structure into models of cladogenesis and lineage extinction.

The techniques that we have described are very general. They can be applied to reveal long-term evolutionary trends in phylogenetic trees, recent patterns of local population history, and the epidemic history of infectious diseases. In this article, we have focused on phylogenetic epidemiology. Because of its obvious applicability to contemporary epidemiology, we can expect phylogenetic epidemiology to become an applied tool, enabling more informed policy decisions about disease control. For the moment, it seems, the data are probably accumulating faster than are the techniques that will enable us to interpret them.

Acknowledgements
We thank Eddie Holmes and Andrew Rambaut for their help with the work reported here, and the AFRC, the SERC (GR/H3658) and the Wellcome Trust (38468) for financial support.

References

A new epoch in joint studies of social evolution: molecular and behavioural ecology of aphid soldiers

Yosiaki Tò

Yosiaki Tò is at the School of Arts and Sciences, Okinawa University, Kokuba, Naha 902, Japan.

Studies on social evolution in animals have developed rather independently of biochemistry and molecular biology, except for the use of allozyme electrophoresis since the end of the 1970s, to evaluate intra- and intercolony relatedness. There have been a few joint works involving theoretical discussions between ecologists and biochemists/molecular biologists, because the former have wanted only to use established biochemical techniques.

DNA fingerprinting and other related techniques to determine kin relations, extraband copulation, paternity, etc. (see Refs 3 and 4 for reviews) created a new era. A lack of priority in paternity of top-ranked males in Japanese macaque troops, a fact that was not previously believed by behavioural ecologists, was found by cooperation of ecologists and molecular biologists. Use of the polymerase chain reaction to determine the number of reproductive queens and the use of microsatellites to evaluate relatedness are other examples of successful joint studies between ecologists and molecular biologists.

Discovery of aphid soldiers

One of the important discoveries that has stimulated active discussions about social evolution was that of sterile soldiers in aphids. Although soldiers of Pemphigus sylvestri are known to clean the inside of their galls, foraging for food is not necessary in aphid colonies and the role of sterile caste in aphids is limited to the defence of their colonies. Mothers of Pseudogregma koshunense, a bamboo aphid with sterile soldiers, produce normal (to-be-reproductive) larvae first and soldiers second, in complete reverse to the reproductive strategies of other eusocial insects, wasps, bees, ants and termites, which produce workers first and reproductives second. This reversal is, however, considered to be a good strategy for aphid mothers, because small, just-established colonies may be not discovered easily by natural enemies. But if colonies become large, they may at tract many enemies, and the soldier production becomes beneficial. Although they produce soldiers first, possibly to protect their galls, two Australian thrips, Oncothrips tepperi and O. habrus also have soldiers only, as they don't need foragers. These discoveries have raised a new set of debates about the evolution of soldier castes.

Aphid soldiers without endosymbions

Most aphids harbor microbial endosymbions (Buchnera aphidicola complex) in mycocytes, huge cells in the abdomen specialized for this purpose. In addition, many species have two types of the symbionts primary and secondary. Primary symbionts are found in almost all aphid species, while secondary symbionts are found only in some species. Molecular biological data suggest that the primary symbionts have been derived from a prokaryote that was acquired by the common ancestor of aphids.

Using immunoblot analysis and immunohistochemical techniques, Fukatsu and Ishikawa found that soldiers and males of a eusocial aphid, Colophina armata, lack the primary symbiont. In C. arma, the male is dwarf and lacks mouthparts, and the soldier has a short proboscis, possibly causing difficulties in sucking the phloem sap (soldiers of C. clematis, a relative of C. arma, excrete little honeydew, suggesting that they cannot suck the phloem sap). There are two possible explanations of lack of endosymbiont in soldiers. The first, the host selection hypothesis, assumes that the host aphids reject the symbiont's infection. As the plant phloem sap is nutritionally quite unbalanced, the presence of the symbiont is necessary for aphids to synthesize essential nutrients. But, if the aphid does not feed, the symbiont is unnecessary and it may be better for the host to reduce the costs of harboring symbionts. The second is the symbiont selection hypothesis, which assumes that the endosymbionts selectively infect the embryos that will become reproductive female but avoid those destined for males and soldiers (intracellular symbionts of aphids are transmitted solely through the female line). This hypothesis is interesting, because such selfish behaviours of extra-nuclear elements have been known in host-parasitoid relationships. However, the fact that soldiers of another