Research News

Soldier aphids go cuckoo

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Aphids hold a special place in the study of social evolution, because they include the only eusocial animals that are clonal. We might expect social aphid colonies, if they consist of pure clones, to be free from reproductive conflict. A fascinating new study by Abbot and colleagues shows that there can be high levels of clonal mixing within colonies of a social aphid. The intruding aphids cheat on the host clone by not helping in gall defence and instead invest singlemindedly in growth and reproduction. Now that aphid soldiers have been shown to cheat, as well as to defend, clean and repair their galls, it is perhaps time to admit them ungrudgingly to the elite cadre of the truly social insects.

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Aphids would seem to be the epitome of defencelessness. Small soft cushions of haemolymph, they huddle on leaves and stems, ready to be ripped apart by ladybirds, sucked dry by lacewings, hoovered up by hoverflies and punctured by wasps. The discovery that certain species have aggressive soldiers therefore came as a surprise: nobody ever expected the soft cushions to fight back [1]. Soldier aphids are rare (only ~1% of the 4500 species have them) but they are impressively diverse in the weapons and behaviour that they use [2], and they have evolved independently ~17 times (T. Fukatsu, pers. commun.).

The distinguishing feature of aphid societies is that, provided they comprise a pure clone, there should be no reproductive conflict. In all other societies, there is inevitably conflict among individuals, because they are not all equally related to each other's offspring. However, the assumption that social aphids live in pure clonal groups has never been properly tested. This is what Abbot *et al.* have done [3]; they have shown that the clones do mix, and with fascinating consequences.

They studied the aphid *Pemphigus obesinymphae*, which form long-lived galls on cottonwood *Populus* trees in North America [4]. The genus *Pemphigus* occurs throughout the North Temperate region (including the UK) and includes several soldier-producing species [3]. Individual females, which we can legitimately call 'queens', make a globular gall on the leaf, in which they asexually produce up to 300 first-instar soldiers. The *P. obesinymphae* queen cannot escape from the gall, but the soldiers can come and go through a small ostiole. This hole is the Achilles Heel of the gall: it is essential for the aphids to get rid of their waste products (honeydew) [5], but it is also large enough to allow predators to get in and eat the queen. The gall remains in this condition for several months, during which time the soldiers effectively, and often suicidally, defend their home from attack by predators that can be much larger than them (Fig. 1). At the appropriate time, the soldiers resume their development and mature into winged aphids that leave the gall and fly to another, herbaceous, host plant.

Abbot *et al.* have shown, by direct observation, that soldiers leave their natal galls in appreciable numbers and infiltrate other galls inhabited by aphids to whom they are not at all related. The authors used aphids marked with coloured powders and by using sticky bands on the twigs: some aphids were

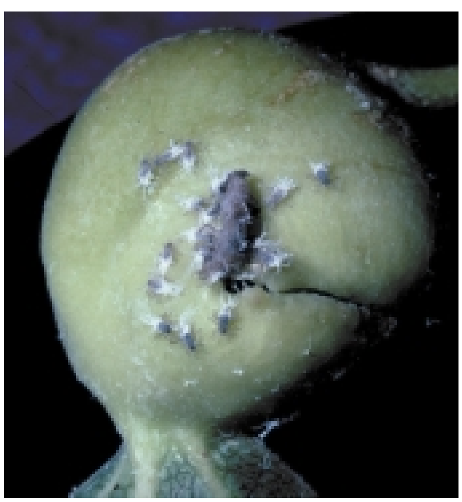

Fig. 1. First-instar soldier aphids attach a fly larva on the surface of a gall of *Pemphigus obesinymphae*. Gall diameter is ~1.6 cm. Note exit hole of gall just to the right of the larva. Photograph reproduced with permission from Patrick Abbot.

able to walk nearly 2 m. They also used genetic markers [single-nucleotide polymorphisms of the aphid bacterial endosymbiont *Buchnera*, and multilocus intersimple sequence repeats (ISSR) on the aphids themselves] to reveal that the level of clonal mixing was high. In seven galls analysed by ISSR, on average 38% of the aphids were from alien clones and five of the seven galls contained intruders from more than two other galls. Although this is a small sample from a restricted locality, it is clear that soldier behaviour can be maintained in an aphid species even when the level of clonal mixing is high.

Even more interesting than this demonstration of extensive clonal mixing, are the results of their experiments on how the intruding aphids behave. Abbot *et al.* inserted *Drosophila* larvae into natural galls and, after a few minutes, removed them, together with the soldier aphids that had attacked and were still stuck to the larvae. They then genotyped all the aphids that had been in the gall and found that the intruder aphids were far less likely to attack the fly larva. Although ~36% of the aphids in the gall were intruders, only 2% of the attacking aphids were not native to the gall. Clearly, the alien aphids had decided to let the native soldiers take care of gall defence. Furthermore, the intruding aphids do not spend much time as first instars, but accelerate their development into winged adults that leave the gall to reproduce on other hosts.

Although this kind of selfish behaviour is exactly what one would expect on the basis of kin selection theory, it is nevertheless a remarkable result. It means that the aphid clones have a condition-dependent altruistic strategy. In your own gall, you should grow slowly and be prepared to fight. But if you have dispersed to another gall, cheat on your new mates, do not risk your life attacking, but develop and leave the gall as quickly as you can. It would be interesting also to know whether the intruders shirk on the normal housekeeping duties of soldier aphids. The vital task of pushing

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honeydew out of the galls is usually performed in gall-living aphids by the early instars, but this is a risky business and one might predict that the intruders would leave this to their hosts.

These results are important to those conducting manipulative experiments on social aphids. It is unclear what proximate mechanisms underlie the change in behaviour of the aphids, but it is possible that this is triggered by simply being out of contact with the queen aphid. The same research group has previously shown, in this species, that the death of the queen allowed the soldiers to develop rapidly [6], and it is possible that walking between galls has the same effect and, in addition, causes them to stop defending. The aphids might well have quite subtle responses to their immediate environment, which researchers will need to be wary of.

Why do the host aphids allow intruders into their galls? It might just be that they cannot recognize them as intruders. All attempts to demonstrate kin recognition in aphids have so far failed [7]. Such a constraint argument is unsatisfactory: after all, kin-recognition systems are widespread in clonal organisms [8]. It is possible that the costs of allowing even quite large numbers of alien aphids into your gall are not very high, especially if this is likely to occur toward the end of the season. There is a clear selective asymmetry here: the costs to the intruder of not getting in will always be severe. If gall invasion is a common strategy for these aphids, there might be strong selection on the clones not to reveal their genetic identity, thus allowing them ready access into alien galls. A parallel argument has been advanced to explain why very young gull chicks are not recognized by their parents [9].

It is now clear that these social aphid clones have a complex strategy that combines defence and dispersal. Given the high risk of clonal extinction by gall death, there will be strong selection for investment in what Hamilton [10] called 'self-propelled cuckoo eggs', which can extend the clone's reproduction by parasitizing nearby galls. And, for gall-living aphids, the run-on costs of producing extra juveniles will be very small. The parallel with birds is even stronger than Hamilton's characteristically vivid phrase might suggest: there are examples of birds that transfer their eggs into neighbours nests, possibly as a bet-hedging strategy, and indeed of juveniles that walk or fly into nearby nests [11].

Because these aphids are adopting a combined strategy, we should not expect to see any clear relationship between the degree of clonal mixing and the extent of soldier behaviour. Investment in defence and dispersal will be favoured by similar ecological conditions, for example high predation, and will lead to convergent aphid phenotypes of toughness and mobility. We should therefore not be surprised to find aphid species that have high numbers of soldiers combined with relatively high levels of clonal mixing, and other species without soldiers where mixing is low. *Pemphigus populi*, which maintains a completely closed gall until just before the aphids fly out, does not have soldiers and almost certainly has zero clonal mixing (N. Pike, pers. commun.). Nevertheless, the gall environment, by providing reasonably high levels of clonal purity, was almost certainly important for setting the stage for the evolution of soldiers in aphids. It would now be especially interesting to look at the level of clonal mixing in the horned soldier aphids, which live in free colonies on herbaceous plants and which are unique as the only social insects that do not live in some kind of nest [12].

The maintenance of clonal purity is a fundamental issue in the evolutionary history of most living organisms [13]. The very first societies almost certainly comprised genetically identical individuals, and we could regard multicellularity as the most successful experiment in social behaviour in the history of life on Earth. Conflicts of interest among clonally reproducing organisms are commonplace. Slime mould clones fight their way into the fruiting structure [14]; colonial marine invertebrates fuse only with their clone-mates [8]; and it is conceivable that the avoidance of conflict among nuclear and mitochondrial genomes has led to the fundamental asymmetry of male and female gametes [15]. Aphids are unique among these clonal societies in that they comprise clones whose individual members are independent of each other and are highly mobile. They provide a link between the animal societies studied by behavioural ecologists and the molecular systems studied by developmental biologists. The study of them, using the techniques of both these fields, should provide fresh insights into the genetic conflicts of interest that permeate so much of biology.

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