

Library of Congress Cataloging-in-Publication-Data

Waldbauer, Gilbert.
Millions of monarchs, bunches of beetles : how bugs find strength in numbers / Gilbert Waldbauer.
p. cm.
Includes bibliographical references.
ISBN 0-674-00090-0 (cloth)
ISBN 0-674-00686-0 (pbk.)
1. Insects—Behavior. 2. Social behavior in animals. I. Title.
QL496.W36 2000
595.7156–dc21 99-42453

Contents

Strength in Numbers



Leafcutter ants carrying pieces of leaves to their nest

Two especially memorable experiences with insects stick in my mind. Early one morning, when I was still a teenager in Fairfield County, Connecticut, I watched a procession of eastern tent caterpillars leave their tent in the main fork of a wild black cherry sapling, and crawl along branches and twigs to a spray of leaves on which they commenced to feed. The caterpillars moved nose to tail in single file. The procession was orderly, one might even say stately. It reminded me of the parade that marched down Main Street in nearby Bridgeport every Memorial Day. Years later, long after I had become a professional entomologist and while I was on sabbatical leave in Colombia, I watched, for the first time, a column of leafcutter ants move over the ground to the huge mound of soil that marked the entrance to their underground nest. The column was long. "Empty-handed" workers moved out, and returning workers delivered inch-wide pieces of green leaves that they held in their jaws and carried over their heads like parasols. I knew from my reading that the nest was inhabited by a highly organized society of agriculturists that use leaf fragments to make a rich mulch on which they cultivate the fungus that is their only food. These two processions impressed me because the caterpillars and the ants—which most of us think of as *lowly* insects—quite obviously operated as organized groups that acted in concert.

People pay particular attention to insects or other animals that occur in groups. Who would not be awed by a swarm of desert locusts so immense that it blocks the sun? Early visitors to the western plains of the United States were so impressed by the huge herds of bison they saw that they sent home excited reports of these vast assemblies. Who would not marvel at a group of beetle larvae (the immature, growing stage) that join together to repel predators or at a group of caterpillars that cooperate to build a silken tent to live in? Scores of writers have extolled the virtues of the social honey bees. And how many children—adults, too—have been fascinated by the many organized activities that go on in a glass-sided ant farm?

Entomologists interested in insect groups have focused most of their attention on the highly organized societies of ants, bees, wasps, and termites, probably because of the obvious and inevitable comparisons between them and human society. Such comparisons have been made for millennia. In the Bible we read (Proverbs 6:6), "Go to the ant thou sluggard; consider her ways, and be wise." In *King Henry V,* Shakespeare wrote, "for so work the honey bees, creatures that by a rule of nature teach the act of order to a peopled kingdom."

Honey bees and ants, such as my leafcutters, as well as termites and bumble bees and some wasps, form the most complex and cohesive of all insect societies. Their study is an immense field, only touched upon in this book, but thoroughly covered by several authoritative and readable books: among them two on social insects in general by Edward O. Wilson, two on ants jointly written by Bert Hölldobler and Wilson and another by A. F. G. Bourke, two on honey bees by Karl von Frisch, a more recent one on honey bees by Thomas Seeley, one on all social bees by Charles Michener, and another on social wasps by Kenneth Ross and Robert Matthews.

Less attention has been paid to more or less unorganized groups and simple societies such as that of the eastern tent caterpillar, probably because the comparison with human society is less obvious. But from a biological point of view, these groups, the main focus of this book, are as interesting as the more complex societies, and there is much we can learn from them. Group living at any level is important in the ecological scheme of things, because it enhances survival.

In the 1920s in a tropical forest in British Guiana (now the independent nation of Guyana), Maud Haviland watched a group of tiny leaf beetle larvae ward off predators by "circling the wagons." The beetle larvae feed in a compact cluster on the upper surface of a leaf of a cecropia tree, and, according to Haviland, they form a tight circle with their heads all directed inward and their armored tail ends thrashing to and fro at the periphery of the circle as they nibble on the leaf. The last segment of a larva's body is armored, broadly expanded to form a hard, impenetrable, shovel-shaped shield. The chief enemies of the leaf beetle larvae, insect-eating stink bugs, lurk nearby, waiting for an opportunity to lunge forward and spear a larva on their long, thin, piercing-sucking beaks. As Haviland put it, "As long as the circle of [shields] is unbroken, the bug stands little chance, for his [beak] cannot penetrate their polished armour and he cannot reach the soft bodies beyond." But as the larvae consume more and more of the leaf, they must back away from the center of the circle, thus widening it and leaving broader gaps between their armored shields, although the circle remains intact to the end. Eventually a stink bug or two penetrates the defensive formation and spears a larva, but most of the larvae survive because they are almost fully grown and ready to escape the stink bugs by descending to the soil to metamorphose to the pupal stage of the life cycle, the transformation stage that bridges the larval and adult stages. Haviland did not mention the name of these beetles, but according to Pierre Jolivet and Trevor Hawkeswood, leaf beetles of the genus *Coelomera* occur in Guyana and the larvae are known to use this defense.

High in the Canadian Arctic, about 5,000 miles north of Guyana, a herd of muskoxen grazes on a windswept slope on Ellesmere Island, eating grasses and other tundra plants such as the prostrate Arctic willow, which the oxen expose by scraping away the thin covering of snow with their hooves. When a pack of wolves appears, the great, shaggy grazers—some weigh over 700 pounds—quickly come together in a defensive formation. According to an idealized account that has been passed down from author to author, the muskoxen use a ring defense much as do Maud Haviland's beetle larvae, gathering in a tight circle with the adults facing outward, and the calves inside the circle or huddled between the adults. But Anne Gunn, a biologist who studies muskoxen in the Canadian Arctic, told me that the defense is seldom that orderly. In response to a pack of wolves, muskoxen do gather in a tight bunch with the calves in a protected position, but the adults tend to mill about and jostle each other and seldom form a circle. Their massive heads are lowered and their sharp, down-curved horns—those of the cows are almost as formidable as those of the bulls—are formidable weapons, ready to gore or rip open any wolf that comes too close. From time to time, a bull dashes out to attack one of the wolves, trying to kill or disable it with a sweep of his horn. Although a pack of wolves sometimes manages to kill a lone muskox, the defensive formation of a herd is virtually impregnable to attack, and the wolf pack eventually becomes discouraged and moves away.

Maud Haviland's leaf beetles and muskoxen have discovered—quite independently of each other—that there is strength in numbers, that an individual can benefit by belonging to a group and participating in group actions. The similarity in the defensive tactics of these two unrelated animals, one a tiny insect and the other a huge mammal, is a striking example of convergent evolution, of different creatures independently evolving similar solutions to similar problems, in this case the ring defense or some approximation of it.

Other kinds of animals also form defensive groups when threatened. Among them are the nasute soldiers of certain species of termites, which form rows of protective flanks on either side of the columns of workers that leave the nest to forage for food. The head of a nasute, a name derived from the Latin for large nose, is drawn out into a long, forward-pointing tube that can squirt a toxic and very sticky substance onto any insect or other creature that threatens the column of foragers.

The predaceous larvae of owlflies (not really flies but relatives of the antlions and aphidlions) stay together in a defensive huddle during the first few days of their lives, forming a tightly packed cluster on a twig near the egg mass from which they hatched. Charles Henry described how they hang head downward on and above their empty egg shells, "overlapping like shingles in such a manner that only the heads and jaws of individual larvae are visible." They capture and eat small insects such as fruit flies and midges that happen to come close. But in response to ants or other predators, they raise their heads and rapidly snap their long, sickle-shaped jaws. After about a week, the owlfly larvae descend to the ground, separate, and henceforth lead a solitary existence as they sit hidden in debris waiting to ambush passing insects.

Young Colorado potato beetle larvae cluster together more or less tightly as they feed on a leaf, and as E. R. López and his coauthors noted, they defend themselves by moving closer together when approached by flies that can infest them with lethal parasitic maggots. At the approach of one of these flies, which the beetle larvae can detect from a distance of about 20 inches, they rear up on their hind legs in unison and flail their front legs, thereby fending off the flies about 45 percent of the time.

If the leaf beetle larvae in Guyana are ever outmaneuvered by some predaceous insect that evolves a way of broaching their defensive formation, they may be doomed to ultimate extinction. They may, however, evolve some new way to defend themselves. But if the hunted, the leaf beetle larvae in this case, evolve new ways to defend themselves, the hunters, in this case stink bugs or other predaceous insects, must evolve new ways to circumvent the new defenses of their prey, switch to other prey, or perhaps even face starvation and extinction. Such escalating evolutionary arms races between hunters and hunted, still going on today, are pervasive chapters in the history of the evolution of life on earth.

Evolution is the central and unifying concept of biology, the science of life, the science through which we seek to understand ourselves and our fellow creatures, to know where we came from, what we are, and how we are inextricably bound to all other life on earth. We cannot completely understand ourselves unless we understand nature, and we cannot truly comprehend nature unless we understand evolution. How, then, does evolution work?

The driving force of evolution is Charles Darwin's concept of natural selection, also known as the survival of the fittest. The success, or fitness, of an animal, not necessarily achieved by proficiency with fang and claw, is measured by the number of progeny that it leaves behind. Natural selection produces new species much as livestock breeders produce new breeds by artificial selection, by choosing only animals with desirable, heritable traits, traits that are fixed in the genes, to be the parents of the next generation. Similarly, natural selection tends to eliminate poorly adapted individuals and to favor the survival of those that are best adapted to their environment because they are better able to avoid its hazards or take advantage of the opportunities it offers. For example, a butterfly with a longer than usual tongue can sip from the blossoms of more kinds of nectar plants than can a shorter-tongued individual of the same species and may, therefore, be better fed than a shorttongued individual and thus likely to produce more progeny; a more deceptively camouflaged individual is less likely to be noticed by a predator and, therefore, more likely to survive to become a parent than is a less well camouflaged individual of the same species. In this way, nature selects the parents of the next generation, and if the advantageous characteristics of the parents are heritable, they will be passed to their children, grandchildren, and on into the distant future. Even if the selective advantage is small, a favorable characteristic will, given enough time, replace a less favorable one. There is no shortage of new heritable traits. They constantly arise as mutations caused by certain chemicals, radioactivity, ultraviolet light, cosmic rays, or by intrinsic factors in the genetic material itself. Some mutations are favorable and some are not. Natural selection tends to eliminate the unfavorable ones and generally preserves the favorable ones.

The fossil record, which tells the story of evolution, is incomplete. In other words, there are gaps that are often referred to as "missing links." If you view a fossil record as a chain, you can see that there are many missing links but that there are also many links that are not missing, often enough of them to form a respectable segment of chain, a complete or nearly complete and convincing record of how an organism evolved to become a new species.

Scientists refer to the *theory* of evolution, but they don't use this word in its everyday sense. To a scientist, a theory is a concept that is strongly supported by evidence and about whose validity there is very little doubt, such as the theory of gravity. A hypothesis, on the other hand, is an idea that is not as well supported by data, but that *can be tested* by experimentation or observation and that may some day be so strongly supported by data that it advances to the status of a theory. The proviso that it must be possible to test a hypothesis by experimentation and observation is all important. No scientist can take seriously a hypothesis or other form of explanation that is not testable. One of the great strengths of science is that scientists are—or should be—both conservative, cautious about accepting new theories, and open-minded, willing to consider new data. They recognize that their understanding of almost any matter can be improved through more experimentation and observation, as is the case with our comprehension of evolution. There is no doubt that living things evolved and continue to evolve, but much remains to be learned about the details of the process.

Three levels of natural selection are recognized: *selection on the individual,* as just described; *kin selection,* which enhances an individual's *inclusive fitness;* and the controversial but reasonable concept of *group selection,* selection that operates on the group as a whole rather than only on the individuals in a group.

Kin selection, a brilliant concept first expounded by William F. Hamilton, recognizes that any individual that sacrifices itself for the good of its relatives will enhance its own inclusive fitness by contributing to the survival of those relatives, which contain many of the individual's genes. A well-known example is the honey bee worker that dies defending the colony against a marauding mammal, injuring herself mortally when her barbed stinger penetrates the marauder's skin and tears away from her own body. As you know, the fitness of an individual is usually considered to be a matter of how many offspring it leaves behind. Offspring are the bearers of their parents' genes, the very genes that programmed the anatomical, physiological, and behavioral characteristics that promoted the survival and reproductive success of their parents, and it is through these offspring that these genes will be passed on to future generations. But, as Hamilton pointed out, the ultimate measure of an individual's evolutionary success is its inclusive fitness, which is measured by the survival of its genes, whether they are contained in its own body or in the bodies of relatives. Each parent gives each of its offspring half of its genes: thus brother and sisters share half of their genes; first cousins share one eighth of their genes with each other; and one quarter of a grandparent's genes appear in each grandchild.

As Elliott Sober and David Sloan Wilson pointed out in *Unto Others,* the concept of group selection has its roots in the writings of Charles Darwin, who invoked it sparingly and with a critical eye. But Darwin's successors "were less abstemious, invoking the process [of group selection] widely and often uncritically." V. C. Wynne-Edwards, for example, argued that animals come together in groups so that they can judge the size of their population, and if it is too large they can, as Sober and Wilson expressed Wynne-Edwards' idea, "restrain themselves from consuming food and reproducing, so that the population can avoid crashing to extinction." A backlash against this and other obviously improbable ideas gave the concept of group selection an undeserved bad name. Nevertheless, some observations and experiments with organisms ranging from bacteria to vertebrates cannot be explained without invoking group selection. The antipathy to group selection is gradually disappearing, but still persists in some quarters.

A good example of group selection occurs in the fungus-growing desert leafcutter ant of Arizona, *Acromyrmex versicolor.* A new colony of this species is founded by a group of several *unrelated* queens, usually in the shade of a tree that is likely to attract the foundresses of several other colonies. One of a colony's founding queens acts as the forager that collects the plant material on which the ants grow the fungus that is their only food. This queen becomes an ever more efficient forager with experience, and can be said to act "altruistically" for the benefit of the colony as a whole, because she leaves the nest and is thus more exposed to dangers such as predators than are the queens that stay in the nest to tend the fungus garden. But her specialized prowess determines the rate at which the new colony develops—a crucial factor because only one of the colonies under the tree survives, the one that first produces a contingent of adult workers. These first workers destroy the other colonies under the tree, raiding them to steal their brood, larval and pupal workers, which they raise as their own to augment their force of workers. Kin selection cannot explain the cooperation between the founding queens of a colony because, as genetic tests have shown, they are not related to each other. Group selection seems to be the only plausible answer.

Insect groups may be relatively small, consisting of anywhere from less than a dozen individuals, as in a feeding group of jack pine sawflies, to a hundred or more, as in a family of aphids or a sleeping aggregation of wasps. Others may be huge, including thousands or even millions or billions of individuals, as do swarms of periodical cicadas or the grasshoppers known as migratory locusts.

A group may form only because its members grow and develop synchronously, as do some mayflies, and thus appear together at the same time in the same place, or it may form because, as is the case with chinch bugs, a number of individuals gravitate to the same resource. Groups also form because members of the same species attract each other, as when thousands of fireflies gather in the same tree to attract others by flashing in synchrony. There may be little or no interaction between the members of a group, as is the case with mayflies and chinch bugs; there may be moderately complex interaction, as in a subsocial group of tent caterpillars; or there may be highly complex and all-pervasive interaction, as in the eusocial ("truly social") colonies of termites, ants, honey bees, bumble bees, and some wasps.

Even groups that are seemingly incidental and have little or no internal organization may, nevertheless, be favored by natural selection because they increase the probability of finding a mate or reduce the likelihood that an individual will fall to a predator because it is less vulnerable in a crowd. Thus if the individual benefits from being a member of an unstructured aggregation, natural selection may tend to perpetuate and enhance the formation of such aggregations, not by favoring individuals that are attracted to each other but, rather, by tightening the response to an outside synchronizing stimulus by eliminating stragglers that respond either too early or too late.

Groups of aphids consisting of from a few dozen to a hundred or more siblings form on their food plants because newly born aphids do not move far from the mothers that gave birth to them. In some species, an aphid that is attacked by a predator gives its nearby siblings warning by emitting a special odorous pheromone—a chemical signal released by one member of an animal species that provokes some physiological or behavioral response in another member of the same species.

Immature mayflies lead independent lives in the muck at the bottom of lakes or rivers, but because of their tightly synchronized emergence from the water, they occur together as swarms of flying adults, often in astronomical numbers. Their emergence is so synchronized because every individual is triggered to molt to the adult stage and leave the water on the same day and at the same time by the same extrinsic environmental stimulus or stimuli, perhaps by the length of the day or the temperature of the water. Dead mayflies sometimes accumulate under lights along the shores of the Great Lakes or the banks of midwestern rivers in great piles that may be several feet deep. The unfortunate insects are irresistibly drawn to the lights during the night and beat themselves to death.

Monarch butterflies are solitary during much of their adult stage and always as eggs, caterpillars, and pupae, but they survive the winter by migrating to form huge aggregations of adults clustered in trees in the mountains of Mexico or along the coast of California. In the 1970s a 5.5 acre overwintering site in Mexico was found to contain about 22.5 million monarchs, clustered so tightly that they obscured the foliage and made the trees on which they rested look orange rather than green.

The adult 17-year periodical cicadas—sometimes incorrectly called locusts—that emerged synchronously in the vicinity of Chicago in 1956 (brood XIII) numbered from well over 100,000 to about 1.5 million individuals per acre, as determined by Henry Dybas and D. Dwight Davis of the Chicago Natural History Museum. Since this brood extended over several hundred square miles, and there are 640 acres in a square mile, the total emergence consisted of many billions of cicadas. During the 17 years of their immature stage, these insects led solitary lives underground, sucking sap from the roots of trees.

True locusts, which are actually certain kinds of grasshoppers, are usually solitary and rather sluggish, but when they are crowded they enter a gregarious and highly active migratory phase. A swarm of migratory locusts that appeared in North Africa in the 1950s was estimated to include about 8 billion individuals and calculated to weigh 20,000 tons in the aggregate. Wherever the locusts landed, they ate almost everything that was green, leaving the land as barren as if it had been burned over.

Being part of a group can enhance an individual's fitness in a number of different ways, by helping it to satisfy, in one way or another, one or more of the three ecological imperatives that circumscribe the life of any living thing: it must eat and grow; it must avoid being eaten; and it must reproduce itself.

Group living can facilitate feeding. Just as a pack of wolves can subdue a large prey animal that one wolf could not overcome, perhaps a moose or a lone muskox, a column of army ants in South America or driver ants in Africa can overpower an insect or even a vertebrate that is too large for a single ant to handle. Some insects may even need to overpower the plants on which they feed, by joining forces to overcome special defenses that are effective against individual attackers. As John Byers noted, if enough bark beetles attack a tree at the same time, they can weaken it sufficiently to slacken the flow of resin that would otherwise drown them in the tunnels they excavate just beneath the bark.

A group of animals may also find food more quickly than can an individual. Birds, probably more so than other terrestrial animals, often benefit from foraging in flocks. A young bird may gain from associating with a more experienced flock member that is more adept at locating food, and the whole flock may benefit from the good luck of an individual that happens to make a lucky find. Honey bees, among the most highly social of all animal species, are the epitome of cooperative foraging. When a scout bee finds a new source of nectar or pollen, she returns to the hive and does a dance, known as the waggle dance, that communicates the distance and direction of the newly discovered patch of flowers to other foragers that cluster close to her and follow her as she dances. These followers, the new recruits, then proceed to the indicated food source, and, upon their return, they repeat the waggle dance, but only if they found the flowers to be productive. Thus poor food sources are ultimately abandoned and ever increasing numbers of workers are recruited to good sources. In this way, the attention of the colony is focused on a few productive patches of flowers.

Joining a group can help an individual avoid becoming a meal for a predator. Muskoxen, *Coelomera* beetles, termites, and owlflies put up active defenses, but there are other less obvious ways in which membership in a group tends to help individuals elude predators. For one, a predator that an individual does not notice might be discovered by another member of the group, who will then sound the alarm. Two pairs of eyes are better than one—as are two noses or two pairs of ears.

The mere presence of others—even if they are passive and neither give warnings nor participate in an active defense—decreases the probability that an individual will be taken by a predator. In effect, the individual gets lost in the crowd. Some insects, such as periodical cicadas and migratory locusts, are so numerous that the resident predators can eat only a small fraction of them. The appetites of the predators are thus saturated, so that there is only a small probability that any given individual will be eaten. A member of a group can benefit even if its com-