

Table 3. Male *O. cincta* spermatophore predation. The treatments were compared with mean rank values of a Kruskal-Wallis test ($H = 18.85$, $p > 0.001$)

| Treatment | Predation (%) | Mean rank | No. of males tested |
|-----------------|---------------|-----------|---------------------|
| Control | 59.0 | 26.7 | 15 |
| Reproductive | 95.0 | 11.6 | 15 |
| Nonreproductive | 41.3 | 30.7 | 15 |

groups have overcome negative genetic effects of inbreeding, since they will have had at least ten generations (two generations per year⁹) in a five-year-old heap of twigs. Hence, inbreeding can be favored within aggregates of Collembola and they can maintain adaptations to the local habitat as long as it exists.

Evidently, a female *O. cincta* can actively choose a mate, but how can a male maximize his chances of fertilizing eggs? Male Collembola have been observed to eat spermatophores, but the behavior has been interpreted in terms of the removal of old ones⁵. We tested whether this behavior was directed towards their own spermatophores or those of others.

O. cincta males were collected in the field, placed individually in cups ($d = 4$ cm, $h = 3$ cm) and reared at 15 °C. Males that deposited spermatophores within 24 h before every test situation were classified as reproductive; others were considered nonreproductive.

First, as a control treatment, the male was removed and five spermatophores were moved within the rearing cup and placed along the periphery, while the rest were destroyed. The male was returned and the remaining spermatophores counted after 20 min. Second, five spermatophores, less than 24 h old and produced by another

male, were placed along the periphery of the rearing cup. Third, the procedure was repeated using the same males but in a nonreproductive instar. The same 15 animals were used in all three treatments and the treatment sequence for a single animal was randomized.

Reproductive *O. cincta* males discriminated between spermatophores of different origin by preferentially destroying spermatophores of other males (table 3). The fact that female *O. cincta* hardly ever eat spermatophores and the comparatively low rate of nonreproductive male 'grazing' on spermatophores both indicate that Collembola do not need spermatophores for nutritional reasons. The differential sperm predation could rather be considered as a kind of sperm competition. As such it could be an important mechanism to increase male fitness.

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Two related butterfly species avoid oviposition near each other's eggs

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Summary. Some butterfly species avoid egg-laying on plants which already bear conspecific eggs, and thus reduce food competition between their offspring. In two *Pieris* species the females produce in their accessory glands an oviposition-detering pheromone (ODP), which is combined with the egg during oviposition. The ODP collected from eggs or accessory glands of *P. brassicae* inhibits oviposition by *P. rapae* and vice versa. The ODP of either species stimulates tarsal receptors in both species. The antennae of the two pierids respond to the volatiles of their own and each other's eggs. Thus the ODPs of the two species may reduce not only intraspecific, but also interspecific food competition between their larvae.

Key words. Oviposition deterring pheromone (ODP); butterflies; pierids; oviposition; interspecific effects.

The early observation that the large white butterfly (*Pieris brassicae*) oviposits on a host plant 'not without the.... precaution of ascertaining that it is not pre-occupied by the eggs of some other butterfly'¹ remained un-

noticed for more than 100 years. Recently, it was found that a chemical associated with the eggs of this insect inhibits oviposition in conspecific females². This water soluble oviposition deterrent pheromone (ODP) is pro-

Table 1. Behavioral and electrophysiological responses of *Pieris brassicae* and *P. rapae* to egg washes, accessory gland and fat body washes (control) from both species

| Stimulus | <i>P. brassicae</i> | | | <i>P. rapae</i> | | |
|-------------------------------------|---------------------|------------|-----------------|-----------------|------------|-----------------|
| | N | ODP-index | B-hair response | N | ODP-index | B-hair response |
| Egg wash <i>P. rapae</i> | 8 | 54% * | ++ ¹ | 9 | 72% * | ++ |
| Accessory gland <i>P. rapae</i> | 3 | 67% * | + | 10 | 20% * | ++ |
| Fat body <i>P. rapae</i> | | not tested | 0 | 4 | -8% | 0 |
| Egg wash <i>P. brassicae</i> | 9 | 85% * | ++ | 11 | 84% * | ++ |
| Accessory gland <i>P. brassicae</i> | 4 | 79% * | ++ | 2 | 45% * | ++ |
| Fat body <i>P. brassicae</i> | 7 | 14% | 0 | | not tested | 0 |

¹ ++, +, 0: strong, medium, and no response, respectively. *p ≤ 0.01 (Chi-square test).

duced in the female's accessory glands, and is secreted onto the eggs during egg deposition³. The ODP promotes an even distribution of egg batches in this species, thus decreasing the risk of food competition between conspecific larvae. The ODP is detected by antennal olfactory receptors³ as well as contact chemoreceptors located on the tarsi of female butterflies³⁻⁵.

Adults of the small white butterfly (*Pieris rapae*) which, in contrast to *Pieris brassicae*, lay their eggs singly, have also been found to coat their eggs with an ODP⁶. Since in Europe the two species occur together and depend largely on common host plant species, i.e. cabbage and some other cruciferous plants⁷, it seemed interesting to determine whether the two *Pieris* species respond to each other's ODP.

The ODP of each species was collected by gently shaking 500 eggs in 1 ml of methanol or water for 5 min. The egg wash was sprayed on a cabbage leaf which, together with a control leaf, was offered to 2-5 ovipositing females in a cage. From the distribution of eggs an ODP index can be calculated, using the formula: % deterrence = (A - B) × 100 / (A + B), in which A and B represent the numbers of eggs (or egg batches) laid on control and treated leaves, respectively. An ODP index of 100% indicates that the butterflies have laid all eggs on the control leaf, whereas 0% indicates no preference. Extracts from accessory glands were prepared by bathing 2 freshly excised paired glands in 1 ml of water for 2 h. As a control a comparable amount of undamaged fat body tissue was bathed in 1 ml of water. Electrophysiological experiments were conducted to test tarsal chemosensilla, the so-called B-hairs⁸, for their sensitivity to ODP, using the tip recording technique⁹. Antennal responses to egg volatiles were measured by recording electroantennograms (EAGs)¹⁰.

Behavioral as well as electrophysiological tests showed that the two pierids react to each other's ODP (table 1). When the behavioral responses to the conspecific and heterospecific egg washes are compared, no significant differences can be found in either species. The results of tests using accessory gland extracts confirm the conclusion that both species react to the heterospecific ODP. (The low behavioral response of *P. rapae* to its own accessory gland extract is at present unexplained, but it

should be noted that in electrophysiological tests this extract also produced strong responses).

When stimulated with egg washes or accessory gland extracts from either species the tarsal B-hairs of both *Pieris* species show marked neuronal activity predominantly in one receptor cell. Since these responses are dose-dependent¹¹, this receptor can be regarded as an ODP-sensitive receptor. It can be distinguished from the glucosinolate receptor^{4,8}, the sugar receptor (note; in contrast to an earlier report⁸ both *Pieris* species have a sugar receptor in these sensilla) and a salt-sensitive cell. The ODP-sensitive receptor reacts not only to the ODP of the two pierids, but also to a plant-derived strophanthidin glycoside, known to be a potent oviposition deterrent⁵. Therefore this receptor seems to function as a general detector of oviposition deterring compounds, rather than as a specific ODP-receptor.

When stimulated with air which had passed through a glass tube containing eggs of one of the two species, the antennae of both pierids show dose-dependent EAG responses to their own and to the other species' egg volatiles, whereas no responses were observed to eggs of another cabbage-infesting lepidopterous species, *Mamestra brassicae* (table 2).

The fact that *P. brassicae* and *P. rapae* react to each other's ODP may indicate that the ODPs of the two species are chemically related or even identical. This can only be verified when the chemical structure of the two pheromones has been elucidated. It may be noted that although the two pierids are classified in the same genus, they are probably only distantly related to each other¹². Epideictic pheromones serve to reduce the risk of conspecific competition with regard to food resources¹³. In the case of *P. brassicae*, which lays its eggs in batches of

Table 2. Electroantennogram (EAG) responses (± SEM) to eggs of two pierids and to eggs of *Mamestra brassicae* as a control. As a standard stimulus 0.1% cis-3-hexen-1-ol in paraffin oil was used. EAG responses to egg volatiles are expressed as % of the response to the standard stimulus

| Stimulus | <i>P. brassicae</i> | | <i>P. rapae</i> | |
|---|---------------------|------------|-----------------|------------|
| | N | EAG | N | EAG |
| 0.2 g eggs of <i>P. brassicae</i> | 20 | 17.1 ± 1.3 | 38 | 12.1 ± 0.9 |
| 0.2 g eggs of <i>P. rapae</i> | 20 | 19.5 ± 1.8 | 43 | 10.3 ± 1.1 |
| 0.4 g eggs of <i>Mamestra brassicae</i> | 4 | 1.6 ± 1.1 | 8 | 0.1 ± 0.1 |

up to 150 eggs (average batch size 20–40), the importance of an avoidance mechanism seems obvious. For *P. rapae*, which lays eggs singly and whose larvae remain considerably smaller than those of *P. brassicae*, the need to avoid conspecifics may be less important. On the other hand *P. rapae* may benefit considerably from the capacity to perceive *P. brassicae* egg clutches. The ability of *P. brassicae* to detect the presence of *P. rapae* eggs may appear less functional, but it should be realized that the described responses were obtained with washes from large numbers of *P. rapae* eggs. Moreover, *P. rapae* larvae have been observed to attack and feed upon *P. brassicae* larvae in the presence of their normal food¹⁴. The observation that *P. rapae* butterflies originating from the USA produce the same amount of ODP as females from European stock⁶, in spite of the fact that the American population has existed for more than 100 years in the absence of *P. brassicae*¹⁵, suggests that the ODP serves primarily to deter conspecific females from oviposition close to eggs deposited earlier. The heterospecific effects of the ODPs of the two pierids is, to our knowledge, the first case described in Lepidoptera. These substances seem to serve not only their primary function of promoting an even distribution of conspecifics over available host plants, but also the secondary function of promoting an even distribution of larvae across species. Since the ODP of *P. brassicae* also acts as a kairomone to a parasite¹⁶, this semiochemical

plays a role in an ecological web, involving at least three insect species at two trophic levels.

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Magnetic compass orientation in the subterranean rodent *Cryptomys hottentotus* (Bathyergidae)

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Summary. To test whether mole-rats *Cryptomys hottentotus* were able to use the magnetic field for orientation, laboratory experiments were conducted which were based on the animals' spontaneous tendency to build their nests at the same position in a circular arena. In the local geomagnetic field, the animals preferred the SE-sector. When magnetic north was turned by 120° or by 180°, the mole-rats changed their nest position accordingly. This clearly shows that they can use the magnetic field for direction finding.

Key words. Magnetic compass orientation; mole-rat; *Cryptomys*; subterranean rodents.

The African mole-rat, *Cryptomys hottentotus* (Bathyergidae), a subterranean rodent, digs the longest, permanent underground systems produced by any animal studied so far^{1,2}. In contrast to the radially arranged burrows of many other subterranean mammals, the burrow systems of *C. hottentotus* tend to be linearly arranged, with the nest at one end and a single, long main tunnel, 200 m or more, which forms the major axis¹. In most of the burrows analyzed so far the main tunnel extended roughly southward^{3,4} (and own observations). Each system is

constructed, occupied, extended, and maintained over many years by a eusocially living family group of up to 25 members⁵.

The remarkable ability of *C. hottentotus* to maintain its course while digging long, straight tunnels³ gave rise to speculations on possible orientation cues. Air currents^{6–8} and acoustic cues^{3,9,10} have been discussed; internal mechanisms, like kinesthetic sense and/or vestibular cues^{11,12} may also be considered, yet neither of these mechanisms seems to be able to provide a satis-