development, feeding preference, and food consumption and utilization of tobacco.

In hypersensitive hosts the physiological reactions to TMV infection are more drastic than those with systemic infections, as reflected in the increase and accumulation of toxic quinones at the site of TMV multiplication[24]. Thus, different results might be obtained if hypersensitive host/TMV combinations had been evaluated. The conversion of nicotine to nornicotine[17], if indeed it occurs, may be why the systemic infection of tobacco by TMV does not affect tobacco hornworm larvae. Hare[25] reported that growth rates of fourth instar hornworms were reduced by 27 and 16% when reared on locally and systemically protected tobacco leaves, respectively. These results are not in agreement with those from our study. However, several factors are different between studies. Although not explicitly stated, Hare[25] implies that his experiments were conducted with a hypersensitive tobacco variety, as appears to be in the case in his previous experiments[5]. In addition, differences in levels of TMV infection between locally and systemically protected tobacco leaves are not clear nor is it possible for us to determine if Hare's[25] systemically protected leaves are comparable to our inoculated plants.

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Mate choice and male competition in *Orchesella cincta* (Collembola)

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Summary. Both male and female *Orchesella cincta* (Collembola) were able to discriminate between spermatophores of different origin. Females chose spermatophores deposited by closely related males while males preferentially destroyed spermatophores of other males.
Key words. Mate choice; mating; sperm competition; kin recognition; Collembola.

Sexual selection theories usually assume that female mate choice is based on male fitness expressed by secondary sexual characters. It has also been suggested that characters expressing genetic relatedness between mates may determine the choice[1,2]. An optimal level of inbreeding and outbreeding will strike a balance between the cost of reduced individual heterozygosity and the benefits of maintaining associations of alleles of individuals in a locally adapted population[3,4].

We have investigated whether the Collembola *Orchesella cincta* L. are able to discriminate between spermatophores of different origin. Female *O. cincta* are fertilized by spermatophores (a drop of sperm on a 280-μm high stalk)[5] deposited by males on the substrate without prior contact with any female[6]. The female is fertile for approximately two days during each reproductive period, whereas the male produces spermatophores during five days in each reproductive instar[7].

We collected *O. cincta* from two heaps of twigs and litter, 2 m² in size and five years old, situated 2 km apart in a pine forest near Lund in southern Sweden. The samples are referred to as groups 1 and 2. We assumed that the individuals were more related within than between the groups, as they were aggregated, and were likely to move 2 km, crossing two gravel roads, during one generation.

The tests were performed with animals collected in the field. They were sexed and placed, with the sexes separate, in groups of 3 in plastic cups (d = 6 cm, h = 4 cm) with a moist layer of charcoal:plaster of Paris (1:9, vol:vol) in the bottom. They were fed with algae scraped off twigs and offered on a piece of filter paper, and were kept at 20 °C.

Spermatophores were deposited on the bottom layer. They were transferred to a cup with three females within 48 h, with a little piece of the bottom layer, using a flattened needle. Five spermatophores from each of the two groups were placed alternately along the periphery of the cup containing females. The females were caged in a plastic tube during the transfer. A test was started when the tube was taken away and the females released. The number of remaining spermatophores from each male group was counted after one hour.

The behavior of the females was observed continuously during the first 12 tests, in which 43 spermatophores were taken up, 15 were trodden on and one was eaten. Since those accidentally crushed were visible on the substrate we were confident that more than 95% of the spermatophores that had disappeared at the end of the experiment were taken up sexually by the females.

First, we tested whether the females of both groups discriminated between spermatophores from males of their own group and from the distant group, by offering them spermatophores produced by males from the two groups.

Females (both from groups 1 and 2) preferred spermatophores deposited by males from their own group (table 1). Since they did so, the possibility that the preference depended on some cross-group quality characters, e.g. spermatophore size, could be ruled out. The choice was most likely to have been based on recognition of the origin of the spermatophore.

Second, we tested whether female *O. cincta* avoided mating with sibling males, as optimal inbreeding/outbreeding theories predict[2,3]. The experiment was performed with seven sibling groups (progeny of field-collected animals of group 1) that were reared separately. The adult

siblings were sexed about two months after hatching. Females were placed individually, whereas 3–5 males were kept together. *O. cincta* of group 1 were picked at random from a stock culture containing approximately 80 animals of the field generation. Otherwise they were reared as in the previous experiment.

A female from a sibling group was offered a choice between six spermatophores, half of them deposited by her brothers and the other half by randomly chosen group 1 males. Females of group 1 were given a similar set of spermatophores to test the possibility that other characters than relatedness would influence the choice. Transfer of spermatophores, test duration and statistical treatment were as previously described.

Contrary to our expectations, females of the sibling groups preferred spermatophores deposited by siblings rather than by randomly chosen males, whereas females of group 1 did not discriminate between the spermatophores (table 2). This indicates that their inbreeding/outbreeding level was skewed towards inbreeding. Siblings may not, however, be the choice in the field. According to a model of Bateson[1], a female learns a standard provided by the members of the opposite sex growing up with her. When she matures she will prefer a partner deviating slightly from the standard, but reject a large deviation and avoid one which is too small. If she can differentiate between the two she will prefer the latter. A female *O. cincta* reared together with sibling males will learn such a 'narrow' standard that even other males from the same heap of twigs would deviate too much and be rejected. On the other hand a female reared in a culture of Collembola of group 1 will encounter a much greater male variation and adopt a wider standard. Consequently, she will accept males of sibling groups as well as males of group 1.

The merits of inbreeding are associated with costs of dispersal and genetic effects. Inbreeding will be favorable when the cost of dispersal is higher than the cost of inbreeding depression[8]. Deleterious recessives will gradually (i.e. during a number of generations) be removed from the population. It is possible that the *O. cincta*

Table 1. Female *O. cincta* choice of spermatophores deposited by males from two locations (referred to as groups 1 and 2), 2 km apart. N is the number of tests performed and T_s is the Wilcoxon signed rank statistic.

	No. of tests with mate choice of:		Total No. of accepted spermatophores of:		Wilcoxon signed rank test (2-tail)		
	Group 1 ♂	Group 2 ♂	Group 1 ♂	Group 2 ♂	N	T_s	
Group 1 ♀	11	2	39	24	15	10.0	p < 0.02
Group 2 ♀	2	7	20	27	12	5.5	p < 0.05

Table 2. Female *O. cincta* choice between spermatophores deposited by sibling males and males of group 1. N is the number of tests and T_s is the Wilcoxon signed rank statistic.

	No. of tests with mate choice of:		Total No. of accepted spermatophores of:		Wilcoxon signed rank test (2-tail)		
	Group 1 ♂	Siblings ♂	Group 1 ♂	Siblings ♂	N	T_s	
Sibling ♀	8	19	29	50	34	92.0	p < 0.02
Group 1 ♀	9	7	18	16	20	62.5	n.s.

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 year[9]) 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 ones[5]. 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-deterring 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 unnoticed for more than 100 years. Recently, it was found that a chemical associated with the eggs of this insect inhibits oviposition in conspecific females[2]. This water soluble oviposition deterrent pheromone (ODP) is pro-