source of carbon with low δ^{13} C values in the gold mines, especially as bacteria may have lived and died in the hydrothermal systems that eventually degassed during metamorphism to give rise to auriferous fluids. Yet the discussions of carbon in carbonate from Archaean gold lode deposits usually ignore any biological effects.

The debate will continue: perhaps soon the paths of CO₂ movement will be mapped better and we will understand much more about the history of CO. degassing. The new work will be useful for

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finding gold, which should be profitable. More than that, in revealing the way in which the Earth manages its carbon budget, the work will aid our understanding of the history of the biosphere and the continents.

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Evolutionary biology Learning in parasitic wasps

H.C.J. Godfray and J.K. Waage

ABOUT one out of every ten forms of metazoan life is an insect parasitoid, most of these being parasitic wasps. Insect parasitoids lay their eggs in, or on, the bodies of other insects which act as food for their developing offspring. Parasitoids and their hosts are small animals living in a very complex vegetational environment: the chances of finding hosts by random searching are remote. As a consequence, parasitoids have evolved a wide array of searching strategies, often making use of cues that indicate the presence of a host or a suitable environment for a host. Although it was once thought that these strategies involved innate responses of great specificity, evidence is now that parasitic wasps accumulating frequently learn from their experiences. On page 257 of this issue¹, Lewis and Tumlinson provide an excellent example of how wasps use their experience to improve searching strategies.

The commonest type of cues used by

parasitic wasps are chemical, although examples are known of the use of visual, vibrational and auditory cues (see refs 2,3 for reviews). Chemicals used by searching, parasitic wasps can be volatile attractants which lead them to areas containing hosts, or non-volatile arrestants, usually called 'contact' chemicals, which cause them to concentrate movement in these areas. Attractant chemicals are often produced by the host themselves, usually incidentally in their frass (excrement) or salivary secretions, but sometimes the wasps subvert the host's own chemical communication system by homing in on sexual or aggregation pheromones. Volatiles produced by sources associated with the host, such as its food plant, can also provide attractant stimuli, and some parasitoids are capable of sniffing out the infested plants in a crop, because of chemical changes in the plant caused by the host.

The value of certain stimuli to parasitic



Left, female Microplitis croceipes wasp following an odour plume to locate the host caterpillar feeding on a bean plant leaf. Right, chemicals (first detected as odours in the air, later on plant surfaces) lead the wasp to sting its caterpillar host. As the wasp stings, an egg is oviposited into the caterpillar which will ultimately kill it. (Courtesy of Lewis and Tumlinson/Tim McCabe.)

wasps varies depending on local conditions. Imagine a wasp that parasitizes several different host species. The abundances of the host species will change both spatially and over time, so that an associational cue, such as the host's food plant, will vary in its information content. The wasp can obtain some information about the local distribution of hosts by noting the volatile stimuli in the environment where she developed. Perhaps this learning takes place in the larval stage, but it is more likely to occur immediately after the adult wasp emerges from the pupa. The wasp may also note which volatile chemicals are present in an area where it has found hosts, and subsequently follow these attractants in the hope that they will lead to further hosts.

There have been several studies on learning in parasitic wasps (see ref. 4 for review), one of the best being the work of Vet and her collaborators⁵⁻⁷ on parasitic wasps attacking Drosophila larvae, which develop in fungi and fruit. One species of wasp is normally attracted to the odour of decaying fungi, but if cultured on a yeast medium, the adult wasps show an increased attraction to the yeast odour characteristic of rotting fruit. The attraction is substantially increased if the wasps encounter and parasitize hosts in a yeast medium. This learning suggests that parasitoids can shift over several generations between the Drosophila faunas of fungi and fruits: the searching strategy is an example of a culturally transmitted trait.

In their paper in this issue, Lewis and Tumlinson describe for the first time an example of a wasp learning to associate volatile stimuli, not with its place of development or the host itself, but with the host's frass, a very strong indication of the presence of the host (see figures). The wasp innately recognizes a non-volatile compound in the frass and then associates it with any volatile present, which it uses as attractants in the future. Lewis and Tumlinson show that even completely alien substances such as vanilla can be used by the wasp. The wasp used in their study attacks a host with a wide variety of food plants. The most likely advantage of this behaviour is that it enables the wasp to learn the food plants that, at that time and place, are being most used by the host. \Box

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