Doklady Biological Sciences, Vol. 375, 2000, pp. 644–646. Translated from Doklady Akademii Nauk, Vol. 375, No. 4, 2000, pp. 571–573.

GENERAL BIOLOGY

Effect of Red Wood Ants on Carabid Behavior: Experimental Studies at the Individual Level

Zh. I. Reznikova and E. A. Dorosheva

Presented by Academician V.K. Shumnyi March 21, 2000

Received March 21, 2000

Being not only an active predator, but also a real competitor with predatory herpetobionts such as spiders and various species of beetles, the red wood ant *Formica polyctena* has a great impact on other members of invertebrate communities. The location of anthills and foragers' paths pervading ant territories largely determines the spatial distribution of herpetobionts [1–4]. Carabid beetles move swiftly and consume very diverse foods. Their behavior exhibits high plasticity [5–7]. It is natural to expect that they are capable of promptly reacting to interaction with ants, the more so as the mortality among beetles once bitten by ants is significantly higher than that of intact specimens [8]. However, the behavioral aspects of carabid interaction with ants were addressed only in laboratory experiments by Gridina [9], which provided just a general description of carabid behavior, without revealing the specific characteristics of their avoidance response. The data from that study do not allow us to compare carabids with other predator herpetobionts in this respect. Presented in this work are the results of (1) field experiments in which we marked beetles and mapped their movements and (2) laboratory experiments in which ants were allowed to interact with carabids in mazes. This is the first report indicating that not only ants, but also carabids use specific behavioral strategies when interacting with their competitors and are capable of learning to avoid encounters.

Experimental setup. All results were obtained during 1996–1998. Field experiments were carried out in the territory of a *Formica polyctena* colony in a woodland, namely, in the park zone of Akademgorodok (Novosibirsk). The spatial distribution of carabid beetles in the ants' territory was studied in ten-day-long surveys using 30 Barber's soil traps placed at various distances from the anthill and foragers' paths. We distinguished three zones occupied by the ant colony: central (zone I, in the closest vicinity of the hill and foragers' paths), intermediate (zone II), and peripheral (zone III). In laboratory experiments, we used two-arm mazes, in one of which we tied an ant with a thin thread. A beetle was attacked if it approached the tethered ant. The beetle was also tested in a control maze containing no ant. A total of 145 beetles were tested, and the relationships between various elements of their behavior were analyzed. Mazes with electrodes in both arms were used to study whether carabid beetles were capable of learning to avoid danger or to find shelter. A weak electric current was supplied through one of the electrodes, to which a low voltage was applied. A total of nine specimens belonging to three species were studied using this maze technique. We also used mazes containing only positive stimuli, i.e., mazes providing a possibility of sheltering. The specimens (n = 16) tested in such mazes belonged to six species. In field experiments, we released carabids of three species (n = 38) near ant paths and recorded their trajectories and responses to encounters with ants. The procedure was repeated five times at half-hour intervals. A total of 380 trajectories were mapped. Their sinuosity was estimated as a ratio of the distance between its start and end points to the trajectory length (the sinuosity coefficient, SC; see [10] for details). We also recorded the speed at which each beetle moved. Reference data were obtained in control plots that were beyond the range of influence of ants and were covered with a similar substrate.

Carabid distribution over the ant territory as a basis for topic competition. Carabids of three mixophytophagous species (*Amara nitida*, *Harpalus smaragdinus*, and *H. pygmaeus*) and four predatory species (*Pterostichus magus, P. niger, P. oblongopunctatus,* and *Carabus regalis*) were observed in the ant territory. Only large *Carabus regalis* beetles, the largest of these seven species, reached zone I. Most of the captured beetles of each species were from traps placed in zone III. The deeper into the ant territory, the lower the beetle density. On average, *Pterostichus* beetles were captured at frequencies of 38, 5.2, and 0 specimens per 10 trap-days in zones III, II, and I, respectively (pooled data for two species). The *C. regalis* distribution was as fol-

Institute of Systematics and Animal Ecology, Siberian Division, Russian Academy of Sciences, ul. Frunze 11, Novosibirsk, 630091 Russia

Novosibirsk State University, ul. Pirogova 2, Novosibirsk, 630090 Russia

0012-4966/00/1112-0644$25.00 © 2000 MAIK "Nauka / Interperiodica"

lows: 1.5, 1.0, and 0.33 specimens per 10 trap-days in zones III, II, and I, respectively. For *A. nitida*, this distribution was 0.5, 0.06, and 0. Interestingly, the percentage of specimens captured during the periods of ant daytime activity averaged 33% for genus *Harpalus* beetles and 67% for *A. nitida*. Carabids of the genus *Pterostichus* were mostly nocturnal. However, as they were very abundant, even those of them that remained active during the daytime were more abundant than any of the other carabid species in the ant territory. It is likely that ants caused carabids to retreat to the periphery of their colony, as we observed previously in other situations [1–4].

Specific elements of carabids' behavior allowing them to avoid encounters with ants. The learning ability of carabids proved to be high in simple mazes. However, it became clear only from ant-interaction experiments how diverse their behavioral patterns could be. When tested in mazes with electrodes, beetles did not avoid the dangerous arm. However, when coming into that arm, they stopped in front of the electrode and turned back. This behavioral pattern was observed immediately after the second session and from then onward in 89% of the *C. regalis* specimens tested, 92% of the *P. magus* specimens, and 100% of the *P. niger* specimens. In mazes with only positive stimuli, all specimens visited the shelter-containing arm during the second and all subsequent sessions four to six times more often than the other arm. After one or two conflicts, most beetles learned to avoid encounters with the tethered ant. They either stopped coming into the arm where an ant was tethered or began to behave differently when approaching the source of danger. In these experiments, 14 out of 31 *C. regalis* specimens, 32 out of 52 *P. magus* specimens, 9 out of 20 *P. niger* specimens, and 30 out of 42 *P. oblongopunctatus* specimens were able to learn. Preliminary experiments with the herbivorous *Amara* suggested that these beetles, unlike carnivorous carabids, could not learn to avoid ants. We distinguished the following strategies used by beetles capable of avoidance learning: (1) trying to bypass the ant; (2) turning away from the ant after touching it with antennae; (3) turning back by a distance of 1 cm or greater from the ant; (4) avoiding coming into the arm with the ant inside; and (5) freezing in the least vulnerable posture. Large beetles (*C. regalis*, *P. niger*) were unlikely to step aside to let the ant pass, which was the preferred strategy in the small *C. regalis* and *P. oblongopunctatus*. This strategy was effective in natural environments but not in the maze, where it was used less frequently. Unlike strategy 1, strategies 2 and 3 were used in the maze more often; in addition, strategies 4 and 5 appeared. The smaller the carabid and the closer its size to the ant size, the more diverse the set of avoidance strategies displayed by specimens of this species. Using Student's *t*-test, we compared the fractions of specimens that used each particular strategy in *C. regalis, P. niger, P. magus*, and *P. oblongopunctatus*. This analysis revealed that the sets of preferred strategies were species-specific. The species significantly differed in the relative rates at which they used specific strategies. The only exception was strategy 3, which was observed equally frequently in all species. We are inclined to interpret these data as reflecting species-specific differences in carabid behavior, rather than the distinctions between carabid life forms (for their definition see [11]). In fact, while belonging to the same life form of zoophagous stratobionts, *P. magus* and *P. oblongopunctatus* significantly differed in the use of behavioral strategies. Our previous study [12] was the first in which insect antennal contacts were described. Such contacts suggest that ants and small beetles are capable of recognizing each other as specific objects (like dogs and cats; see [12]).

In field experiments, different patterns of carabid movements were observed in areas with high and low dynamic densities of ants. In the ant-controlled territory, the beetles made more turns (which corresponded to lower SC values), ran more quickly, and stopped only rarely. These differences in the beetles' behavior were species-specific. The SC characterizing *C. regalis* trajectories changed slightly, from 0.85 to 0.77. The SC changes in the other species were greater. *C. regalis* are large beetles. They did not bypass ants; rather, they crossed ant paths at a high speed, taking advantage of their relatively safe external body covering (compared with that in other species). Larger changes in the SC were observed in smaller species: from 0.84 to 0.57 in *P. oblongopunctatus* and from 0.87 to 0.62 in *P. magus*. The average speed of movement increased from 7.1 ± 5.3 to 16.3 ± 3.6 cm/s in *C. regalis* and from 4.8 ± 3.5 to 11.7 ± 5.4 cm/s in *P. oblongopunctatus*. The percentage of time *P. oblongopunctatus* beetles spent without moving in the ant territory was 5% (versus 11.5% in control plots). There were pauses in the running activity of *C. regalis* in control plots; however, in the ant territory, the beetles moved without stopping. Unlike these two species, *P. magus* specimens spent more time without moving in the ant territory (38 versus 27.5%), because their avoidance behavior included freezing, a response in which they stayed motionless, with antennae and legs tucked underneath their bodies. However, this strategy was successful only at relatively low ant densities. For *Carabus*, the optimal strategy in "crossing the road" was to increase the speed of their movement, whereas *Pterostichus* used a combination of strategies. If the beetle was able to learn, it ran quickly and turned abruptly when bypassing ants. This behavior resulted in no more than two bites in five tests. The specimens that were unable to learn were bitten up to six times. Therefore, behavioral flexibility of predatory carabids and their individual learning capacities make the basis allowing them to avoid encounters with ants.

ACKNOWLEDGMENTS

This work was supported by the Russian Foundation for Basic Research (project no. 99-04-49713) and the

Program "Universities of Russia" (project no. 991-049).

REFERENCES

1. Cherix, D. and Bourne, J.D., *Rev. Suisse Zool.*, 1980, vol. 87, pp. 955–973.
2. Savoläinen, R., Vepsäläinen, K., and Wuorenrinne, H., *Oekologia*, 1989, vol. 81, pp. 481–486.
3. Suvorov, A.A., *Osobennosti zhivotnogo naseleniya pochv Moskovskoi oblasti* (Specific Features of Animal Soil Biota of the Moscow Oblast), Moscow: Nauka, 1994.
4. Rybalov, L.B., Rybalov, G.L., and Rossolimo, T.E., *Usp. Sovrem. Biol.*, 1998, vol. 118, no. 3, pp. 313–322.
5. Sergeeva, T.K., Trophic Relations, Structure, and Mechanisms of Resistance in the Communities of Rapacious Invertebrates, *Doctoral (Biol.) Dissertation*, Moscow, 1994.
6. Lövei, G.L. and Sunderland, K.D., *Annu. Rev. Entomol.*, 1996, vol. 1, no. 41, pp. 231–256.
7. Gryuntal', S.Yu., *Byull. Mosk. O-va. Ispyt. Prir., Otd. Biol.*, 1998, vol. 103, no. 3, pp. 25–33.
8. Kolbe, W., *Entomol. Z.*, 1969, no. 7, pp. 269–280.
9. Gridina, T.I., *Memor. Zool. Acad. Pol. Sci.*, 1994, vol. 48, pp. 91–97.
10. Reznikova, Zh.I., *Mezhvidovye otnosheniya u murav'ev* (Interspecific Relations in Ants), Novosibirsk: Nauka, 1983.
11. Sharova, I.Kh., *Zhiznennye formuly zhuzhelits (Coleoptera, Carabidae)* (Life Forms in Ground Beetles; Coleoptera: Carabidae), Moscow: Nauka, 1981.
12. Reznikova, Zh., Novgorodova, T., and Dorosheva, E., Abstracts of Papers, *Proc. Annu. Meeting of the Eur. Sociobiol. Soc., Moscow, 1998*, Moscow: Russian State Univ. for Human, 1998, pp. 18–19.