Social animals

Earth: Planet of the Ants

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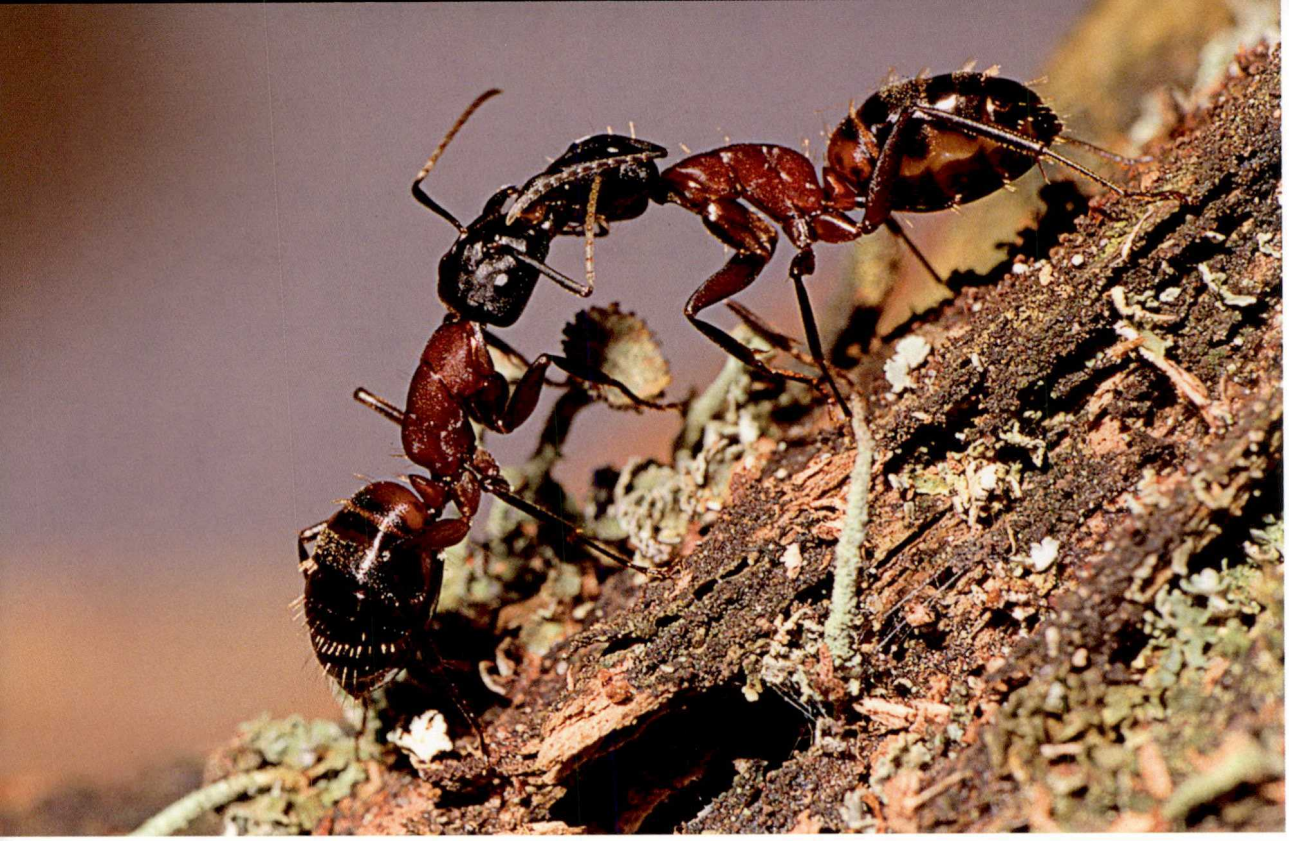
Even if we are indeed the most advanced social species on this planet, we must remember that the greatest system of cooperating individuals to be found on Earth was not created by humans

We usually perceive ants as laborious, hard-working creatures that are engaged in painstaking, endless toil, patient and highly sociable. This last trait is especially apt: ant societies do sometimes attain astonishing dimensions. In particular, some ant species form huge coalitions called „supercolonies." Within a supercolony workers and queens can move freely from one nest to another. Until recently, the largest known ant supercolony was found on the Ishikari Coast, on the Japanese island of Hokkaido. It was created by mound-building red wood ants of the species *Formica yessensis* and was composed of 306 million workers and more than a million queens, living in 45,000 interconnected nests. This sounds enormous, but two years ago an even vaster ant supercolony was discovered in south-western Europe. This supercolony, created by tiny imported Argentine ants of the species *Linepithema humile*, extends along about 6000 km of the Mediterranean coast - from Western Italy, around the Iberian coastline, all the way to the Atlantic coast of Portugal and north-eastern Spain. It consists of millions of interconnected nests inhabited by billions of individuals - the largest system of cooperating individuals so far identified on Earth.

Can scientists cope with studying such a complex insect society? Our knowledge of social phenomena observed in ants is already fairly advanced, but it is still very far from being complete. In particular, the neuro-

Marek W. Kozłowski

"Go to the ant, thou sluggard; consider her ways, and be wise; which having no guide, overseer, or ruler, provideth her meat in the summer, and gathereth her food in the harvest" – encourages us the Biblical Book of Proverbs (Proverbs 6: 6-8)



Tomasz Szczuka

Ants kissing? No, it's a specific form of contact, called "trophallaxis." During this act social insects exchange liquid food and chemical substances. Ultimately all members of the colony acquire a uniform mixture of substances, used to distinguish their nestmates from strangers

biological mechanisms underlying ant social behavior are only now starting to be unraveled.

Engineering society

One of the most important breakthroughs in modern biological thinking consists in the realization that information flow between the various levels of organization encountered in biological systems is multidirectional: from the molecular and submolecular level up to the social level, and vice-versa.

Our current research on ant social behavior carried out in the Laboratory of Ethology at the Nencki Institute of Experimental Biology focuses on two sets of problems, related to the two main directions of information flow between the various levels of organization encountered in insect societies. We are interested both in the social context's "downward" influences on the expression/suppression of behavior, and in the "upward" neurobiological mechanisms underlying the social ties and social cohesion that characterize ant colonies.

The profound influence of social context on the expression/suppression of various behavior patterns has already been reported in many social insect species. The main method employed in these studies consists in experimental modifications of some chosen element (s) of the social environment of the individual, such as colony size or age, the ratio of workers characterized by some particular morphological trait (s), and/or by a particular specialization, the presence/absence and number of queens, etc. Such manipulations are denoted by various terms: i.e. "pseudomutant technique", "demographic manipulations" and "social engineering."

We recently reported one striking example of particularly clear-cut and predictable effects of social context modifications on the expression/suppression of a single behavior pattern: the sequence of predatory behavior shown by common red wood ants of the species *Formica polyctena*. In ant colonies, mature workers mainly feed on carbohydrate food, and retrieval of animal prey is usually strictly related to the protein demands of queens (who need protein for egg production) and developing larvae. We were thus rather surprised to discover that *F. polyctena* workers may continue to retrieve dead insect prey not only when living in entire colonies, but also when reared in laboratory conditions in relatively small groups composed exclusively of mature workers. However, we observed complete sequences of predatory behavior only in groups exceeding size of about 35-45 individuals. In smaller ant groups predatory behavior was expressed in an incomplete form, terminating at the stage of transport, biting, or only exploratory contacts with the prey.

We also demonstrated that the behavioral effects of modifications in group size are wholly reversible. If a large group was split into several smaller ones, with the size dropping below the threshold level of 35-45 individuals, ants rapidly ceased to retrieve insect prey. But if these small groups were then fused once more into a single large group, the expression of the complete sequence

Marek W. Kozłowski

Ants do their best to free their nestmate captured by the larva of the ant--lion. Similar rescue actions were extensively studied as an example of social context influencing individual ant's behavior

of predatory behavior rapidly reappeared again. The phenomenon we described - flexible, reversible and highly predictable changes in the expression of predatory behavior induced by manipulating the group size - thus provides a convenient model for future research into the influence exerted by social context on behavioral, physiological and neurobiological processes in social insects.

Rescue your nestmate!

Another interesting finding concerning the effects of social context on the expression/suppression of ant behavior was reported in another of our recent studies, carried out in collaboration with Professor Wojciech Czechowski from the Museum and Institute of Zoology, PAN and Professor Marek Kozłowski from the Warsaw Agricultural University. We discovered that a particular behavior pattern, the so called nestmate rescue behavior, is expressed in ants of the species *Formica fusca* only in a heterospecific social context: in workers reared as slaves within a colony of another ant species.

What do we mean by "nestmate rescue behavior"? We observed that when an worker ant happens to be captured by a predator, a larva of the ant-lion (*Myrmeleon formicarius*) hiding inside a sand pit, its nestmates often rush to its rescue: they pull at it while it struggles with the attacker, and dig frantically in the sand gradually burying it. We observed such behavior in ants of the species *Formica sanguinea* and *Formica cinerea*, but never observed it in workers of yet another ant species, *Formica fusca*, living in normal, monospecific colonies. The situation was totally different, however, in the case of workers of *F. fusca* which had been captured at the pupa stage by ants of another species, *F. sanguinea*, and then reared by them as slaves in a mixed colony composed of workers belonging to these two species. Such enslaved *F. fusca* workers participated readily in rescuing their heterospecific nestmates, *F. sanguinea* workers. This finding implies that the behavioral repertoire of *F. fusca* still contains the nestmate rescue pattern, but such behavior is entirely suppressed in monospecific societies of this species. It only becomes expressed in the modified social context of a mixed colony. Sadly, when an enslaved *F. fusca* worker is captured by an ant-lion larva, its nestmates leave it on its own.

Passionate kisses

As has already been pointed out, we are interested not only in the downward influences of the social context on individual behavior, but also in processes that run in the opposite direction. Our current research devoted to the neurobiological mechanisms underlying social ties between nestmates and social cohesion in ant colonies is focused on the ethopharmacological analysis of the neurochemical mechanisms underlying trophallaxis. This specific form of social contact, widespread in insect societies, involves a close mutual contact of mouthparts between two or more individuals, resembling a "kiss." During such trophallactic contact, the partners exchange liquid food and/or so-called cuticular hydrocarbons, specific compounds synthesized by each adult individual and then stored in the so called postpharyngeal glands located in its head. Via trophallaxis and, to a lesser degree, via other forms of social contacts these compounds are exchanged among colony members, ultimately

forming a uniform mixture common for the colony. During subsequent grooming, this mixture is spread all over the body surface of the ant, and then acts as a so-called "colony visa," allowing ants to distinguish their nestmates from individuals that come from alien colonies.

Extasy of an ant

In his classical book *The Life of the Ant*, the famous Belgian writer and philosopher Maurice Maeterlinck speculated that ants engaging in trophallaxis experience feelings of "extasy", representing the equivalent of orgasmic experiences. This is an interesting idea: as is well known, in some vertebrates sexual contacts do play an important role not only in reproduction, but also in social bonding. Unfortunately, these speculations cannot be subjected to direct, rigorous experimental testing. However, we may try to shed some light on the question of whether trophallactic contacts between nestmates are associated with neurobiological processes which might correspond to the phenomenon of "social reward," so far studied only in vertebrates.

In a series of experiments carried out in collaboration with the team of Professor Alain Lenoir from the Francois Rabelais University in Tours (France), and with the team of Professor Abraham Hefetz from Tel Aviv University (Israel), we investigated the behavior of workers of several species of carpenter ants of the genus *Camponotus* using the method of so-called "reunion tests," during which two ants from the same colony were reunited after a period of social isolation. Such ants showed increased readiness to engage in trophallactic contacts, even if they had had unlimited access to food during the whole isolation period. We dubbed this phenomenon "isolation-induced trophallaxis." In subsequent experiments we demonstrated that isolation-induced trophallaxis may be significantly reduced by abdominal injections of octopamine, a biogenic amine involved in controlling many aspects of insect physiology and behavior.

Why does octopamine reduce isolation-induced trophallaxis in ants? One of the several possible explanations for this finding is related to the fact that octopamine is known to play a crucial role in the reward system involved in the associative olfactory learning of another social insect, the honeybee. It is thus possible that octopamine reduces isolation-induced trophallaxis in ants by mimicking the possible octopamine-mediated rewarding effects of their trophallactic interactions with nestmates. The octopaminergic system may thus be involved in the phenomenon of so-called social reward, so far described and analyzed only in vertebrates. However, it must be stressed that this is only one of the possible hypothetical explanations for our data, and the issue remains open for further research.

A famous story, dating from medieval times, tells us how the great conqueror Tamerlane, defeated by his enemies, had to seek shelter in a deserted manger while enemy troops searched the countryside. As he was laying there, Tamerlane watched a tiny ant carrying a large grain. She tried to carry it up the wall, but kept falling down. However, she did not give up and after her 70th try, the ant was at last successful! Her perseverance inspired Tamerlane with new hope: he decided to resume his fight, and in the end he triumphed over his enemies. We hope that by following this example we will finally unravel many futher secrets of ants' social relations. ■

Further reading:

Boulay R., Soroker V., Godzińska E. J., Hefetz A., Lenoir A. (2000). Octopamine reverses the isolation-induced increase in trophallaxis in the carpenter ant Camponotus fellah. *Journal of Experimental Biology* 203, 513-520.

Czechowski W., Godzińska E.J., Kozłowski M. W. (2002) Rescue behaviour shown by workers of Formica sanguinea Latr., F. fusca L. and F. cinerea Mayr (Hymenoptera: Formicidae) in response to their nestmates caught by an ant lion larva. *Annales Zoologici* 52, 423-431.

Szczuka A., Godzińska E. J. (2004). The role of group size in the control of expression of predatory behavior in workers of the red wood ant Formica polyctena (Hymenoptera: Formicidae). *Sociobiology* 43, 295-325.

Marek W. Kozłowski

Worker ants separated from the entire colony demonstrate only incomplete predatory behavior