

Aphid soldiers discriminate between soldiers and non-soldiers, rather than between kin and non-kin, in *Ceratoglyphina bambusae*

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Soldiers have evolved at least four times in aphids (Aoki 1987). For this altruistic caste to be adaptive, soldiers must preferentially protect kin. Individuals of many species of social Hymenoptera ensure that they are altruistic towards relatives by discriminating between kin and non-kin and excluding non-kin from the colony or preferentially directing care towards kin (Breed & Bennet 1987). Below we discuss an examination of kin discrimination and colony defence in the soldier-producing aphid species *Ceratoglyphina bambusae* (= *Astegopteryx styracicola*, see Aoki & Kurosu 1989; Aphididae: Hormaphidinae: Cerataphidini).

Aphids of *C. bambusae* form conspicuous cauliflower-shaped galls (see photographs in Moffett 1989) on trees of *Styrax suberifolia* (Metachlamydeae: Styracaceae). Mature galls often contain more than 100 000 individuals (Aoki et al. 1977; Aoki 1979a), all parthenogenetically derived from a single foundress (U. Kurosu and S. Aoki, unpublished data). About half of these individuals are soldiers (Aoki et al. 1977; Aoki 1979a). All non-soldiers reside within the gall and feed on the intricately convoluted gall tissue. Soldiers are morphologically distinct second instar larvae, which never moult and are thus reproductively sterile (Aoki et al. 1977). Most soldiers live inside the gall while others guard on the gall surface, but many soldiers rush to the gall surface when the gall is disturbed. Soldiers quickly attack and kill insect larvae (Aoki 1979a), as well as aphids (personal observation), placed on the gall. Soldiers attack by grasping invaders, piercing them with their mouthparts and presumably injecting saliva (Aoki 1979a).

Our experiments were performed on the surface of a large *C. bambusae* gall (with a diam-

eter of 74 mm) attached to a *S. suberifolia* tree, at Kuangyinshan, Taiwan, on 23, 24 and 26 September 1990. We collected two other *C. bambusae* galls: one from a tree in Kuangyinshan (gall A) and one from a tree at Sun Moon Lake (gall B), located approximately 15 km from Kuangyinshan. Soldiers, wingless adults and non-soldier larvae from galls A and B were marked with a coloured powder and placed on the surface of the test gall, one at a time. To test for discrimination of aphids from the same gall, we cut off a small piece of the test gall and the following day placed soldiers and adults from this dissected piece on the test gall. To test for the effect of the marking powder, we marked only half of the adults, which are much larger than soldiers, from galls A and B. Finally, soldiers and wingless adults from a gall of another soldier-producing species, *Astegopteryx bambucifoliae*, were placed on the test gall. The yellow aphids of *A. bambucifoliae* were easily distinguished from the dark brown soldiers of *C. bambusae*, and were therefore not marked. We scored aphids as attacked or not attacked within 3 min after introduction. If an aphid was attacked, we followed its fate.

The results are strikingly clear cut (Table 1). Soldiers always attacked conspecific non-soldiers, regardless of origin, and never attacked conspecific soldiers. Soldiers almost always attacked individuals of *A. bambucifoliae*. The one *A. bambucifoliae* soldier not attacked within 3 min (see Table 1) was attacked after approximately 3.5 min and eventually displaced from the gall. One *A. bambucifoliae* soldier that was attacked within 3 min escaped from the attack and after 30 min was still found alive on the gall surface. All other attacked aphids were eventually (range = 16–2160 s) displaced from

Table I. Number of introduced aphids attacked by *C. bambusae* soldiers on test gall within 3 min of introduction

| Source of aphids | Soldiers | | Wingless adults | | Larvae* | |
|-------------------------|----------|--------------|-----------------|--------------|----------|--------------|
| | Attacked | Not attacked | Attacked | Not attacked | Attacked | Not attacked |
| Test gall | 0 | 10 | 10 | 0 | | |
| Gall A | 0 | 10 | 10 | 0 | | |
| Gall B | 0 | 10 | 10 | 0 | 10 | 0 |
| <i>A. bambucifoliae</i> | 9 | 1† | 10 | 0 | | |

*First and second instar larvae were introduced.

†Aphid was attacked after 3 min 39 s.

the gall. The marking powder had no discernible effect on the attack behaviour.

Because almost all galls were out of easy reach and observation, we performed these experiments on a single gall. This fact may weaken the generality of our findings, but soldier behaviour was consistent with all our past observations of this species. For example, on 8 July 1990 we tied a branch so that two galls of *C. bambusae*, which were still attached to the tree, were touching one another. Over a 30-min period we observed no aggression between soldiers of the two galls.

We found no evidence of kin discrimination in *C. bambusae*. We performed an assay for a relatively extreme behaviour pattern, mortal attack, and we cannot exclude the possibility that the aphids possess a more subtle form of kin discrimination. Although soldiers do not apparently treat relatives differentially, they actively discriminate against non-soldiers. In addition, this discrimination appears to be context dependent, because the majority of soldiers reside within the gall but apparently do not attack non-soldiers within the gall.

Soldier attack of non-soldiers may effectively exclude unrelated non-soldier aphids from the gall where they would propagate and compete with resident aphids. Inter-gall migration occurs in at least four species of aphids (Aoki 1979b; Setzer 1980; Kurosu & Aoki, in press) and the resulting competition may pose a serious threat to colony success. It is unclear, however, whether the observed pattern of discrimination evolved as a direct response to the threat of inter-gall migration or evolved to repel predators, incidentally conferring defence against the invasion of conspecific reproductives.

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