

THE EVOLUTION OF SOLDIERS IN APHIDS

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I. INTRODUCTION

'... the members of an aphid colony are genetically identical just like the cells of a body. So the existence of sterile workers in aphids is perhaps no more of an evolutionary surprise than the fact that our nose cells do not produce sperms or eggs.' (Krebs & Davies, 1993: p. 331)

The existence of permanently sterile individuals always poses a problem for evolutionary theory. The nature and extent of the problem depends on the natural history of the group in question, but the basic problem can be posed as follows: if natural selection is the survival of the fittest, how could it lead to the production of individuals with a personal fitness of zero? The theoretical solution to this question was provided by Hamilton's (1964) concept of kin selection (Haldane, 1923; Fisher, 1930; Maynard Smith, 1964). If altruists are genetically related to the individuals they help, the indirect fitness gained via these relatives might be enough to offset the direct fitness lost as a result of helping or of being sterile. In this review we are concerned both with the general problem of explaining the taxonomic distribution of extreme reproductive altruism in aphids and with the biological details of this altruism. Understanding the taxonomic distribution of a trait, and particularly the causes for its origin, requires a comparative approach explicitly guided by an historical perspective (for reviews see Harvey & Pagel, 1991; Brooks & McLennan, 1991). We therefore set the biological details of soldier production in an historical, and when possible a phylogenetic, perspective.

Which groups of animals display reproductive sterility, and in which of these groups would it be most profitable to study the origins of this reproductive altruism? The great majority belong to the insect orders Hymenoptera (ants, bees, and wasps) and Isoptera (termites), but sterile castes have also been described in aphids, mole-rats, thrips and bark-beetles (Table 1). Comparative studies can be applied only to those groups that are variable for the character of interest. Therefore, the ants and termites, although they include thousands of eusocial species, are inappropriate groups in which to study the origins of sterility since all species share this trait. In addition, the causes for the origins of altruism are best tested in groups that are variable for primitive forms of reproductive altruism. This consideration again rules out the ants and termites, which all have a relatively advanced level of social organization. Finally, it is helpful if the group under study has experienced several independent gains (and losses) of sterile castes. This rules out the Vespidae, which probably has a single origin of eusociality (Carpenter, 1991). This leaves the bees and the aphids as the two most suitable for

Table 1. *Eusocial* animals*

Taxon	Number of species		Number of origins of eusociality	Genetic system
	Eusocial	Total in taxon		
Hymenoptera				
Ants ¹ (Formicidae)	8800	8800	1	Haplodiploid
Bees ² (Apoidea)	1000	30000	7-9	
Vespids ³ ('higher' Vespidae)†	880	910	1	
Sphecids ⁴ (Sphecidae)	1	6000	1	
Isoptera ⁵	2200	2200	1	Diploid
Hemiptera				
Aphids (Aphidoidea)	43	4400	≥ 6-9	Clonal
Thysanoptera				
Gall thrips ⁶ (Phlaeothripini)	6	2500	2	Haplodiploid
Coleoptera				
Bark beetles ⁷ (Platypodinae)	1	550	1	Diploid
Mammalia				
Mole-rats ⁸ (Bathyergidae)	3	12	2	Diploid

Table shows the number of species in a taxon that are thought to be eusocial together with the total number of species in that taxon, the supposed minimum number of independent origins of eusociality within that taxon and the genetic system of that taxon.

* All species considered eusocial under the traditional definition as well as under more recent definitions (Crespi & Yanega, 1994; Sherman *et al.*, 1994) are included, although we argue in the text that it may be misleading to consider soldier aphids as eusocial.

† Stenogastrinae, Polistinae and Vespinae.

References from which information was obtained: ¹Hölldobler & Wilson (1990); ²Michener (1974); ³Carpenter (1991); ⁴Matthews (1991); ⁵Wilson (1971); ⁶Crespi & Mound (1996), Crespi (personal communication); ⁷Kent & Simpson (1992); ⁸Honeycutt *et al.* (1991).

studying the origins of extreme reproductive altruism: both groups contain a reasonable number of species, both are polymorphic for relatively primitive forms of reproductive altruism, and in both groups altruism has arisen independently more than once.

The discovery of soldiers in aphids is relatively recent. In 1977, Aoki demonstrated that the aphid *Colophina clematis* Shinji (Pemphigidae) produces sterile first-instar soldiers, and since then sterile soldiers have been discovered in a number of other aphid species (Tables 2, 4). We have argued elsewhere (Stern & Foster, 1996) that it is probably inappropriate to classify soldier-producing aphids as eusocial. The term eusociality was originally created to explain a set of phenomena associated with particular taxonomic groups, namely the highly social Hymenoptera and the Isoptera. The definition, therefore, incorporates natural history that is specific to these groups but irrelevant to aphids, as well as thrips (Crespi, 1992). Recently two groups of authors have redefined eusociality in two very different ways (Crespi & Yanega, 1995; Sherman *et al.*, 1995) to incorporate the natural history of the newly discovered highly social animals (thrips, beetles, and naked mole rats) and to attempt a unification of the study of social behaviour across all animals. We do not present a review of this controversy but note that although we believe these definitions will be useful in some circumstances, all three ignore a crucially important detail of aphid natural history, clonality. We will argue that aphid clonality forces us to think about soldier evolution in new ways and does not allow the aphids to be easily fit into any of the definitions of eusociality.

In this review, we will examine the question: why do colonies of some aphid species

Table 2. *A classification of soldier-producing aphids*

Taxon	Primary hosts	Secondary hosts	Number of species	Genera known to have defender morphs	Genera where defender morphs are unknown
Hormaphididae					
Cerataphidini	<i>Styrax</i>	Araceae, Balsaminaceae, Compositae, Gramineae, Loranthaceae, Orchidaceae, Palmae, Pandanaceae, Zingiberaceae	81	<i>Astegopteryx</i> , <i>Cerataphis</i> , <i>Ceratoglyphina</i> , <i>Ceratovacuna</i> , <i>Pseudoregma</i> <i>Tuberaphis</i>	<i>Aleurodaphis</i> , <i>Chaitoregma</i> , <i>Glyphinaphis</i>
Hormaphidini	<i>Hamamelis</i>	Betulaceae	8	<i>Hamamelistes</i>	<i>Hormaphis</i>
Nipponaphidini	<i>Distylium</i>	Fagaceae, Lauraceae, Moraceae	82	<i>Distylaphis</i> , <i>Nipponaphis</i>	<i>Euthoracaphis</i> , <i>Mesothoracaphis</i> , <i>Metanipponaphis</i> , <i>Neohormaphis</i> , <i>Reticulaphis</i> , <i>Schizoneuraphis</i> , <i>Sinonipponaphis</i> , <i>Thoracaphis</i>
Pemphigidae					
Eriosomatinae					
Eriosomatini	<i>Ulmus</i> <i>Zelkova</i>	Compositae, Grossulariaceae, Pomaceae, Rosaceae, etc.	58	<i>Colophina</i> , <i>Eriosoma</i> , <i>Hemipodaphis</i>	<i>Aphidounguis</i> , <i>Byrsocryptoides</i> , <i>Colopha</i> , <i>Gharesia</i> , <i>Paracolopha</i> , <i>Shizoneura</i> , <i>Shizoneurata</i> , <i>Shizoneurella</i>
Tetraneurini	<i>Ulmus</i>	Cyperaceae, Gramineae, Labiatae	38	None	<i>Kaltenbachiella</i> , <i>Tetraneura</i>
Pemphiginae					
Pemphigini	<i>Populus</i>	Compositae, Primulaceae Umbelliferae, etc.	81	<i>Epipemphigus</i> , <i>Pemphigus</i>	<i>Mordvilkoja</i> , <i>Thecabius</i>
Prociphilini	Woody angiosperms	Conifers	65	<i>Pachypappa</i>	<i>Gootiella</i> , <i>Pachypapella</i> , <i>Prociphilus</i>
Fordinae					
Fordini	<i>Pistacia</i>	Gramineae, Leguminosae, Solanaceae	48	<i>Smynthuroides</i>	<i>Aploneura</i> , <i>Forda</i> , <i>Geoica</i>
Melaphidini	<i>Rhus</i>	Mosses	9	None	<i>Melaphis</i> , <i>Nurudea</i> , <i>Schlechtendalia</i>

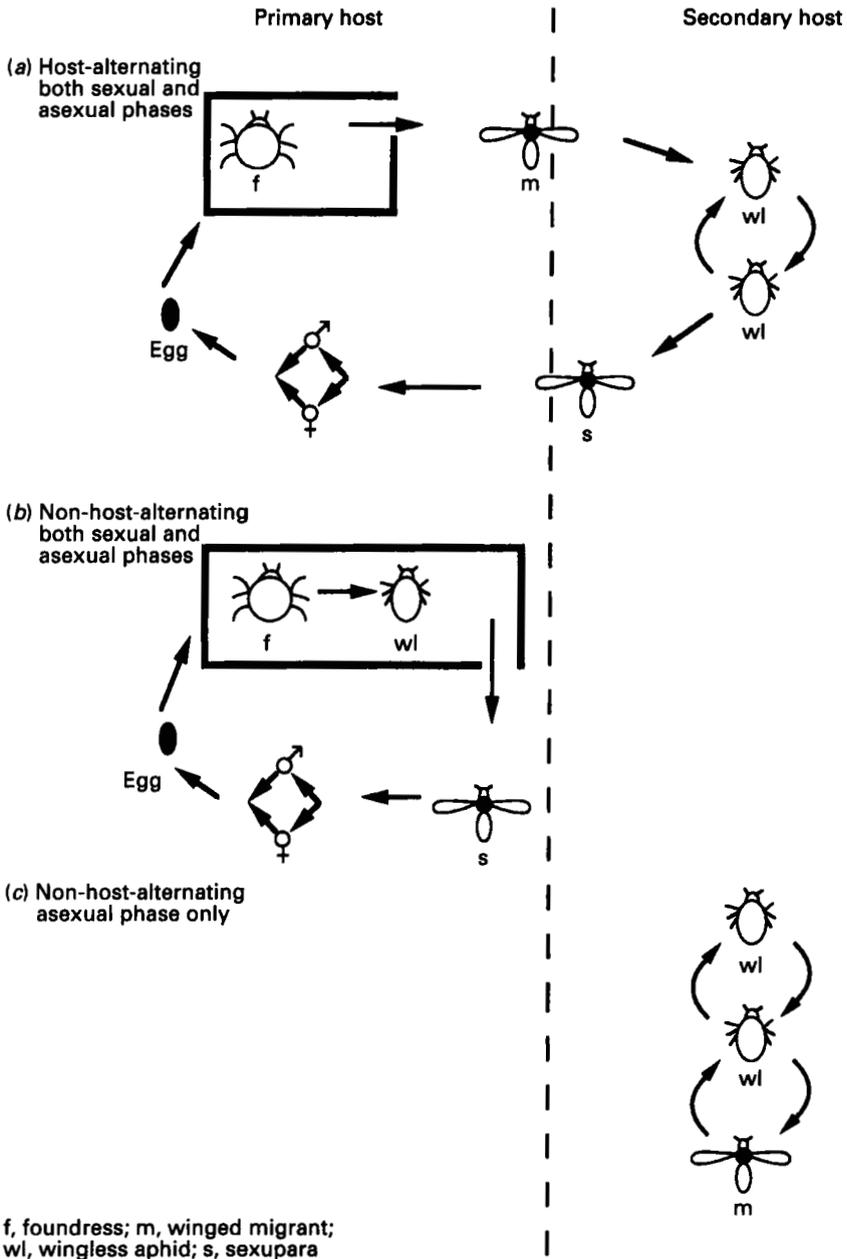


Fig. 1. Simplified diagram of the life cycles of Hormaphididae and Pemphigidae. The adults of the succeeding generations, and the egg, are shown. The rectangular box represents a gall. (a) The most complete, and presumed ancestral, life cycle of the two families consists of an alternation of a single sexual generation with multiple parthenogenetic generations and host alternation, typically from a woody primary host (sometimes called the winter host) to an herbaceous secondary host (the summer host). Note that although we indicate only a single generation in the gall (typical for pemphigines) some species produce several generations of wingless aphids within the gall. (b) A variant of the complete life cycle in which there is no migration to the secondary host. (c) A variant of the complete life cycle in which there is no migration to the primary host and the sexual phase has been lost. Further variant life-cycles are known. For example, in variant (c) there may be occasional, facultative production of sexuparae that return to the primary host.

invest in reproductively sterile defensive individuals (soldiers) whereas colonies of other species do not? As Hamilton (1987) has written 'a particularly valuable check on kin selection theory will come when it is possible to contrast colonies [of aphids] that have soldiers with those that don't.' In addition, the aphids are an ideal group in which to use the comparative method to combine phylogenetic information with observations on behavioural ecology and genetics. We will review what is currently known about soldier production in aphids and describe how this comparative study might be undertaken.

(1) *General aphid biology*

Aphids are small (1–10 mm) sap-sucking insects of the suborder Homoptera and order Hemiptera. They are, in general, characterized by cyclical parthenogenesis (the alternation of a series of parthenogenetic generations with a single generation of sexual reproduction), telescoping of generations, and viviparity (see Dixon, 1985). These mechanisms, combined with a short generation time (~ 10 d), allow aphid colonies to grow very quickly. Many aphids also alternate between two hosts from very different plant taxa: the primary or 'winter' host, where sex occurs, and the secondary or 'summer' host, where successive, entirely parthenogenetic, generations of females develop (Fig. 1). The primary hosts are usually woody and tend to be taxonomically highly conserved for each of the major aphid groups, whereas the secondary hosts are usually much more diverse. For example, all the species of the Pemphigini use poplar (*Populus*) trees as their primary hosts, but plants from a wide variety of families, including composites, umbellifers, legumes, Primulaceae, and Ranunculaceae, as their secondary hosts (Table 2).

The life-cycles of the two soldier-producing families, the Pemphigidae and Hormaphididae, are very similar (Fig. 1). The foundress hatches from an egg laid on the primary host where she forms a gall in which one or more generations of females are produced parthenogenetically. Winged migrants leave the galls, usually at about midsummer in temperate regions, and fly to the secondary host where they give birth parthenogenetically to wingless aphids. Several more parthenogenetic generations are then produced and, in the autumn, colonies produce specialized winged migrants, the sexuparae, which fly to the primary hosts where they give birth parthenogenetically to sexual males and females. These sexuals undergo several moults and mate (Foster & Benton, 1992). Each female lays a single egg, which overwinters and hatches the next spring as the foundress.

It should be pointed out that parthenogenesis in aphids, as in most cyclically parthenogenetic groups, is apomictic and therefore strictly clonal. It had been suggested that there might be some form of crossing over ('endomeiosis') in the maturation of the parthenogenetic aphid egg (Cognetti, 1961), but subsequent cytogenetic, biochemical and morphogenetic studies have provided no evidence for genetic recombination and segregation within parthenogenetic lines of aphids (Blackman, 1979, 1987).

(a) *The instability of aphid taxonomy*

Aphid nomenclature has historically been highly unstable. This is due, in large part, to the fact that aphids produce many different morphs during the life cycle and can look

very different when feeding on the primary and secondary hosts. This instability can cause confusion when attempting to decipher the primary literature. Table 3 is a synonymic list for all known soldier-producing species and we highly recommend referring to this table when delving into the primary literature.

II. REPRODUCTIVE ALTRUISM IN CLONAL ANIMALS

Aphids are the only taxa in Table 1 that reproduce asexually, or clonally, for the majority of their life cycle. Extreme forms of reproductive altruism ought to be commonplace in clonal organisms: since the members of a clone are genetically identical, any kind of altruism that pays more than it costs ought to be selected for (Hamilton, 1987). And yet altruism is rare in clonal organisms. Why? In answering this question, it might be useful to think of communities of potentially altruistic units as being arranged along a continuum, with the cells of a typical metazoan individual at one extreme and a colony of highly eusocial insects at the other. This continuum emphasizes first the permanence of spatial relationships between interactants and second the genetic relatedness between these interactants (cf. Hamilton, 1987). As both the permanence of spatial relationships and genetic relatedness decrease, the incidence of extreme altruism declines.

In a metazoan, the genetically identical cells are in close permanent contact with each other and, although there may be a clear division of labour between the germ-line and the sterile soma, there is no genetic conflict and no real possibility of invasion by cells of unrelated conspecifics. In modular colonial invertebrates, such as sponges, siphonophores, bryozoans and ascidians, the individuals may be highly specialized for particular functions, such as defence, feeding or reproduction, but they are nevertheless clearly attached to each other in one unit, and they can not be readily invaded by unrelated conspecifics (e.g. Wilson, 1975; Hughes, 1989; Harvell, 1994). A similar example can be found in the polyembryonic parasitic wasps of the family Encyrtidae that produce precocious larval defender morphs (Cruz, 1981, 1986). Here, many thousands of embryos are derived clonally from a single egg deposited in a host. Some of these embryos develop rapidly into aggressive larvae with enlarged mandibles that will attack heterospecifics and unrelated conspecifics, thereby securing the host for the sole use of their clone-mates. Here the host cuticle provides a reasonable barrier against clonal mixing and when a second clone is introduced the larvae apparently recognize and attack until only one clone remains.

In some clonal invertebrates, the individuals are clearly capable of independent existence but may remain close to each other in relatively immobile clonal aggregations. A good example is provided by the sea anemone *Anthopleura elegantissima*. Clonal mixing appears to be prevented by the behaviour of specialized sterile warrior polyps that fight polyps from unrelated clones (Francis, 1976, 1979). A further stage in our hypothetical continuum might be represented by the prokaryotic slime bacteria (Myxobacteria) and the eucaryotic slime moulds (Acrasiales), in which separate, mobile individuals may come together under certain conditions to form a fruiting body, with some members of the clone forming the stalk and others the reproductive spores at the tip (Bonner, 1974; Wireman & Dworkin, 1975).

In the aphids, the parthenogenetically produced individuals are clearly separate from each other and usually fairly mobile, so that there is enormous potential for clonal

Table 3. *Nomenclature of aphid species with soldiers*

Currently accepted name	Other, previously used names
Hormaphididae	
Cerataphidini	
<i>Astegopteryx bambucifoliae</i> (Takahashi) [<i>Oregma</i>]	<i>Astegopteryx bambusifoliae</i> (Takahashi) ¹ , <i>Astegopteryx sasakii</i> Takahashi
<i>Astegopteryx roepkei</i> Hille Ris Lambers	
<i>Astegopteryx setigera</i> Noordam	
<i>Astegopteryx styracophila</i> Karsch	
<i>Cerataphis fransseni</i> (Hille Ris Lambers) [<i>Astegopteryx</i>] ²	<i>Cerataphis variabilis</i> ³ , <i>Cerataphis palmae</i> ³ , <i>Aleurocanthus palmae</i> ⁴ , <i>Cerataphis lataniae</i> ⁴
<i>Cerataphis vandermeermohri</i> (Hille Ris Lambers) [<i>Astegopteryx</i>] ⁶	
<i>Ceratoglyphina styracicola</i> (Takahashi) [<i>Astegopteryx</i>] ⁵	<i>Ceratoglyphina bambusae</i> Van der Goot ⁵
<i>Ceratovacuna floccifera</i> Noordam	
<i>Ceratovacuna japonica</i> (Takahashi) [<i>Oregma</i>] ²	<i>Ceratovacuna pseudostyracophila</i> (Shinji) ⁷ [<i>Astegopteryx</i>] ²
<i>Ceratovacuna lanigera</i> Zehntner	<i>Oregma lanigera</i> Van de Goot ⁴
<i>Ceratovacuna longifila</i> (Takahashi) [<i>Oregma</i>] ²	
<i>Ceratovacuna nekoashi</i> (Sasaki) [<i>Astegopteryx</i>] ²	
<i>Ceratovacuna</i> sp. C Takahashi	
<i>Pseudoregma alexanderi</i> (Takahashi) [<i>Oregma</i>] ²	
<i>Pseudoregma bambucicola</i> (Takahashi) [<i>Oregma</i>] ²	<i>Pseudoregma bambucicola</i> (Takahashi) ¹ [<i>Oregma</i>] ⁴ , <i>Oregma bambusae</i> ⁴
<i>Pseudoregma koshunensis</i> (Takahashi) [<i>Oregma</i>] ²	<i>Pseudoregma shitosanensis</i> (Takahashi) ⁸ [<i>Astegopteryx</i>] ⁹
<i>Pseudoregma montana</i> (Van der Goot) [<i>Oregma</i>] ²	
<i>Pseudoregma panicola</i> (Takahashi) [<i>Oregma</i>] ²	
<i>Pseudoregma pendleburyi</i> (Takahashi) [<i>Oregma</i>] ²	
<i>Pseudoregma sundanica</i> (Van der Goot) [<i>Oregma</i>] ²	<i>Pseudoregma nicolaiiae</i> (Takahashi) ⁶ [<i>Oregma</i>] ²
<i>Tuberaphis coreana</i> (Takahashi) [<i>Astegopteryx</i>] ¹¹	<i>Tuberaphis taiwana</i> Takahashi ^{6,11}
<i>Tuberaphis leeuweni</i> (Takahashi) [<i>Astegopteryx</i>] ¹	
<i>Tuberaphis styraci</i> (Matsumura) [<i>Astegopteryx</i>] ¹⁰ [<i>Hamiltonaphis</i>] ⁶	<i>Ceratovacuna styraci</i> ¹⁰
<i>Tuberaphis sumatrana</i> (Hille Ris Lambers) [<i>Astegopteryx</i>] ¹	
<i>Tuberaphis takenouchii</i> (Takahashi) [<i>Astegopteryx</i>] ¹² [<i>Aleurodaphis</i>] ¹	<i>Rappardiella plicator</i> Noordam ¹³

Hormaphidini

Hamamelistes betulinus makabae (Inouye) [*Mansakia*]¹

Nipponaphidini

Distylaphis foliorum (Van der Goot) [*Schizoneuraphis*]⁴

Nipponaphis distyliicola Monzen

Pemphigidae

Eriosomatinae

Colophina arma Aoki

Colophina clematicola (Shinji) [*Pemphigus*]¹⁴

Colophina clematis (Shinji) [*Pemphigus*]²

Colophina monstrefica Aoki

Eriosoma moriokense Akimoto

Hemipodaphis persimilis Akimoto

Colopha sp. near *caucasica*¹⁵

Pemphiginae

Epipemphigus niisimae (Matsumura) [*Pemphigus*]¹

Pachypappa marsupialis Koch

Pemphigus dorocola Matsumura

Pemphigus monophagus Maxson

Pemphigus obesinympae Aoki & Moran

Pemphigus spyrothecae Passerini

*Pemphigus borealis*¹⁶, *Pemphigus bursarius*¹⁶

Pemphigus spirothecae Passerini²

The presence of parentheses around author indicates transferred species, and the genus from which they were transferred follows in square brackets. Superscript numbers indicate reference that documents the synonymy or name change. The following names, though considered synonyms of species above, are currently used to denote other species: *Cerataphis lataniae*, *Pemphigus borealis*, and *P. bursarius* (Aoki, personal communication).

References: ¹ Aoki (personal communication); ² Eastop & Hille Ris Lambers (1976); ³ Stern, Aoki & Kurosu (1995); ⁴ Noordam (1991); ⁵ Aoki & Kurosu (1989c); ⁶ Stern, Aoki & Kurosu (unpublished data); ⁷ Aoki & Kurosu (1991b); ⁸ Aoki & Kurosu (1991c); ⁹ Aoki (1982b); ¹⁰ Aoki, Kurosu & Fukatsu (1993); ¹¹ Aoki & Kurosu (1993); ¹² Aoki & Usuba (1989); ¹³ Kurosu, Aoki & Fukatsu (1994); ¹⁴ Kurosu & Aoki (1988b); ¹⁵ Akimoto (1983); ¹⁶ Aoki (1975).

mixing. At the final point on this continuum are the colonies of sexually reproducing individuals, represented in their most advanced form by ant and termite colonies. Here, although the members of the society are related, they are not genetically identical, and we would expect, and indeed find, considerable intracolony reproductive conflict (e.g. Seger, 1991).

The aphids occupy a particularly interesting position along this spectrum of social organization. Because individuals are mobile, aphid clones represent the simplest groups in which we would expect clonal mixing to create problems for the evolution of altruism. Up to this point, we would expect altruism to be rife; beyond it, we would expect it to be increasingly unlikely to have evolved.

In thinking about the evolution of altruism in clonal animals, we need to use a conceptual model that is somewhat different from the one that is applied to sexually reproducing animals. Conventionally, selection for altruism is considered to act on individuals. Helping behaviour will be selected for if the following inequality (Hamilton's Rule) is satisfied:

$$\frac{b}{c} > \frac{r(\text{donor to own offspring})}{r(\text{donor to beneficiary's offspring})}$$

where b is the increase in the number of the beneficiary's offspring as a result of the helping behaviour, c is the decrease in the number of the donor's offspring as a result of the helping behaviour, and r is relatedness (Starr, 1979).

In clonal animals, we must take a clone's-eye-view. An altruistic act performed by members of the clone, for example investing in soldiers, will be selected for, provided that the benefit to the clone is greater than the cost. Relatedness, in the classical sense, drops out of the picture: other individuals are either members of the same clone ($r = 1$) or they are not (r effectively equals 0). The relatedness between the altruist and recipient is still important but for a very different reason. Clonal mixing will act to reduce the benefit of altruism to the clone: as the extent of clonal mixing increases, the benefits will be increasingly diluted because they are wasted on unrelated individuals. Therefore, we expect a clone to take account of the extent of clonal mixing before performing an altruistic act, such as investing in soldiers, *only* because the mixing dilutes the benefits of the soldiers for that clone. That is, the clone is entirely uninterested in the effects of its altruistic act on an unrelated beneficiary's offspring.

III. THE BIOLOGY AND NATURAL HISTORY OF SOLDIER APHIDS

(1) *Which aphid species have soldiers?*

There are roughly 4400 species of aphids, and of these approximately 50 have been reported to have soldiers (Tables 2, 4). The species with soldiers are confined to two families, the Hormaphididae and the Pemphigidae (Fig. 2). It is generally accepted that the two families are closely related: they share a number of apomorphic characters, such as the possession of dwarf, wingless sexuals and a distinctive life-cycle (see below and Fig. 1) and wing venation (see Heie, 1987). The Pemphigidae and Hormaphididae are both rather ancient groups, whose shared derived habits – e.g. gall formation and their host-associations and life-cycles – probably originated over 65 MYA in the Cretaceous (Heie, 1987).

In most soldier-producing species, the soldiers occur in the galls on the primary host,

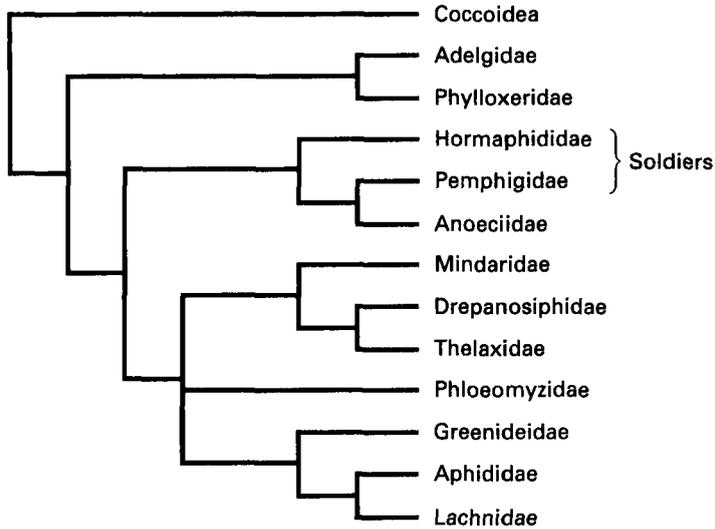


Fig. 2. Phylogeny of the aphids with the families of the soldier-producing species indicated. The phylogeny was reconstructed by Heie (1987) based on fossil evidence and consideration of morphological traits and life-cycle variation of extant taxa. The Coccoidea was used as an outgroup. Although there is some uncertainty in the tree, the close relatedness of the Pemphigidae and Hormaphididae is strongly supported.

but in two tribes – the Cerataphidini and the Eriosomatini – soldiers are also produced on the secondary host (Table 4). Evolutionary loss of the secondary host or more commonly the primary host has occurred in many soldier-producing species. The loss of alternate hosts has consequences for several components of the life cycle, most notably the loss of sexual reproduction in species that have lost the primary host (Fig. 1*b, c*; for review see Moran, 1992).

(2) *Studying the evolutionary origins of soldiers*

There are several reasons for studying soldier evolution within a phylogenetic setting. (1) A phylogeny allows investigation of the sequence of origin of related traits and the possible influence of one trait on the evolution of a second trait (Donoghue, 1989; Maddison, 1990; Pagel, 1994). (2) Phylogenetic information allows determination of independent evolutionary events so that robust statistical tests of associations between traits can be carried out (Harvey & Pagel, 1991). (3) By mapping trait origins onto a phylogeny we can develop a rough idea of the trait's evolutionary 'lability', or the frequency with which it has been gained and lost over evolutionary time, as well as information on morphological and behavioural convergence. For example, aphid soldiers on the secondary host from the two cerataphidine genera *Ceratovacuna* and *Pseudoregma* are very similar in appearance and behaviour. By mapping the character 'soldier production' onto a phylogeny of the Cerataphidini we can examine whether this similarity is due to homology or convergence (see Fig. 3 and below). (4) A phylogenetic view of trait evolution may allow rejection of specific one-tailed hypotheses for trait origins. For example, the hypothesis that soldiers evolve when a species switches to a host that lowers its rate of increase could be rejected by demonstrating that

Table 4. *Aphid species in which soldier behaviour has been observed*

Species	Primary host	Secondary host	Primary host soldiers*				Secondary host soldiers*				References
			Instar	di/mono	Sterile	Weapons	Instar	di/mono	Sterile	Weapons	
Hormaphididae											
Cerataphidini											
<i>Astegopteryx bambucifolia roepkei</i>	<i>Styrax suberifolia</i>	Bamboos	II	di	Sterile	styl	I	mono	Not sterile	styl	Aoki & Kurosu (1989 <i>b-d</i>), Kurosu & Aoki (1991 <i>a</i>)
<i>setigera</i>	<i>Styrax benzoin</i>	Monoecious	II	di	?	styl					Kurosu & Aoki (1995)
<i>styracophila</i>	<i>Styrax benzoin</i>	?	II	di	?						Noordam (1991), Stern (personal observations)
<i>Ceratophis fransemani</i>	<i>Styrax benzoin</i>	Palms	II	di	Sterile	styl					Noordam (1991), Stern <i>et al.</i> (1995)
<i>vandermeermohri</i>	<i>Styrax serrulata</i>	?	II	di	?	styl					Aoki & Kurosu (personal communication)
<i>Ceratoglyphina styracicola</i>	<i>Styrax suberifolia</i>	Bamboo (<i>Pleioblastus</i>)	II	di	Sterile	styl					Aoki <i>et al.</i> (1977), Aoki (1979), Aoki & Kurosu (1989 <i>b, c</i>), Aoki <i>et al.</i> (1991), Kurosu & Aoki (1991 <i>b, c</i>)
<i>Ceratovacuna floccifera japonica</i>	?	Bamboo					I	di	Sterile	Horns, fl	Noordam (1991)
<i>lanigera</i>	<i>Styrax japonica</i>	Bamboos (<i>Pleioblastus chino</i>)	II	di	Sterile	styl	I	di	Sterile	Horns, fl	Aoki <i>et al.</i> (1981), Aoki (1987), Aoki & Kurosu (1989 <i>b</i>), Kurosu <i>et al.</i> (1990), Aoki & Kurosu (1991 <i>b</i>)
<i>longifila nekoashi</i>	Unknown	<i>Miscanthus sinensis</i> (sugar cane)					I	mono	Not sterile	Horns	Aoki <i>et al.</i> (1984), Aoki & Kurosu (1987), Arakaki (1989)
sp. C	Unknown	A bamboo					I	di	Sterile	Horns, fl	Aoki & Kurosu (1989 <i>b</i> , personal communication)
sp.	Unknown	<i>Microstegium vimineum</i>	I	mono	Not sterile	styl					Kurosu & Aoki (1988 <i>a</i> , 1990 <i>b</i>)
<i>Pseudoregma alexanderi</i>	Unknown	<i>Sasa veitchii</i>					I	di	Sterile	Horns, fl	Aoki & Kurosu (1989 <i>b</i>)
<i>bambucicola</i>	<i>Styrax suberifolia</i>	<i>Bambusa sp.</i> (bamboo)					I	di	?	Horns, fl	Stern (personal observations)
<i>koshunensis</i>	<i>Styrax suberifolia</i>	<i>Bambusa</i> (bamboos)	II	di	Sterile	styl, fl	I	di	Sterile	Horns, fl	Aoki <i>et al.</i> (1984), Aoki & Kurosu (1987), Sakata & Itô (1991), Sakata <i>et al.</i> (1991), Noordam (1991), Aoki & Kurosu (1992 <i>a</i>)
<i>montana nicolaiiae</i>	Unknown	<i>Bambusa</i> sp. (bamboos)	II	di	Sterile	styl, fl	I	di	Sterile	Horns, fl	Aoki <i>et al.</i> (1981), Aoki (1982 <i>b</i>), Aoki & Kurosu (1991 <i>c</i>), Arakaki (1992 <i>b, c</i>)
<i>panicola</i>	Unknown	Bamboo					I	di	?	Horns, fl	Noordam (1991)
<i>pendleburyi sundamica</i>	Unknown	Zingiberaceae					I	di	?	Horns, fl	Stern (personal observations)
<i>Tuberaphis coreana leeuweni</i>	<i>Styrax suberifolia</i>	<i>Oplismenus</i> spp.					I	di	Sterile	Horns, fl	Aoki <i>et al.</i> (1981), Aoki (1982 <i>a</i>)
		<i>Cyrtococcum</i>					I	di	?	Horns, fl	Noordam (1991)
		Bamboos					I	di	?	Horns, fl	Noordam (1991)
		Zingiberaceae	II	di	Sterile	styl	I	di	?	Horns, fl	Noordam (1991), Schütze & Maschwitz (1991), Stern, Aoki & Kurosu (unpublished data), Aoki (personal communication)
	<i>Styrax formosana</i>	Loranthaceae	II	di	Sterile	styl					Aoki & Kurosu (1989 <i>b</i>), Stern, Aoki & Kurosu (unpublished data)
	<i>Styrax serrulata</i>	Monoecious	II	di	Sterile	styl					Aoki <i>et al.</i> (ms.)

<i>styraci</i>	<i>Styrax obassia</i>	Monoecious	II	di	Sterile	styl						Aoki & Kurosu (1989a, b, 1990)
<i>sumatrana</i>	<i>Styrax serrulata</i>	?	II	di	?	styl						Aoki & Kurosu (personal communication)
<i>takenouchii</i>	<i>Styrax japonica</i>	Loranthaceae	II	di	Sterile	styl	I	mono	Not sterile	styl		Aoki & Usuba (1989), Kurosu <i>et al.</i> (1994), Stern, Aoki & Kurosu (unpublished data)
Hormaphidini <i>Hamamelistes betulinus makabae</i>	Unknown	<i>Betula maximowicziana</i>					I	?	?	styl		Inouye (1963), Akimoto (personal communication)
Nipponaphidini <i>Distylaphis foliorum</i>	<i>Distylium stellare</i>	Leaves of <i>D. stellare</i>	I	mono	?	styl, fl						Noordam (1991)
<i>Nipponaphis distyliicola</i>	<i>Distylium racemosum</i>	<i>Quercus</i> spp.	I	mono	Not sterile	styl						Itô (1989), Aoki (personal communication)
Pemphigidae Eriosomatinae, Eriosomatini <i>Colophina arma clematicola</i>	<i>Zelkova serrata</i>	<i>Clematis stans</i>	II	mono	Not sterile	styl, fml	I	di	Sterile	styl, fml		Aoki (1977b, 1980b)
<i>clematis</i>	<i>Zelkova serrata</i>	<i>Clematis terniflora</i>					I	mono	Not sterile	styl, fml		Kurosu & Aoki (1988b), Kurosu & Aoki (1991d)
<i>clematis</i>	<i>Zelkova serrata</i>	<i>Clematis apiifolia</i>	II	mono	Not sterile	styl, fml	I	di	Sterile	styl, fml		Aoki (1977a, b, 1980b)
<i>monstrifica</i>	Unknown	<i>Clematis floribunda</i>					I	di	Sterile	styl, fml		Aoki (1983)
<i>Eriosoma moriohense</i>	<i>Ulmus davidiana</i>	<i>Sedum</i> spp.	II, III	mono	Not sterile	styl						Akimoto (1983)
<i>Hemipodaphis persimilis</i>	<i>Zelkova serrata</i>	Unknown	I	mono	Not sterile	styl, fml						Aoki (1978), Akimoto (1983, 1992)
Fordinae Fordini <i>Smynturodes betae</i>	<i>Pistacia atlantica</i>	Gramineae, Leguminosae, Solanaeae	Adult	mono	Not sterile	styl, fmhl						Inbar (ms), Burstein & Wool (1993)
Pemphiginae Pemphigini <i>Epipemphigus nisimae</i>	<i>Populus maximowiczii</i>	???	I	mono	Not sterile	styl						Aoki (personal communication) Akimoto (personal communication)
<i>Pemphigus dorocola</i>	<i>Populus maximowiczii</i>	Unknown	I	mono	Not sterile	styl, hl						Aoki (1978, 1980a)
<i>monophagus</i>	<i>P. angustifolia</i> , <i>P. balsamifera</i>	Monoecious	I	mono	Not sterile	styl, hl						Aoki & Kurosu (1988)
<i>obesinympxae</i>	<i>Populus fremonti</i>	Unknown	I	mono	Not sterile	styl, fmhl						Moran (1993)
<i>spyrothecae</i>	<i>Populus nigra</i>	Monoecious	I	di	Not sterile	styl, hl						Aoki & Kurosu (1986), Foster (1990), Foster & Benton (1992)
Prociphilini <i>Pachypappa marsupialis</i>	<i>Populus maximowiczii</i>	Unknown	I	di	Not sterile	styl						Aoki (1979)

• These columns show, in sequence, whether: the soldiers are I or II instars, larvae are mono or dimorphic, sterile or not, and the weapons used (styl [stylets], f, m, hl [fore-, mid-, hind-legs]), horns.

soldiers are gained upon acquisition of hosts that allow a greater rate of increase. (5) If considerable evidence on current utility is available from extant taxa, then it may be possible to determine the causes of trait origins (Coddington, 1988; Baum & Larson, 1991). Below, we briefly discuss phylogenetic reconstruction of trait histories and then illustrate approaches (2) and (3) with a real example from aphids.

It is important to keep in mind that any estimate of phylogeny has some associated error due to inconsistencies in the data set and inadequacies in the models used to reconstruct the phylogeny. If this associated error is sufficiently large, then we must be sceptical of any comparative analysis that utilizes this estimate of the phylogeny (cf. McLennan & Brooks, 1993). With the phylogeny in hand it is then necessary to reconstruct the presumed evolution of the trait along the branches of the phylogeny. Such reconstructions are usually pursued using parsimony which assigns character states at each node on the phylogeny so as to minimize the total amount of evolutionary change required to explain the observed distribution of character states among extant taxa (Maddison & Maddison, 1992). This process is also vulnerable to inaccuracies, especially when traits follow non-parsimonious evolutionary routes, although these errors are much more difficult to detect and correct. With a reconstruction of trait histories we are ready to investigate trait origins.

(a) *Patterns of origins of soldier production*

For the following discussion we utilize the phylogenies provided by Heie (1987) and Stern (1994) and the classifications of Eastop (1977) and Heie (1980). Heie's phylogeny of the Aphidoidea (Fig. 2) was constructed using information both from fossils and extant taxa and represents the best current estimate of aphid family relationships. From Heie's phylogeny it is clear that soldier production has a phylogenetically limited distribution. Soldier production has been found only in the families Pemphigidae and Hormaphididae (Fig. 2). However, a closer look reveals a more interesting story.

Stern (1994) has constructed a phylogeny for 14 species of the Hormaphididae based on mtDNA sequence data. His phylogeny reveals that soldiers have been gained at least five times, with one loss, in this family (Fig. 3). Stern discusses three reasons for why this is probably an underestimate of the true number of origins and losses of soldiers. First, many soldier-producing hormaphidines were not included in this phylogeny. This is particularly important for the Hormaphidini and Nipponaphidini where recently discovered soldier-producing species (e.g. the nipponaphidine *Distylaphis foliorum*, (Noordam 1991) and the hormaphidine, *Hamamelistes betulinus* Inouye, (S. Akimoto, personal communication)) will probably have a large impact on our estimate of soldier evolution in this family when incorporated into the phylogeny. Secondly, the life cycles of many soldier-producing species are poorly known so that we do not know whether they produce soldiers on both hosts (see Fig. 3). As we discuss below, it seems highly likely that primary- and secondary-host soldiers of the Cerataphidini represent separate evolutionary events. Finally, Stern sampled only two species from the genus *Ceratovacuna*, which is polymorphic for secondary-host soldier production. Further analysis of this genus may reveal further origins and losses of soldiers. This phylogeny supports the hypothesis that soldiers evolved separately on the primary and secondary hosts in the Cerataphidini (Aoki, 1987; Aoki & Kurosu, 1989b). We discuss this hypothesis in further detail later.

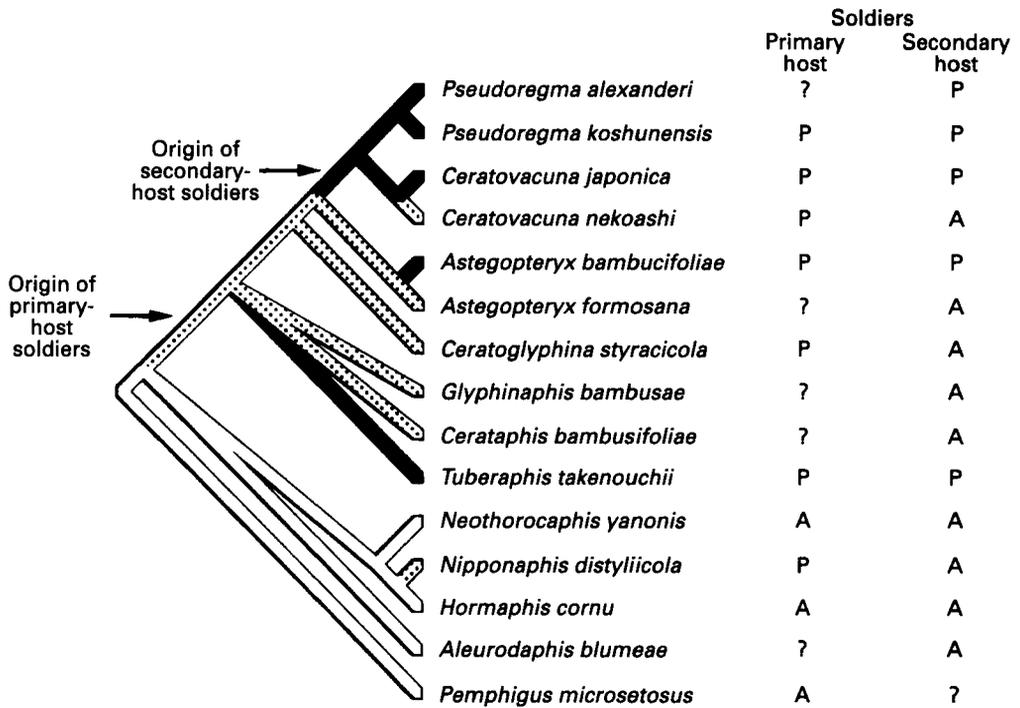


Fig. 3. Phylogeny of selected species of the Hormaphididae reconstructed on the basis of mtDNA sequence data (modified from Stern, 1994 with permission). P, presence of soldiers, A, absence of soldiers. Soldier evolution is reconstructed on the phylogeny using parsimony. Stippled branches represent lineages producing primary-host soldiers, black branches represent lineages producing both primary-host and secondary-host soldiers. This reconstruction requires five origins of soldiers and one loss (in *Ceratovacuna nekoashi*). [Note that *Astegopteryx formosana* and *Ceratoglyphina styracicola* were originally published in Stern (1994) under the junior synonyms *A. unimaculata* and *C. bambusae* (see Table 3). In addition, soldiers in the secondary-host generations of *Tuberaphis takenouchii* were reported after the original publication of the phylogeny.]

To examine soldier production within the Pemphigidae we have converted the classifications of Eastop (1977) and Heie (1980) into a phylogeny, assuming that each taxonomic group is monophyletic (Fig. 4). For simplicity, we assume that the distribution of soldier-producing species can be accounted for by a single evolutionary event (either a gain or a loss) within each tribe. Because we lack detailed phylogenetic information, however, the reconstructed transitions are dependent on assumptions about the relative frequency of origins versus losses. If we assume that the evolution of soldiers was rare, but that loss was relatively common, then the reconstruction in Fig. 4*b*, requiring one origin of soldiers and six losses, makes the most sense. In contrast, if we assume that gains and losses are equally likely, the traditional parsimony assumption, then the reconstruction requires four evolutionary origins and no losses (Fig. 4*a*). Because soldier-producing species are relatively rare within each tribe, this latter reconstruction seems more likely. Combining the analyses of the Hormaphididae and Pemphigidae, it is clear that soldiers have evolved a minimum of six to nine times, but probably many more times.

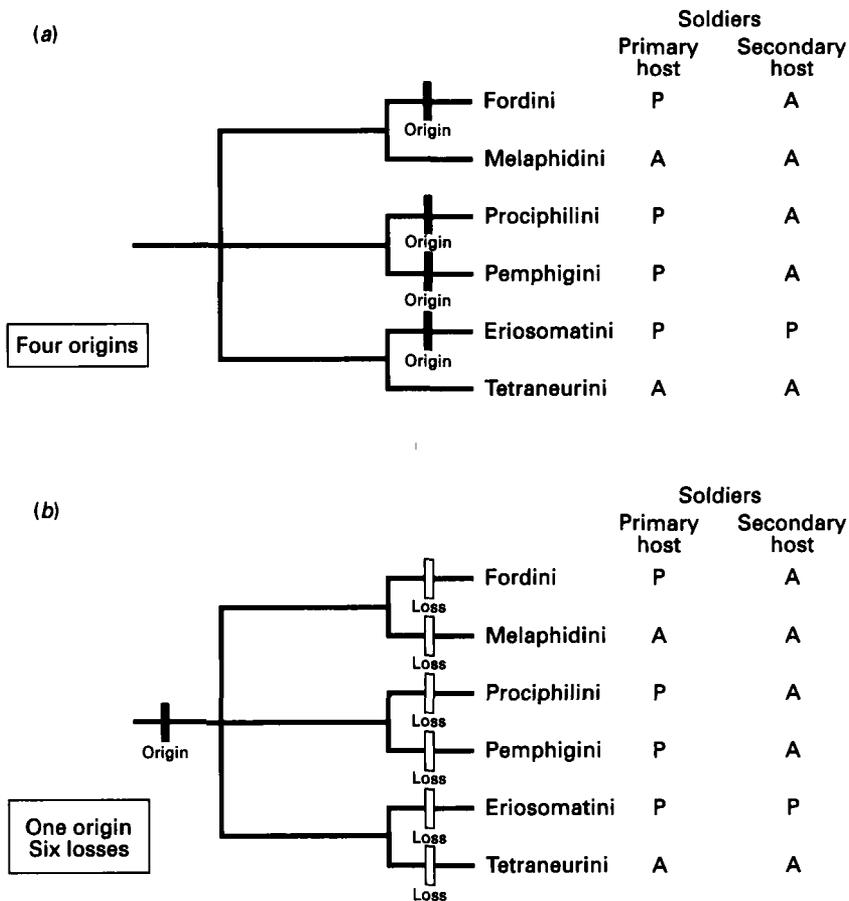


Fig. 4. The taxonomic relationships of the Pemphigidae [from Eastop (1977) and Heie (1980)] represented as a hierarchical tree, assuming all taxonomic categories are monophyletic. The minimum number of evolutionary events leading to the current distribution of soldiers is indicated for two extreme scenarios. (a) If we assume gains and losses are equally likely then a minimum of four events (all origins) is required. (b) If, however, we assume that losses are more likely than gains then we require seven events (one origin and six losses). The lack of phylogenetic resolution does not allow discrimination between these alternatives but this example demonstrates the importance of the evolutionary assumptions used to reconstruct character evolution.

(3) *A classification of aphid soldiers*

The defensive morphs of most aphid species are immatures: they are usually first or second instars, although in *Eriosoma moriokense* they include third instars (Akimoto, 1983) and in *Smynthurodes betae* they are adults (M. Burstein, unpublished). The defensive morphs can be either obligately or facultatively sterile and they can either differ (larvae are dimorphic) or not differ (larvae are monomorphic) from conspecific non-soldier larvae of the same instar. Obligately sterile morphs do not moult to the next instar and therefore are not able to reproduce. Facultatively-sterile morphs can moult to the next instar and are thus potentially able to reproduce, although they may die whilst soldiering. This classification scheme gives rise to three categories of soldiers: monomorphic, facultatively-sterile morphs; dimorphic, facultatively-sterile morphs;

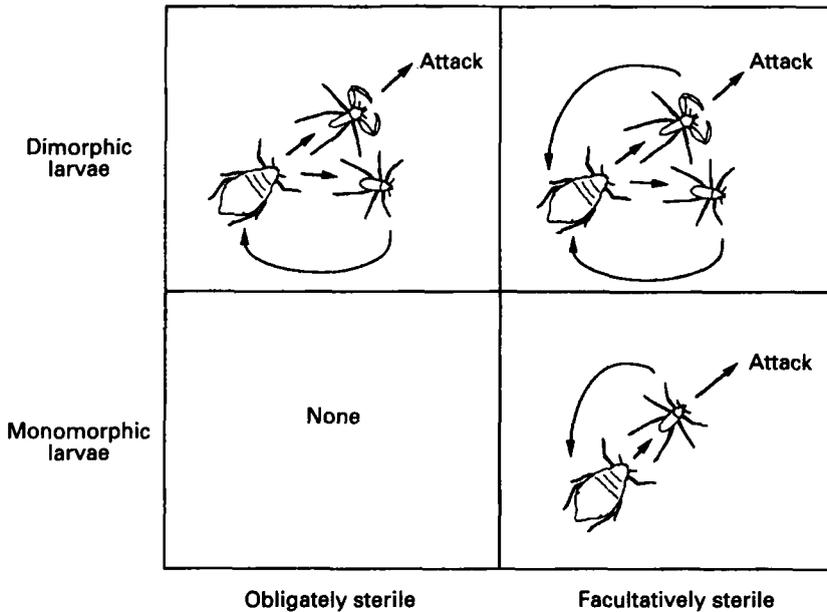


Fig. 5. A simple categorization of soldiers. Soldiers can be either a morphologically or behaviourally specialized caste (Dimorphic larvae) or not (Monomorphic larvae). Morphologically specialized soldiers can be either facultatively sterile or obligately sterile. Facultatively sterile soldiers have the ability to molt, continue development and reproduce, but they may not always do so.

and dimorphic, obligately-sterile morphs (Fig. 5). It has been common to restrict the term 'soldier' to the obligately sterile morphs (e.g. Aoki, 1987). However, it is important to realize that all of these defensive morphs incur similar costs on a clone. The general cost of defence to a clone is a decrease in the growth rate of the colony and a concomitant reduction in the number of migrants. These costs are manifested as increased risk of death or injury to defensive individuals, increased investment in cuticular weaponry and body size, increased development time required by moulting defensive morphs, and sterility. To single out one of these costs – sterility – as the only criterion of a soldier does not seem justified, and we will therefore use the term 'soldier' to describe all the different defensive morphs. We discuss the analogous costs of all types of soldier production in more detail later. Here we present a categorization of the chief types of aphid soldiers based primarily on taxonomic categories but including morphological and behavioural traits (Table 4).

(a) *Pemphigus* type (*Pemphigidae*)

These relatively unspecialized soldiers (Fig. 6a) are always restricted to the generations in galls on the primary host; they are facultatively sterile, and they are almost always first instars. They attack predators by piercing them with their stylets and by squeezing them with their enlarged and heavily sclerotized hind-legs and attempting to rupture the predator's cuticle with their well-developed hind-claws (Foster, 1990) or all six legs (Moran, 1993). The least specialized *Pemphigus*-type soldiers are found in *Pemphigus dorocola*: Aoki (1978) showed that the monomorphic first instars (and a few second instars) attacked a lepidopterous larva placed in the gall.

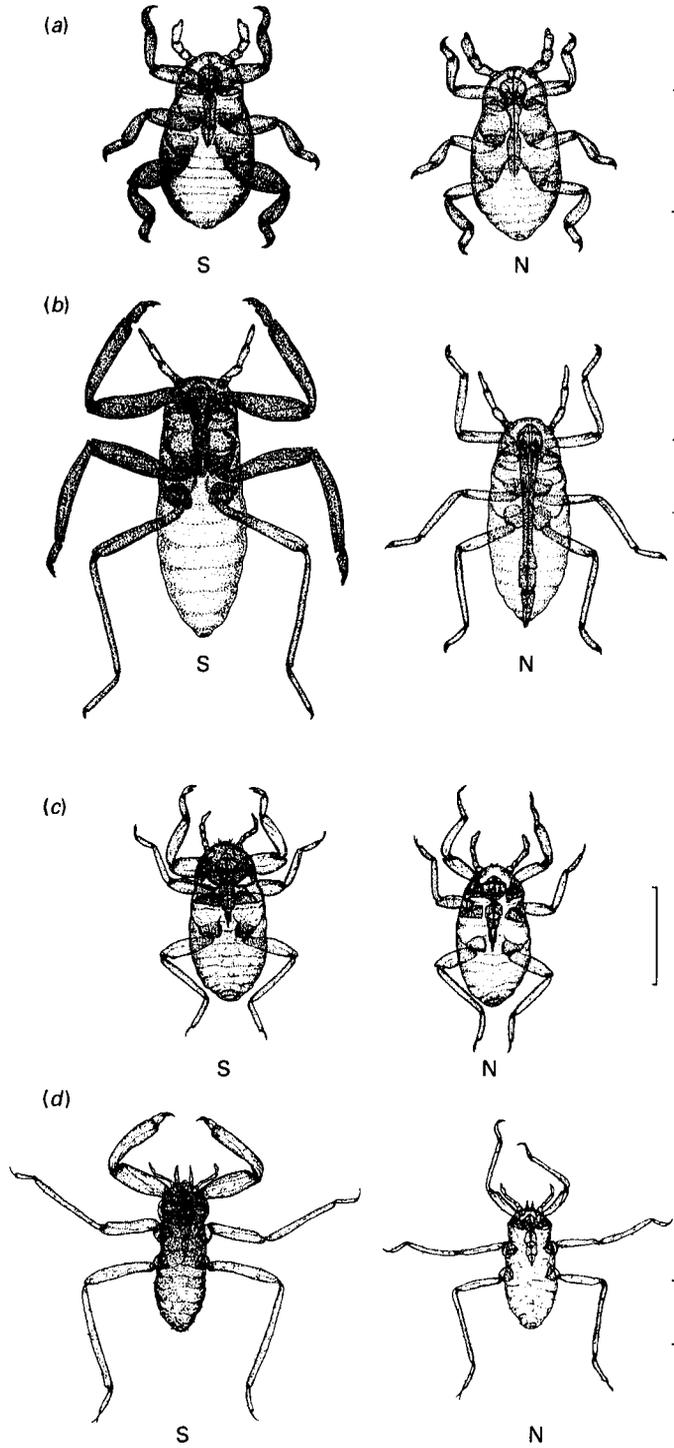


Fig. 6. (a) First-instar larvae of *Pemphigus spyrothecae* from galls on the primary host, *Populus nigra*. Soldier (left) has enlarged legs and a thickened cuticle relative to the normal larva (right). Scale = 0.5 mm. (b) First-instar larvae of *Colophina monstrifica* from the secondary host, *Clematis floribunda*. Soldier (left) is considerably larger than the normal larva (right), and has a shorter rostrum and a thickened cuticle.

In *P. monophagus* there are three generations of aphids in the gall, and two types of first instars, thick- and normal-legged, and it is presumed that the thick-legged larvae behave as soldiers (Aoki & Kurosu, 1988). These larvae, however, are not strictly dimorphic, since they are produced by different generations: the thick-legged first instars are produced by the foundress and the normal-legged ones by later generations. More specialized are the soldiers of *P. spyrothecae*; larvae are dimorphic (both normal and soldier first-instars are produced in the third gall generation (Lampel, 1968–9)) and soldiers effectively defend the colony against natural predators (Aoki & Kurosu, 1986; Foster, 1990). The soldiers produced towards the end of the season may be functionally obligately sterile since, although they are able to moult, they probably do not have time to develop to adulthood (Foster & Northcott, 1994; cf. Akimoto, 1992). The most specialized *Pemphigus* type soldiers so far described are those of *P. obesinymphae* (Moran, 1993). The foundress produces monomorphic soldiers throughout the very extended gall-inhabiting phase. These soldiers remain as first instars throughout this period, which may last several months, aggressively defending the gall against predators by using all three pairs of legs.

(b) *Eriosomatini* type (*Pemphigidae*)

Soldiers of this type (Fig. 6b) occur on both the primary and the secondary hosts. They hold predators firmly with their enlarged, well-sclerotized fore- and mid-legs, and pierce the predator's cuticle with their stylets, which are supported by a short, powerful rostrum (Aoki, 1977a, b). The soldiers on the secondary host are always first instars. The least specialized soldiers of this type are probably those of *Colophina clematicola*, which are monomorphic and facultatively sterile (Kurosu & Aoki, 1988). More specialized are the soldiers of *C. arma*, *C. clematis*, and *C. monstrefica*, which are obligately sterile and morphologically differentiated from normal larvae (Aoki, 1976, 1977a, b, 1980b, 1983). The soldiers on the primary host are less specialized: they are always monomorphic and never obligately sterile. They are either first (*Hemipodaphis*) or second instars (*Colophina*) (Aoki, 1978, 1980b; Akimoto, 1983, 1992). Because the soldiers on the primary and secondary hosts are morphologically similar and use similar weapons, it is generally assumed that they are homologous and represent a single origin of defensive behaviour.

It is possible that the 2nd- and 3rd-instar larvae of *Eriosoma moriokense* represent a further independent origin of soldier activity (Akimoto, 1983). The defensive behaviour is not very well-developed: the larvae clutch the predators and appear to attack them with their stylets.

(c) *Styrax-gall* type (*Hormaphididae*: *Cerataphidini*)

These soldiers (Fig. 6c) occur in galls on the primary host (*Styrax*): they use their stylets as their only weapons, the larvae are usually dimorphic, and soldiers are second instars and are usually obligately-sterile (e.g. Aoki, Yamane & Kuichi, 1977; Aoki & Kurosu, 1992a). Aphids from a range of cerataphidine genera produce this type of

Scale = 0.5 mm. (c) Second-instar larvae of *Pseudoregma bambucicola* from galls on the primary host, *Styrax suberifoliae*. The soldier (left) has enlarged legs and a thickened cuticle relative to the normal larva (right). Scale = 0.5 mm. (d) First-instar larvae of *Pseudoregma bambucicola* from the secondary host, bamboo. The soldier (left) is larger than the normal larva (right) and has enlarged horns on the head and a thickened cuticle. Scale = 0.5 mm.

soldier (Table 2; Aoki & Kurosu, 1989*b*). An interesting variant on these soldiers are the so-called 'outsiders' which have been reported in three cerataphidine species [*Ceratovacuna nekoashi*, *Astegopteryx bambucifoliae* and *Ceratoglyphina styracicola* (Kurosu & Aoki, 1988*a*, 1991*a*, *b*)]. These are first instars produced relatively late in the season by the foundress, and their role is to defend against predators on the surface of the gall. Larvae are monomorphic and they are usually functionally obligately-sterile, since the subgalls are closed by the time they are born (although the outsiders of *A. bambucifoliae* are able to enter the subgalls) and they apparently cannot feed outside the gall.

(*d*) *Horned type (Hormaphididae : Cerataphidini)*

These soldiers (Fig. 6*d*) are first instars and they only occur on the secondary hosts. They have strongly sclerotized tergites, enlarged, greatly thickened fore-legs armed with strong claws, and they use a novel weapon – horns on the front of their heads. They grasp predators with their fore-legs and tear the predator's cuticle with their frontal horns (e.g. Aoki & Miyakazi, 1978). They may be either obligately or facultatively sterile, and larvae may be mono- or dimorphic. The first instars of *Ceratovacuna lanigera* are the least specialized of the horned soldiers: larvae are monomorphic, facultatively sterile, and they appear to specialize in attacking predator eggs, which are a relatively easy target (Aoki, Kurosu & Usuba, 1984; Aoki & Kurosu, 1987), although they will also attack predatory larvae (Arakaki, 1989). The most specialized horned soldiers, indeed arguably the most specialized of all soldier aphids, are the soldiers of some of the *Pseudoregma* species. These are obligately sterile, larvae are dimorphic and in one species, *P. alexanderi*, it is possible that there are two soldier subcastes (Aoki & Miyazaki, 1978; Stern, Moon & Martinez del Rio, unpublished data). In some species, soldiers aggressively attack a range of predators (Aoki, Akimoto & Yamane, 1981; Schütze & Maschwitz, 1991).

Even though some species (e.g. *Pseudoregma* spp.) may have both *Styrax*-gall type soldiers on the primary host and horned type soldiers on the secondary host, Aoki (1987) and Aoki & Kurosu (1989*b*) have argued strongly that these two types of soldiers are not homologous but represent independent origins of soldier behaviour. First, the primary-host soldiers are second instars, whereas the secondary-host soldiers are first instars. Secondly, the morphology of the two types of soldier is very different: the *Styrax*-gall soldiers use their stylets to pierce predators, whereas the soldiers on the secondary hosts have enlarged fore-legs and tear predators with their frontal horns. Thirdly, the *Styrax*-gall soldiers almost certainly inject something into the predators, whereas the horned aphids do not. Finally, the taxonomic distribution of the two types of soldiers hints that they might have evolved independently. This hypothesis was independently supported by two phylogenetic analyses, one based on mtDNA sequence data (Fig. 3; Stern, 1994) and a second based on the morphology of endosymbionts and galls (Fukatsu *et al.*, 1994).

(*e*) *Other secondary-host cerataphidine types (Hormaphididae : Cerataphidini)*

Two other types of soldiers have been found on the secondary hosts within the Cerataphidini. Aoki & Kurosu (1989*d*) reported that monomorphic horned first-instar larvae of *Astegopteryx bambucifoliae* produced on the secondary host occasionally attack

predators with their stylets. Kurosu, Aoki & Fukatsu (1994) reported soldiers from *Tuberaphis takenouchii* produced in pseudo-galls on the mistletoe secondary host. Monomorphic first-instar larvae were found to attack lepidopterous larvae introduced into the gall by clinging to the larvae and stinging them with their stylets. Attacks by both species have not been proven to kill or deter predators although the fact that the larvae will attack predators is significant. In the future, it will be very important to demonstrate, preferably based on experimental evidence, whether such stylet attacks by this and possibly other horned larvae (e.g. *Ceratovacuna silvestrii*, Agarwala, Saha & Ghosh, 1984) are truly altruistic defensive behaviour which deters or kills predators.

(f) *Other types*

Inbar (unpublished manuscript) recently discovered unusual adult soldiers from the tribe Fordini (Pemphigidae). *Smynthurodes betae* West produces two galls sequentially on the primary host, *Pistacia atlantica* (Anacardiaceae). The foundress that hatches from the sexual egg produces a small round gall on the leaf midrib and the next generation first-instars leave this gall to found final galls on the leaf margins. It is these second generation individuals that are aggressive both as first instars and as adults. The first instars defend their gall initiation site against conspecific and interspecific first instar aphid invaders. They use a variety of fighting techniques including face-to-back kicking, back-to-back kicking, face-to-face kicking, and escalated fights where the larvae grab each other and roll over several times. First instars do not remain aggressive for the entire duration of the instar, but after some time they appear to become apathetic to the presence of other invaders. This territorial defence is similar to aggressive behaviour among gall foundresses in other species (see below). However, when these larvae develop into adults they adopt a slightly different aggressive behaviour that can, perhaps more properly, be termed soldiering. The adults defend the gall against conspecific first instars, first-instar anthocorid bugs and psyllidinquilines. The defensive behaviour is unique among soldiers; the adults grab the invader and pull it close to its body with all six legs. The soldier then rolls over onto its back and attempts to insert its stylets into the invader (Fig. 7). This represents the first report of soldiers from the Fordinae and the first report of defensive behaviour in adults, and it will be well worth looking for soldiers in other gall-forming species from this subfamily.

It is likely that soldiers have evolved independently within the Nipponaphidini (Hormaphididae), but there have been few critical studies of soldiers in this tribe. Kurosu *et al.* (unpublished, reported in Itô (1989)) found that first instars of *Nipponaphis distyliicola* attack invading predatory moth larvae. Noordam (1991) describes a soldier first-instar larva in the gall formed by *Distylaphis foliorum*. The soldier is very distinctive, with enlarged, heavily sclerotized fore-legs bearing fused first and second tarsal segments and with relatively short, robust stylets. The behaviour of soldiers of this second species is unknown. The phylogenetic position of these species (see Fig. 3 for *N. distyliicola*) and their distinctive morphology suggests that they represent at least one independent origin of soldier behaviour.

Finally, there are preliminary reports of soldiers from the hormaphidine aphid *Hamamelistes betulinus makabae* Inouye (S. Akimoto, personal communication) in pseudo-galls on the secondary host *Betula maximowicziana*. This is the first report of soldiers from the tribe Hormaphidini and almost certainly represents an independent

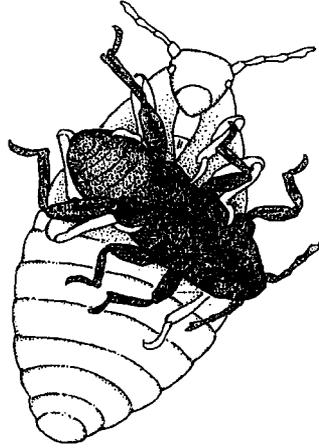


Fig. 7. Adult of *Smynturodes betae* (Fordini: Pemphigidae) attacking conspecific larva (from Inbar, ms with permission). The adult grabs the larva, rolls over onto its back and attempts to puncture the larva with its stylets.

origin of soldiers. Importantly, if soldiers are not produced during the primary-host generations, then this will be the first species known to produce soldiers on the secondary host and not on the primary host.

(g) *Summary of soldier classification*

In summary, a wide range of aphid taxa produce soldiers and these soldiers vary greatly in morphology, behaviour, larval instar, and presence or absence of obligate-sterility and larval dimorphism. Our classification is clearly rudimentary but reflects the major categories, primarily along taxonomic lines, that can be drawn at the current time. In the future, as we learn more about soldiers, it may be possible to construct a more functional classification of soldiers. It will become increasingly important as we gain more phylogenetic information on soldier-producing taxa to study convergence, not only of soldiers as a broad category, but also of the details of soldier morphology, behaviour and life-history.

New soldier-producing aphids are being discovered every year and we expect this trend to continue for some time. As the community of known soldier-producing aphids increases it becomes imperative to document the natural history of soldier-producing species and related species known to not produce defensive larvae. Findings of a lack of defensive behaviour in a species are as significant as findings of soldiers and play a critical role in understanding why some species evolved soldiers. We, therefore, encourage investigators to publish the findings of all surveys for soldier production whether soldiers are found or not. Only then will robust comparative studies be possible.

(4) *Galls and soldier aphids*

All soldier-producing aphid species induce galls on their host plants, although not all soldiers are produced during galling generations. Foster & Northcott (1994) discuss how living in a gall might affect the social organization of aphids and facilitate the evolution of soldiers. It is generally argued that if animals live in a home that is costly

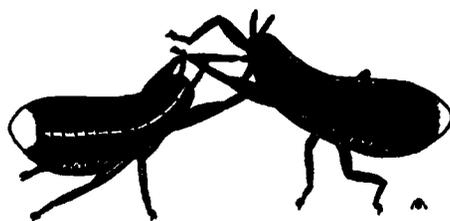


Fig. 8. Fight between first instar foundresses of *Epipemphigus nisimae* (from Aoki & Makino, 1982 with permission).

to produce or simply valuable and defensible then this will favour the evolution of sociality, either because it will be advantageous for the young to remain in the parental home rather than make their own, or because they will only be able to construct a home by cooperating with others (e.g. Alexander, Noonan & Crespi, 1991; Krebs & Davies, 1993). All highly social animals, besides the horned type and some Eriosomatini type soldier species discussed above, live either in nests (Hymenoptera, Isoptera), burrows (mole-rats), tunnels (bark-beetles), or galls (thrips, aphids). However, for clonal animals the argument is subtly different: instead of focusing on an individual's decision to stay or leave the maternal home, or to found a nest singly or jointly, we have to look at the clone's decision to invest or not to invest in defensive individuals. Below we discuss five factors associated with gall-living that might have facilitated the evolution of soldiers. Foundress fighting and intergall migration can be considered preadaptations providing traits that might have been adopted by a soldier morph. Gall cleaning represents a likely gall-associated precursor to soldier evolution that might have also directly selected for soldiers. The last two factors, defendability of the gall and genetic integrity, are gall-associated traits that would directly select for soldiers. (There is not space here to consider the selective advantages of gall-making itself – see Price, Fernandes & Waring, 1987; Forrest, 1987.)

(a) Foundress fighting for gall-initiation sites

Aphids have a ready-made weapon in the form of their stylets, but these are not normally used offensively. An important exception to this is provided by the first-instar foundresses that have been shown to fight each other for access to good sites at which to initiate galls: this has been observed in both soldier-producing and non-soldier-producing species within the two soldier-producing families. For example, first-instar foundresses of *Epipemphigus nisimae* fight each other within immature galls; they fight face-to-face, often to the death, grappling each other with their fore-legs and inflicting lethal damage with their stylets (Fig. 8; Aoki & Makino, 1982). First-instar foundresses of *Pemphigus betae* can fight each other for up to two days, in fierce rear-to-rear shoving and kicking contests using their hind legs (Whitham, 1979). Akimoto (1988) suggests that the foundresses of *Eriosoma yangi* do not form galls but intrude into ready-made galls of other *Eriosoma* species, killing the host foundress. Kurosu & Aoki (1990b) report fighting between first-instar foundresses of *Ceratovacuna nekoashi* in competition for suitable gall-initiation sites; the aphids kick and fight each other, sometimes inflicting fatal injuries with their stylets. It is noteworthy in all these examples that the first-instar foundresses are morphologically specialized for fighting, being heavily

sclerotized and – at least in the case of *E. niisimae* – being endowed with well-developed legs, whereas later instars are not specialized in this way (Dunn, 1960; Aoki & Makino, 1982). It seems, therefore, that in both of the soldier-producing aphid families, there already existed a specialized fighting stage, the first-instar foundress, whose morphology and behaviour could then have been used in later gall generations, not in fighting conspecifics but in defending the clone against predators. This is clearly demonstrated in the recently discovered soldier species *Smynthuodes betae*, discussed earlier, in which the first instars defend their gall initiation sites against competitors and later, as adults, they act as soldiers, defending the gall against invaders and predators (Inbar, unpublished manuscript).

(b) Intergall migration

In an aphid species constrained to live in galls, there might be a considerable selective advantage to those clones that invested some of their resources in individuals that habitually migrated to seek out and colonize other galls (Aoki, 1982*a*). These aphids, described as 'self-propelled cuckoo eggs' by Hamilton (1987), might acquire behaviours and morphology, for example well-developed walking abilities, increased sclerotization to combat desiccation whilst outside the gall, and general breaking-and-entering capabilities, that would be useful for them not only as migrants but also as soldiers. Aoki (1979) describes a specialized migratory morph in the aphid *Pachypappa marsupialis* that fits this scenario remarkably well. The migratory first instars have a long rostrum and sclerotized tergal plates, and Aoki established experimentally that they leave the maternal gall and intrude into empty or successfully developed conspecific galls, where they grow and become emigrant alates. In addition, he observed some of these migrants apparently attacking eggs of syrphids. Aoki (1982*a*) developed an ESS model to describe how much a fundatrix should invest in migrants, and it would be interesting to test this model further.

There is increasing evidence that other species of aphids migrate between galls. Setzer (1980) analyzed allozyme variation of aphids within galls of *Pemphigus populitransversus* and *P. populicaulis* and found that as many as 25 % of the aphids were not of the same phenotype as the fundatrix. Galls that were experimentally isolated with cloth bags had colonies with greatly reduced allozymic variation. Williams & Whitham (1986) demonstrated that immature aphids migrate out of galls, both on abscising and healthy leaves. However, Hebert, Finston & Footitt (1991) found only one gall containing two distinct genotypes from 690 galls of the sumac aphid *Melaphis rhois*, suggesting that migration was occurring at a very low level in this species. In addition, Fukatsu & Ishikawa (1994), using a very sensitive technique based on the polymerase chain reaction, found no evidence for mixing from a sample of five galls of *Ceratovacuna nekoashi*.

(c) Gall cleaning

Although living in a gall might initially have enhanced the microclimate around the clone, enclosure brings with it the novel and potentially fatal problem of death by drowning in honeydew. A partial solution to this problem, adopted by the aphids in the galls of both the soldier-producing families, is to wrap the honeydew in wax to form non-wetting droplets. However, if a colony wishes to persist in a gall for more than one

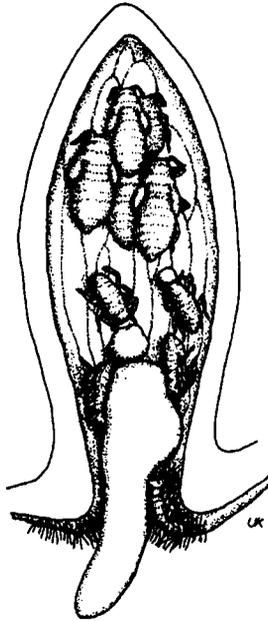


Fig. 9. Larvae (primarily first-instars) of *Hormaphis betulae* pushing honeydew out the gall opening, like toothpaste from a tube (from Kurosu & Aoki, 1991c with permission).

or two generations, these droplets must be removed from the gall. Such active honeydew removal is found in species from both the Pemphigidae and the Hormaphididae. First instars of *Pemphigus dorocola* (Aoki, 1980a) and the soldiers of *Tuberaphis styraci* (Aoki & Kurosu, 1989a) and *Ceratovacuna japonica* (Kurosu, Stern & Aoki, 1990) push honeydew droplets out of galls with their heads. A slightly different method is used by *Hormaphis betulae*: the honeydew is pushed out of the gall mostly by first instars like toothpaste from a tube (Fig. 9; Kurosu & Aoki, 1991c). Benton & Foster (1992) showed that the first instars of *Pemphigus spyrothecae* push out cast skins and dead aphids, as well as honeydew, using different methods for ejecting droplets of different sizes. They established experimentally that the cleaning behaviour is costly to the soldiers who perform it and essential for gall survival.

Two points of general interest emerge from these observations. First, it is almost always the soldiers or, if there are no defenders such as in *Hormaphis*, the first instars that clean the galls. Second, the phylogenetic distribution of gall-cleaning seems to be wider than that of soldier production. For example, soldiers have never been reported in galls on the primary hosts in the Hormaphidini, but gall-cleaning behaviour occurs in at least four species (*Hormaphis betulae*, *Hormaphis hamamelidis*, *Hamamelistes miyabei* and *Hamamelistes kagamii*) (Kurosu & Aoki, 1991c; Gendron, 1993). [Soldiers have been found in one hormaphidine species, *Hamamelistes betulimus makabae*, from pseudogalls on the secondary host, birch, where gall cleaning has not been reported (S. Akimoto, personal communication).] It is possible that the same situation occurs in *Pemphigus*: *P. bursarius*, which apparently does not have soldiers, does clean its gall (Benton & Foster, 1992). However, soldiers of *Ceratovacuna nekoashi* do not clean their gall (Aoki & Kurosu, 1989b).

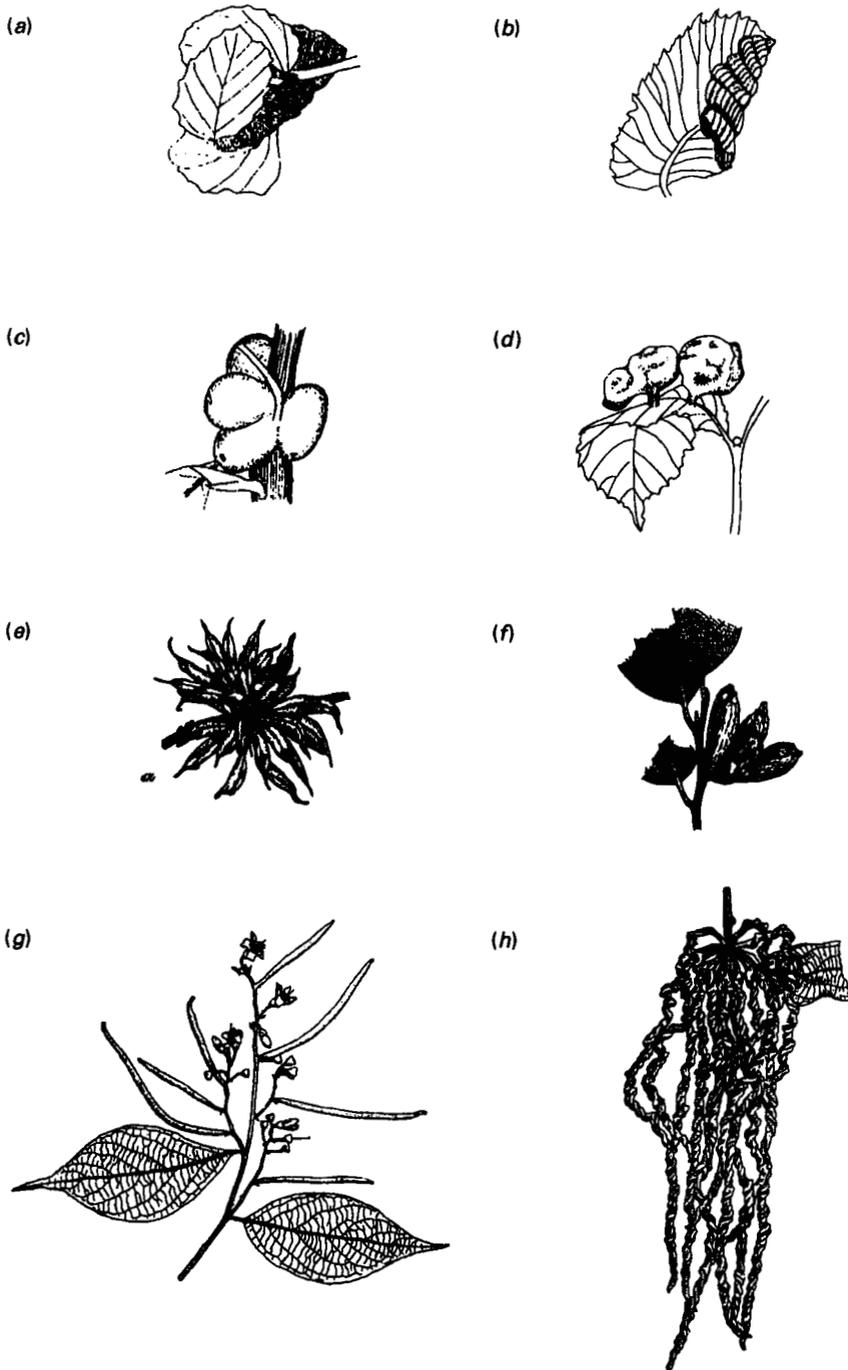


Fig. 10. Examples of galls of differing defendability. (a) *Pachypappa tremulae* on *Populus tremula* (from Tullgren, 1909). (b) *Eriosoma grossulariae* on *Ulmus procera* (from Patch, 1913, as *Eriosoma ulmi*). (c) *Pemphigus borealis* on *Populus laurifolia* (from Tullgren, 1909). (d) *Tetraneura caerulea* on *Ulmus procera* (from Mordvilko, 1935, as *T. rubra*). (e) *Astegopteryx bambucifoliae* on *Styrax suberifolia* (from Kurosu & Aoki, 1991a with permission), (f) *Pseudoregma koshunensis* on *S. suberifolia* (from Takahashi,

Gall-cleaning behaviour, if indeed it has a wider phylogenetic distribution, might therefore have acted as an evolutionary precursor to soldier-behaviour. Some first- or second-instars might have become specialized as cleaners, because they are small enough to work effectively at the gall opening, and in pushing things out of the gall they might have come into contact with predators trying to get in. The necessity for gall cleaning would therefore have brought a particular morph, already committed by the clone to behaving altruistically, into direct contact with predators. And the requirement of a gall opening for ejecting honeydew would allow a wide range of predators access to the colony, thereby selecting for defence.

(d) *Defendability of the gall*

Aphid galls are highly variable in morphology (see Figs 9, 10), and there is a continuum of defendability from blister galls (e.g. those formed by *Pachypappa tremulae*, Fig. 10a), which presumably provide no protection at all, through the various types of leaf-roll galls (e.g. those formed by *Eriosoma grossulariae*, Fig. 10b), to the readily defendable, enclosing galls formed, for example, by *Pemphigus borealis* (Fig. 10c), *Tetraneura caerulescens* (Fig. 10d), and various cerataphidines (Fig. 10e-h). In Section IV(2d) we make specific predictions as to how gall morphology should influence soldier investment.

(e) *Genetic integrity*

The prevalence of intergall migration discussed earlier presents problems for a soldier-producing colony. Invasion of the aphid clone by alien conspecifics will reduce the benefit to the clone provided by soldiers, and will therefore decrease the likelihood that the clone will invest in soldiers. We discuss this general problem in more detail later, but living in a gall might be of great significance in this respect by providing, as it were, a fence around the clone. Enclosure in walls of vegetable matter would help to maintain the integrity of the clone: an aphid in a gall may be more confident that its neighbours are clone-mates than an aphid on an open leaf.

As with defendability against predators, the likelihood of clonal mixing is probably dependent in part on gall morphology. The blister and leaf-roll galls will be accessible to dispersing aphids at all times. Other galls, for example those formed by many cerataphidines (*Ceratovacuna nekoashi*: Kurosu & Aoki, 1990b; *Tuberaphis styraci*: Aoki & Kurosu, 1990) and *Pemphigus* (*P. microsetosus*: Aoki, 1975; *P. bursarius*: Dunn, 1960) close quickly at the beginning of the season and all the colony members will probably initially be of the same clone. However, the galls must eventually open, either to let the alates emigrate or to allow removal of honeydew and debris.

(5) *The evolution of the horned soldiers*

We have already argued that the horned soldiers of the Cerataphidini evolved separately on the secondary host and did not directly arise from soldiers on the primary host. What historical factors might have influenced the evolution of soldier behaviour in these aphids? As Stern (1994) has argued, it seems possible that the presence of

1939), (g) *Tuberaphis leeuweni* on *S. serrulata* (from Docters van Leeuwen, 1922), and (h) *Astegopteryx vandermeermohri* on *S. serrulata* (from Docters van Leeuwen, 1922). The final four species (e-h), all members of the Cerataphidini, produce soldiers in the galls.

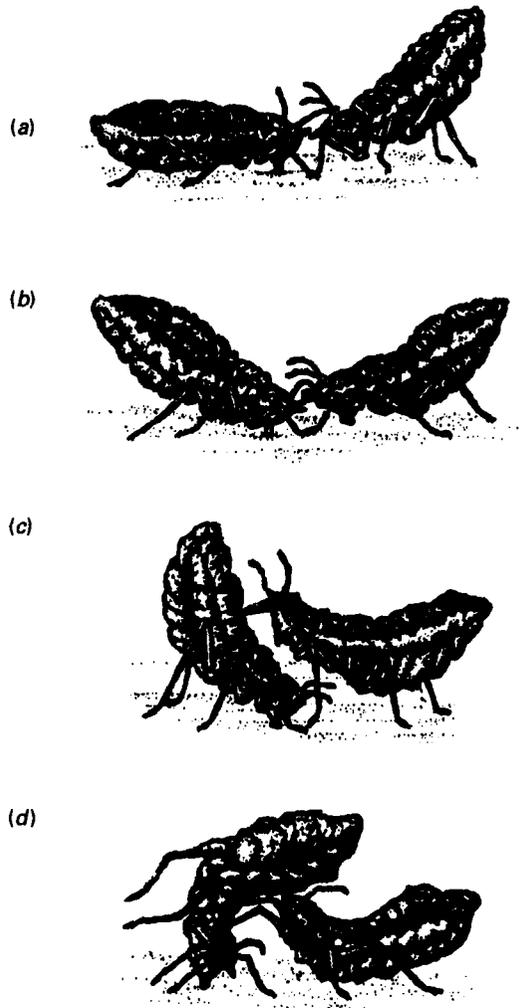


Fig. 11. Head butting in a horned cerataphidine (from Aoki & Kurosu, 1985 with permission). (a) An intruder (right) attacks a feeding aphid (left) by butting with the frontal horns. (b) The feeding aphid lowers its horns. (c) The intruder grabs the feeding aphid with her front legs and butts with her horns. (d) The feeding aphid raises up onto her front legs and flips her abdomen over to ward off the attacker.

soldiers in one stage of the life cycle might have facilitated the evolution of soldiers in a different stage of the life cycle. A general distinguishing characteristic of soldiers is that they tend to attack, rather than run away from, predators. Once this set of behaviours was present in one stage of the life cycle it might easily have been adopted into another stage.

Other morphological and behavioural features might have influenced the evolution of horned soldiers. Cerataphidini of all instars use their frontal horns to fight conspecifics for feeding sites on the secondary host (Fig. 11; Aoki & Kurosu, 1985), and this behaviour occurs in all species that have horns (Aoki, 1987; Foster, Aoki, Kurosu, & Stern, unpublished data). Aphids with this butting behaviour might then have turned their attention to predators, perhaps in the early stages of evolution piercing predator's

eggs, as seen in *Ceratovacuna lanigera* (Aoki & Kurosu, 1987). Defensive behaviour might have become restricted to the first instars because these were also the more active dispersal stage (Aoki, 1987; and see above). The butting behaviour itself might have a more ancient origin in the activity of gall-cleaning. Soldiers of *Astegopteryx setigera* and *Astegopteryx* sp. were observed to push determinedly at everything they encountered in their gall, including the internal gall as well as honeydew and other aphids (Foster & Stern, unpublished observations). It is also possible that the small frontal spine-like setae of these soldiers (see Aoki & Kurosu, 1989a), or perhaps the sockets of these setae (Aoki, 1987), are used in gall cleaning and might be the structural precursors of the frontal horns of the soldiers on the secondary hosts.

(6) *Observations and experiments on defensive behaviour in aphids*

(a) *Can soldiers actually kill predators?*

Because aphids are generally perceived as being weak and defenceless, it was initially necessary to convince people that soldiers were actually able to kill other animals. Aoki (1977a) achieved this in his original observations on *Colophina clematis*, in which he showed that soldiers were able to kill unidentified syrphid larvae in each of seven experiments. However, these were rather artificial experiments and the syrphids were not natural predators of these particular aphids. Since then, it has been shown that soldier aphids respond aggressively to tactile stimulation (e.g. Aoki, 1980b; Aoki *et al.*, 1981; Sakata & Itô, 1991; Schütze & Maschwitz, 1991; Akimoto, 1992), pierce human skin with their stylets (Aoki *et al.*, 1977; Aoki, 1979; Aoki & Kurosu, 1989a, 1993), attack insects that are not aphid predators (e.g. Aoki, 1978, 1980b; Kurosu & Aoki, 1988b; Aoki & Kurosu, 1989b; Kurosu *et al.*, 1990), attack conspecific and heterospecific aphids (e.g. Aoki, Kurosu & Stern, 1991; Aoki & Kurosu, 1992a), attack, and often kill, aphid predators (e.g. Aoki, 1978; Aoki & Miyazaki, 1978; Aoki *et al.*, 1981, 1984; Akimoto, 1983; Aoki & Kurosu, 1987, 1989a, b; Kurosu & Aoki, 1988b; Arakaki, 1989; Foster, 1990; Schütze & Maschwitz, 1991), and attack and kill natural predators of their own species (e.g. Aoki *et al.*, 1984; Ôhara, 1985a, b; Aoki & Kurosu, 1987, 1992a; Foster, 1990; Schütze & Maschwitz, 1991; Moran, 1993).

The most detailed experimental observations on the effectiveness of soldiers against natural predators are those of Foster (1990). Using natural galls of *Pemphigus spyrothecae* containing experimentally manipulated proportions of soldiers and non-soldiers, he showed that the soldiers killed juvenile *Anthocoris minki* (Heteroptera: Cimicidae) that had been introduced into the galls. Experiments also showed that the soldiers were effective both in preventing the predator (*A. minki*) from entering the gall and in killing those that did manage to enter.

(b) *Against what kinds of predators are soldiers effective?*

Aphid soldiers are not equally effective against all types of predators. Soldiers can be effective against syrphid eggs, piercing and killing them either with their frontal horns [e.g. *Ceratovacuna lanigera*, Fig. 12 (Aoki *et al.*; 1984' Ôhara, 1985a, b; Aoki & Kurosu, 1987)] or their stylets [e.g. *Colophina clematicola* (Kurosu & Aoki, 1988b)]. Aoki & Kurosu (1987) showed that, although the soldiers of *Ceratovacuna lanigera* could kill eggs of the generalist aphid predator *Syrphus ribesii* and of *Dideoides latus*, which is probably a specialist predator of this aphid, they were ineffective against the toughened

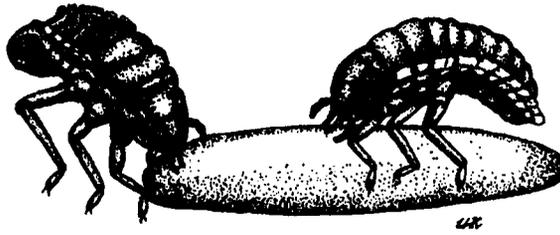


Fig. 12. First-instar larvae of *Ceratovacuna lanigera* crushing a syrphid egg with their horns (from Aoki, Kurosu & Usuba, 1984)

eggs of the specialist predator *Eupeodes kuroi* (formerly *Metasyrphus hakiensis*, authority K. Ôhara (S. Aoki, personal communication)). Predatory larvae are clearly more exacting targets, since they can fight back. For example, soldiers of *C. lanigera* could kill the eggs, but not the larvae, of *Dideoides latus* (Aoki & Kurosu, 1987). However, soldier aphids have been shown to be effective against larvae of syrphids, coccinellids, chrysopids, anthocorids, lycaenids and pyralids (e.g. Aoki, 1978; Aoki *et al.*, 1981; Ôhara, 1985*b*; Aoki & Kurosu, 1987, 1992*b*; Foster, 1990; Schütze & Maschwitz, 1991). In general, later instar predatory larvae and adults are often unaffected by soldiers and can be seen feeding in the colonies, apparently free from harassment. Relatively large larvae (i.e. 8 mm long syrphids and 12 mm long chrysopids) did succumb to mass soldier attack in experiments (Foster, 1990), but the effectiveness of mass attack in a more natural context would be well worth examining.

It has been suggested that the soldiers of the *Styrax*-gall type might be effective in defending the clone against vertebrate predators. Soldiers of *Ceratoglyphina bambusae* readily fall off the gall when it is shaken and cause intense irritation when placed on human skin (e.g. Aoki *et al.*, 1977) and induce vigorous scratching when scattered on mice (Aoki, 1979). Aoki & Kurosu (1991*a*) observed partially damaged galls of this species, which they concluded had probably been attacked by non-human vertebrates, and suggested that the soldiers might have been effective in repelling these predators. More direct observations or experiments are clearly required.

(c) *The effect of defensive behaviour on predators and soldiers*

The mechanism of injury or fatality of predators varies with soldier type. For many species, for example *Pemphigus spyrothecae*, the predators appear simply to bleed to death as a result of multiple lacerations by the soldiers (Foster, 1990). This is also how the horned soldiers kill their predators (e.g. Aoki, 1987). However, the soldiers that fight with their stylets might use chemical weapons; this is presumably how the soldiers of *Ceratoglyphina bambusae* cause irritation to human skin. Kurosu & Aoki (1988*a*) observed that, in five cases, a single 'outsider' of *Ceratovacuna nekoashi* was able to paralyze a non-predatory caterpillar (*Brachmia trimaculella*). Kurosu & Aoki (1991*a*) also observed a first-instar defender in the gall of *Astegopteryx bambucifoliae* attack an unidentified caterpillar which 'became moribund almost immediately'.

A common result of soldier attack is that the predator falls from the plant [e.g. on the secondary host, horned soldiers of *Pseudoregma alexanderi* (Aoki *et al.*, 1981) and *P. bambucicola* (Ôhara, 1985*b*); and on the gall, soldiers of *Pemphigus obesinymphae* (Moran, 1993)]. This will clearly benefit the clone, since, even if the predator does not

die, it will almost certainly not be able to relocate the clone. However, the soldiers will also probably be lost. In some cases, the soldiers may be able to throw the predators off the plant (Schütze & Maschwitz, 1991).

The defensive behaviour of the soldiers exposes them to grave risks. In experiments with predators introduced into galls of *Pemphigus spyrothecae*, Foster (1990) showed that between 9 and 20% of the soldiers died, whereas only between 1 and 6% of the non-soldiers died. Schütze & Maschwitz (1991) reported that, with one exception, all the soldiers of *Pseudoregma sundanica* that attacked larvae of *Coccinella septempunctata* died. Soldiers die either because the predator eats or squashes them or possibly because of contact with toxic substances released from the predator. Ôhara (1985*b*) reported that soldiers of *Pseudoregma bambucicola* died within a few minutes after they clasped a syrphid larva, and Foster (1990) suggested that the haemolymph oozing out of wounded predators might be toxic to soldiers of *Pemphigus spyrothecae*. Finally, Arakaki (1992*c*) showed that soldiers of *Pseudoregma koshunensis* that attacked syrphid larvae (*Betasyrphus nipponensis*) or moth larvae (*Plutella xylostella*) died ten times faster than starved soldiers. He suggested that, because these are not specialist predators, the soldiers' accelerated demise was probably not due to chemicals secreted by the predators but might more likely be due to the rapid use of remaining energy. However, it is possible that generalist predators contain toxic chemicals, for example to prevent predation on themselves, that also affect soldiers.

Despite the rapid death of soldiers that attack predators, soldiers that do not attack seem to have relatively long life spans. Sakata & Itô (1991) found that soldiers of *Pseudoregma bambucicola* live an average of 55 days and a maximum of 116 days, compared with the average duration of the normal first-instar stadium of 17 days. This led Arakaki (1992*b*) to report that soldiers of *P. koshunensis* feed, as Sakata & Itô had inferred for *P. bambucicola*.

(d) The importance of non-lethal defensive behaviour

Although most workers have emphasized the lethality of aphid soldiers, the importance of subtle, non-suicidal defence should not be overlooked. Low-level harassment, including, for example, leg-shaking behaviour against parasitoids and predators attempting to oviposit in the aphid colony, might play an important defensive role.

Soldiers and sometimes other larvae and adults of *Pseudoregma bambucicola* (Sakata & Itô, 1991) and *P. sundanica* (Schütze & Maschwitz, 1992), wave their hind- or fore-legs in response to mechanical stimulation. Some species [e.g. *P. sundanica* (Schütze & Maschwitz, 1992), and *Ceratovacuna lanigera* (Arakaki, 1989)] also release honeydew or exudate from the cornicles when disturbed. We have also observed soldiers of *P. bambucicola* grab and quickly release predatory moth larvae, predacious adult wasps, and the tips of forceps placed in front of them (Stern & Foster, unpublished observations). In addition, as we describe later, many predators have adopted behaviours, for example living beneath silken webs, which probably decrease harassment from soldiers but also lower their feeding rate. By harassing predators enough to reduce the feeding rate of predators or deter them from feeding at that colony, these defensive behaviors may increase the growth rate of the colony. These ideas currently have very little experimental support but deserve further investigation.

We believe that the primary defensive role of most soldiers might be non-lethal defence. If true, this has important implications for our understanding of the evolution of soldiers.

(e) *Defensive behaviour against aphid competitors*

It might be to the clone's advantage to defend itself against other aphids, either of the same or different species, which might compete with it for space and food. This could be particularly important for gall-living species, where it appears there is often a shortage of space and where there might be severe problems of self-fouling with honeydew (e.g. Benton & Foster, 1992). A frequent cause of failure of the clones of *Pemphigus spyrothecae* is honeydew fouling by the aphid *Chaitophorus leucomelas*, which commonly invades the galls toward the end of the year (Foster, unpublished). However, in laboratory experiments *P. spyrothecae* soldiers did not attack *C. leucomelas* (Foster, 1990). In other species, soldiers of both the gall (*Ceratoglyphina bambusae*; Aoki *et al.*, 1991) and the secondary-host generations (*Pseudoregma alexanderi*; Aoki *et al.*, 1981) can effectively attack individuals of the potentially competing aphid *Astegopteryx bambucifoliae*. Soldiers in the gall-forming generations of *Ceratoglyphina bambusae* always attacked non-soldiers of the same species, provided that they encountered them outside the gall; aphids within the gall are presumably not attacked (Aoki *et al.*, 1991). The soldiers did not attack other soldiers. The effect of this will be to exclude unrelated aphids from entering the gall. There is no evidence that aphid soldiers, or indeed any kind of aphid, can directly discriminate kin from non-kin (e.g. Foster, 1990; Aoki *et al.*, 1991; Schütze & Maschwitz, 1992).

(f) *Predator counter-adaptations to aphid attack*

Predators, especially those species that specialize on soldier-producing aphids, will be strongly selected to circumvent the soldier's defences. Some predators may simply attempt to eat the soldiers as rapidly as possible. An interesting variant of this is provided by the bug *Anthocoris minki*, which is able to paralyse aphids (*Pemphigus spyrothecae*) at a rapid rate, apparently by a quick injection of a toxin (Foster, unpublished observations). Predatory pyralid caterpillars seem to escape soldier attacks by living under a nest of silken threads (*Assara formosana*: Aoki & Kurosu, 1992*b*; *Dipha aphidivora*: Arakaki & Yoshiyasu, 1988). *Dipha aphidivora* produce silk runways soon after hatching and only leave these runways to capture aphid prey that they quickly bring back to the runway to consume (Arakaki & Yoshiyasu, 1988). Some predators protect their eggs by producing a toughened egg-shell [e.g. *Eupeodes kuroiwae*: originally reported as the junior synonym *Metasyrphus hakiensis* in Aoki & Kurosu (1987) and as the junior synonym *Metasyrphus kuroiwae* in Arakaki (1992*a*)], by coating their eggs with a protective material such as faeces (e.g. *Pseudoscymnus kurohime*: Arakaki, 1988), or by producing eggs too flat for aphids to attack (e.g. *Dipha aphidivora*: Arakaki, 1992*a*). Other predators lay their eggs on the silk of spiders' webs on which soldiers cannot easily walk (Ôhara, 1985*a*) or oviposit at a safe distance from the aphid colonies (e.g. *Dideoides latus*: Aoki & Kurosu, 1987; *Synonycha grandis*, *Eumicromus navigatorum*: Arakaki, 1992*a*). Ôhara (1985*a*) suggests that the syrphid, *Eupeodes confrater* (originally reported as *Metasyrphus*), can adjust its oviposition behaviour depending on the numbers of soldiers in the aphid colonies: in autumn and

early winter, when the soldiers are active, the eggs are laid on spider's webs, but from mid-winter to spring, when there are few soldiers present, the eggs are laid close to, or in, the colony. More intricate tactics of attack and counter-attack undoubtedly await discovery.

These counter-adaptations are probably very costly to predators. First, soldiers deter attack from the start, therefore eggs must be deposited far from the colony. Travel to the colony is costly and the larva is more likely to die *en route*. Furthermore, predators must feed opportunistically which is likely to lead to predators having slower growth rates when feeding on soldier-producing species than when they feed on non-soldier-producing species. Finally, the silk produced by predators to protect themselves will bear some energetic cost.

(g) *Chemical ecology of soldier aphid defence*

Chemical signals play a major role in many aspects of aphid biology, including the interaction between soldiers and predators. In particular, soldier aphids use a range of chemicals to signal that they are being attacked. For example, Akimoto (1983) states that aggressive behaviour in the defenders of *Eriosoma moriokense* is stimulated by yellow brownish fluid secreted from the aphid's cornicles. Arakaki (1989) describes in detail how an alarm pheromone, secreted by all stages of *Ceratovacuna lanigera*, elicits attacking behaviour in the first-instar soldiers, but escape behaviour in the non-soldiers. When soldiers come into contact with a syrphid larva placed in the colony, they secrete droplets from their cornicles and deposit them on the syrphid's body, which is then vigorously attacked by other soldiers. It is interesting that *C. lanigera* is the only species of *Ceratovacuna* in which the first instars have cornicles (U. Kurosu, personal communication).

The soldiers of *Pseudoregma sundanica* use a cruder chemical alarm signal. The soldiers are stimulated to behave defensively by direct contact with haemolymph oozing from wounded aphids (Schütze & Maschwitz, 1991). The stimulus seems to be very non-specific: haemolymph of any insect releases defensive behaviour. Therefore, as long as no aphids are attacked, the soldiers move innocuously around the colony. Other aphids, aphid-attending ants, and neutral insects are not attacked, and predators are only attacked after they have begun eating in a colony and a soldier contacts a haemolymph-contaminated individual. As Schütze & Maschwitz point out, this means that predators with dainty feeding habits, for example those with sucking mouthparts, will be much less likely to trigger a soldier attack. In addition, this mechanism also prevents soldiers from detecting predator eggs.

(h) *The role of ants in soldier defensive behaviour*

Many species of aphids are attended by ants which collect aphid honeydew (Sudd, 1987). Attendant ants and aphids are primarily mutualistic; aphids provide carbohydrate-rich honeydew to ants and ants provide protection from natural enemies. However, ant tending can have either positive, negative or no effect on aphid colony growth (see review by Bristow, 1991). In addition, ant attendance is highly variable both among and within aphid species. To date, attempts to determine the causes of this variability have met with little success (Bristow, 1991). A possible complicating factor which has not been acknowledged in previous studies is that aphids may sometimes be

providing more than simply waste products, as is normally assumed. It seems highly likely that at least some species either provide ants with nutrients that the aphids also need or manufacture compounds that are particularly attractive to ants (cf. Pierce, 1989) in order to secure protection. This raises the interesting possibility that soldier-producing species must make a trade-off between providing nutrients to ants for protection and using the nutrients to manufacture soldiers. The fact that soldiers and attendant ants of at least one aphid species (*Pseudoregma sundanica*: Schütze & Maschwitz, 1991) attack different suites of predators makes this an intriguing possibility. It is currently relatively easy to quantitatively analyze small volumes of honeydew (Byrne & Miller, 1990; Molyneux, Cambell & Dreyer, 1990) and this promises to be an extremely interesting area for future research.

Despite the current lack of quantitative information on ant attendance and honeydew composition, it is still possible to draw some simple conclusions which enable us tentatively to reject an obvious hypothesis. Because both soldiers and ants normally provide protection from predators we might predict an interspecific negative correlation between ant attendance and soldier production. This simplistic view is almost certainly false; there are reports of ant attendance in the soldier-producing species *Ceratovacuna japonica* (secondary host: Stern, unpublished data; primary-host galls: Kurosu *et al.*, 1990), *Pseudoregma sundanica* (Schütze & Maschwitz, 1991, 1992), and *Pseudoregma bambucicola* (Sakata *et al.*, 1991). Interestingly, colonies of *P. sundanica* appear to be obligately tended by ants from at least nine genera (Schütze & Maschwitz, 1991, 1992). We have also observed ant attendance at colonies of the soldier-producing species *C. lanigera*, *P. nicolaiae*, *P. panicola*, and *P. pendleburyi* (Stern, unpublished data). In addition to the widespread nature of ant attendance in soldier-producing species, many related, non-soldier-producing species are often found without attendant ants (Stern, unpublished data).

Schütze & Maschwitz (1990) report on a very surprising facet of the interaction between ants and soldier aphids. They found that for *Pseudoregma sundanica*, even though soldiers do not seem to discriminate against or attack aphids from other colonies (Schütze & Maschwitz, 1992), the ants attending a colony preferentially removed alien aphids introduced into a colony. It is very difficult to understand why the ants should care whether aphids are derived from 'their' aphid colony or from an alien colony and this phenomenon requires further investigation and examination in other ant-attended species.

(7) *Proximate mechanisms of soldier production*

A complete understanding of how and why soldiers are produced requires an understanding of the mechanisms by which soldiers are produced and the environmental cues that trigger soldier production. At the very least, an understanding of mechanism offers insight into the alternative ways soldiers can be built and why different species build them in different ways. Earlier we discussed the diversity of morphology and behaviour associated with soldiers. It is difficult to believe that all of these differences are entirely due to optimization for the particular conditions encountered by each species. It seems more likely that the phenotypes we currently observe have features that would not be predicted strictly from optimization criteria but instead are limited by the phenotypes, and the mechanisms for producing them, present

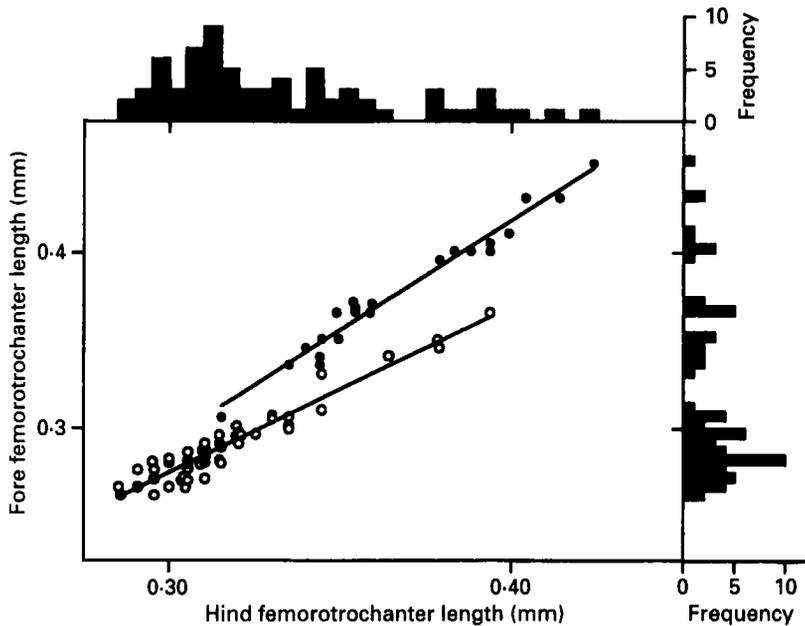


Fig. 13. The morphometrics of larval dimorphism in *Colophina clematis*. The filled symbols represent soldiers and the open symbols represent normal larvae (modified with permission from Aoki, 1976). Both the slopes and the intercepts of the two regressions are significantly different (see text). The frequency histograms suggest that a skewed size distribution of larvae is produced, with most larvae being relatively small normal larvae and with relatively fewer being large soldiers, although it is unknown whether larvae were sampled randomly.

in ancestral species. We discussed one possible example above with regard to the evolution of horned soldiers from a shorter horned non-soldier ancestor. It may be possible to generate similar stories for all soldier-related traits but they will remain stories until we gain an understanding of the mechanism for the production both of soldiers and the ancestral phenotype, normal larvae. Below we discuss the meagre evidence bearing on these questions and point out particularly fruitful avenues of future research.

(a) Morphometrics and allometry

The simplest and most immediate observations that bear on the mechanisms of soldier production are morphometrics. Wheeler (1991) showed how morphometric studies can be used to elucidate developmental mechanisms underlying caste polymorphism in ants. A similar approach may prove fruitful in understanding the development and evolution of soldier aphid castes.

In Fig. 13 we have replotted the only published morphometric data set from soldier-producing aphids (Aoki, 1976). These data were collected and published prior to Aoki's discovery that the specialized larvae are a defensive morph. The aphids were therefore separated into two groups based only on morphological characteristics. An analysis of covariance indicates that the two regressions shown in the figure differ significantly in slope (normal = 0.948, soldier = 1.247; $F = 21.72$, $P < 0.001$) and intercept (normal = -0.001, soldier = 0.080; $F = 9.86$, $P < 0.001$). The slope for the soldiers is approxi-

mately 1.3 times greater than the slope for the normal larvae, indicating that the legs of soldiers and of normal larvae are created using different allometric relationships. That is, the fore legs of soldiers grow faster relative to the hind legs than the legs of normal larvae. It will be extremely interesting to determine whether other species are using similar rules to construct soldiers and to examine in more detail when in ontogeny these shape changes are initiated.

(b) *Cues*

In aphids the production of alternative morphs is often triggered by cues such as day length, temperature, and crowding (Lees, 1966; Dixon, 1985). Several pieces of information suggest that soldier production is sometimes cued by similar external factors. *Pseudoregma bambucicola* (Sunose *et al.*, 1991) and *P. koshunensis* (Tanaka & Itô, 1994) produce soldiers only at certain times of the year and *P. bambucicola* (Sakata *et al.*, 1991) and *P. sundanica* (Schütze & Maschwitz, 1991) produce soldiers primarily in large colonies suggesting that both seasonal factors and crowding may cue soldier investment. It would be interesting to explore the nature of these cues using the techniques developed to understand the cues triggering production of alates and other morphs in aphids.

Tanaka & Itô (1994) studied soldier production by individuals of *P. koshunensis*. They found that some individuals can produce both normal larvae and soldiers and that they produce approximately 30 normal larvae before they begin producing approximately ten soldiers. After producing soldiers they again produce normal larvae. Half of the females did not produce any soldiers although they produced comparable total numbers of larvae.

In galls it seems likely that soldiers are produced only in certain generations. In some species, as reviewed above, the foundress produces soldiers or 'outsiders' that remain outside a closed gall and in some species later generations also produce soldiers. In *Cerataphis fransseni*, soldiers are produced in highly predictable numbers as the gall grows (Stern, Aoki & Kurosu, 1994).

(c) *Symbionts*

Fukatsu and Ishikawa (1992) recently discovered that soldiers and males of *Colophina arma* lack the endosymbionts found in all other morphs. These endosymbionts are apparently necessary for growth and reproduction but their absence in soldiers and males suggests they are not necessary for maintenance. These authors present two hypotheses to explain the absence of endosymbionts in these morphs. First, the 'host's selection hypothesis' proposes that the endosymbionts are costly to maintain or produce and non-moulting morphs do not require the nutritional benefits provided by the endosymbionts. The aphids therefore actively prevent the endosymbionts from entering the embryos of males and soldiers. The 'symbiont's selection hypothesis' proposes, in contrast, that the endosymbionts control their fate and they choose not to be placed in reproductive dead-ends such as soldiers and males. Males represent reproductive dead-ends for the endosymbionts because the endosymbionts are maternally inherited, like mitochondrial genomes. It is therefore possible that it is not in the soldiers' and males' best interest to lack endosymbionts.

We propose a third hypothesis which takes a clone's-eye-view of the problem. First,

it seems highly likely that all the endosymbiont cells of a certain type [most aphids possess two distinct kinds of bacterial endosymbionts (Baumann *et al.*, 1993)] are genetically identical. The endosymbionts should therefore agree among themselves on the optimal allocation of daughter cells. Second, the fate of an endosymbiont lineage is entirely dependent on the aphid clone's fate. Therefore, the aphid clone and the endosymbiont lineage should agree on the optimal investment of endosymbionts in different morphs. Whatever is best for the aphid clone is also, by necessity, best for the endosymbiont lineage. Any endosymbiont lineage that attempts to increase in numbers at the expense of its host, is doomed to failure. This hypothesis predicts not only that some species will have morphs that lack endosymbionts but that different morphs will have different numbers of endosymbionts depending on their requirements. This condition is found in termites where the abundance of gut endosymbionts varies among worker, soldier, nymphal, and alate morphs (Lai, Tamashiro & Fuji, 1983). It may be best to think of aphid endosymbionts as simply an organ which is expanded or atrophied as required by the host.

IV. A MODEL FOR OPTIMAL SOLDIER INVESTMENT

To clarify the selective forces that might have influenced the evolution of soldiers we have constructed a simple model to examine optimal soldier investment strategies. This model incorporates several variables of potential importance: the birth rate, the predation rate, the effectiveness of soldiers in deterring predators, and the proportion of the colonies resources invested in soldiers. For simplicity we have not examined the effects of ant tending.

The model takes a clone's-eye-view of the problem of soldier investment. This approach seems realistic because individual soldiers probably do not have a choice about whether they are produced as soldiers, and they should agree with their mother's choice anyway, as there is no genetic conflict of interest.

As we argued earlier [see section III(3)] the distinction between reproductively sterile soldiers and non-sterile larval attackers is artificial and slightly misleading. There is in fact a continuum of types of attackers from aggressive first instars, to morphologically specialized soldiers that sometimes molt, to morphologically specialized soldiers that apparently never molt. Importantly, all of these strategies are simply defence investment that has an associated cost, a decrease in the intrinsic growth rate of the colony. The colony growth rate is primarily a function of the birth rate and the developmental rate of larvae. A decrease in growth rate can therefore take the form of either decreased developmental rate, as in monomorphic defenders (Akimoto, 1992), or decreased effective birth rate, as in the production of reproductively sterile soldiers. It is interesting that different species produce defenders in one or the other of these ways at different times (see above and Foster & Northcott, 1994) and the reasons for this variation should prove a fascinating subject for future research (Akimoto, 1992).

(1) *The model*

We assume that clones are attempting to maximize r , the intrinsic rate of increase. This seems reasonable as a first approximation because aphids in general follow a pattern of founding new colonies, growing to a large size, and dispersing to found new colonies. Presumably clones are attempting to do this as quickly as possible to escape

predation, to utilize ephemeral resources, and to compete more effectively with other clones for access to new host plants. In essence, the model examines the growth stage of this cycle. We first present a highly simplified form of the model. We then present the optimal solutions for a slightly more complicated version that takes into account soldier efficiency. Finally, we examine the effects of clonal mixing on soldier investment strategies.

If we assume that an aphid colony reaches a stable age distribution quickly after founding and that resources are unlimited, then the intrinsic rate of increase of a non-soldier-producing clone, r_a , is:

$$r_a = b - d_0 - d_p, \quad (1)$$

where b is the instantaneous birth rate, and d_0 and d_p are the instantaneous death rates due to non-predator related death and predator related death, respectively (Dixon, 1987).

For a soldier-producing species we can write r_s , the intrinsic rate of increase for a soldier-producing clone, as

$$r_s = b*(1-c) - d_0 - d_p(1-p), \quad (2)$$

where c is the cost of soldiers, and p (for 'payoff') is the benefit to the colony of having soldiers. The cost of producing soldiers is defined as a proportion of clonal investment and therefore varies from 0 to 1. The payoff term (p) is explored explicitly later.

Note that although the cost of producing soldiers is a reduction in the birth rate we do not specify how this reduction occurs. It can occur directly due to a reduction in the number of reproductive individuals or as a decrease in the developmental rate. If soldiers are larger than normal larvae then it may not be correct to count a single soldier as a cost equivalent to a single normal larvae. It may be more appropriate to compare biomass invested in defenders versus normal larvae, as is usually done when comparing investment in males versus females in sex-ratio studies.

We can now ask when it is better for a clone to produce soldiers by setting $r_s > r_a$ to give

$$\frac{p*d_p}{b} > c \quad (3)$$

As the benefits of soldiers (p) and the death rate due to predation (d) increase, it is easier to satisfy this inequality and producing soldiers is the better strategy. Also, as the birth rate declines it is better to produce soldiers.

(a) *Optimal solutions for the soldier investment model*

We can further explore the dynamics of this model by explicitly defining the 'payoff' term (p). Here we make the link between investment and defence explicit by defining p as a function which translates an investment in soldiers into a reduction in predation or parasitism. We call this translation of investment into defence, 'soldier efficiency', where a more efficient soldier provides better defence for the same investment.

For illustrative purposes we explore the dynamics of our model using the very simple efficiency function $y*c^x$, where $0 < x < 1$ and $0 \leq y \leq 1/c^x$ (for $x > 1$, soldiers are so ineffective they do not pay for themselves). We can then rewrite equation (2) as

$$r_s = b*(1-c) - d_0 - d_p(1-y*c^x). \quad (4)$$

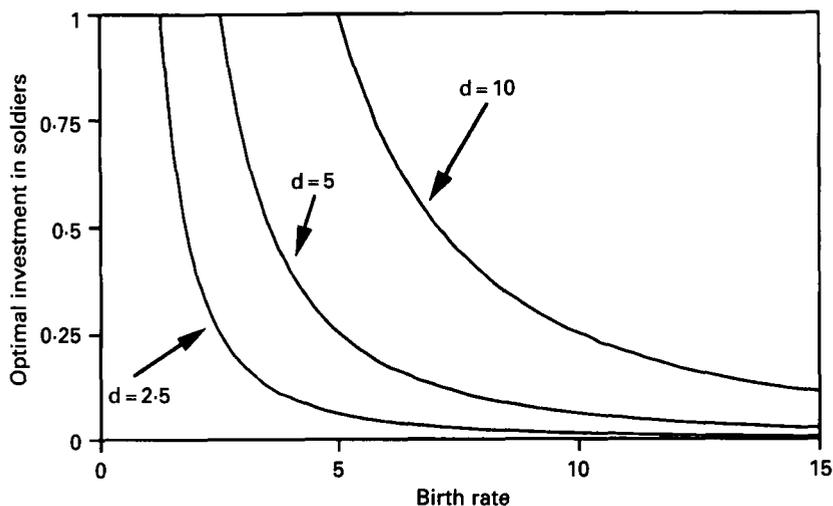


Fig. 14. Predictions of optimal soldier investment from the model described in the text (equation 5). Optimal soldier investment increases with decreasing birth rate and with increasing predation pressure (*d*).

Differentiating equation (4) with respect to *c* and setting $\partial r/\partial c$ equal to 0 to examine the optimum gives

$$c^* = \frac{(x * y * d_p)^{1/(1-x)}}{(b)^{1/(1-x)}}. \tag{5}$$

Most of the results from this analysis are unsurprising given the discussion of equation (3). A decrease in the predation rate shifts the optimum towards a lower investment in soldiers (Fig. 14). Also a decreasing birth rate favours a higher soldier investment (Fig. 14). Interestingly, there is a qualitative shift in soldier strategies with differing soldier efficiencies (Fig. 15). The ability to produce a more efficient soldier does not therefore result in a simple increase in soldier investment, as might be expected intuitively. Instead, investment strategies depend both on soldier efficiency and other factors in a non-linear fashion. This is demonstrated in Fig. 15 by examining the relationship between soldier efficiency and colony birth rate. If highly efficient soldiers can be produced, it is always better to produce a few soldiers and delay massive production until the birth rate is comparatively highly depressed. In contrast, relatively inefficient soldiers should never be produced at higher birth rates but should be produced in very large quantities as the birth rate descends below the predation rate, resulting in an ‘all-or-nothing’ strategy.

(b) Clonal mixing and soldier investment strategies

The model presented above describes how a single clone should invest in soldiers given various ecological parameters. However, colonies of soldier-producing aphids are often likely to contain more than one clone. Here we explore the soldier investment strategies of a single clone in a colony containing multiple clones.

We make several simplifying assumptions. First, we assume that all clones are present in equal numbers. This might be realistic for a colony founded simultaneously

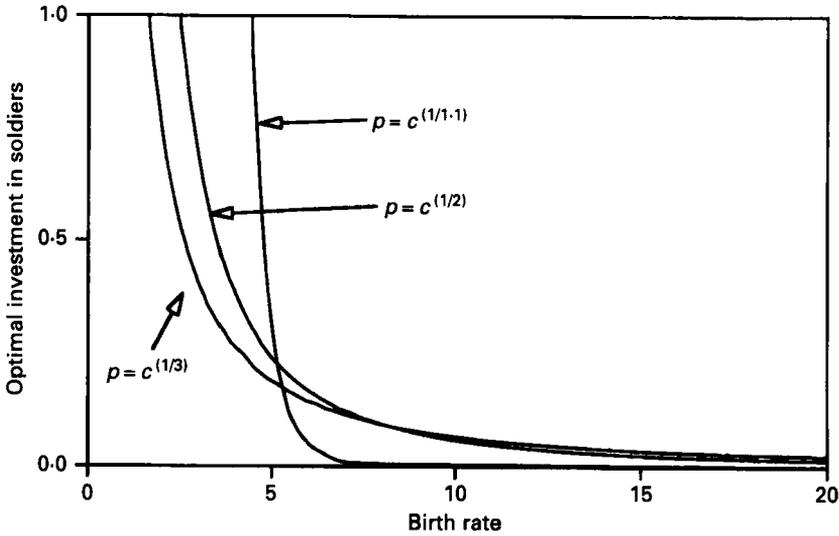


Fig. 15. The effect of soldier efficiency on optimal soldier investment. Low soldier efficiency (e.g. $p = c^{(1/1.1)}$) selects for massive soldier investment only when needed, whereas high soldier efficiency ($p = c^{(1/3)}$) selects for production of a small proportion of soldiers most of the time. The predation rate is constant in this figure ($d = 5$).

		Clone 1	
		Produce soldiers	No soldiers
Clone 2	Produce soldiers	A	B
	No soldiers	C	D

Fig. 16. Payoff matrix for clones in a colony containing two clones. The payoffs (A, B, C, D) are for Clone 2 given that Clone 1 pursues a particular strategy. Soldier production by both clones is evolutionarily stable when $A > C$ or when both $A = C$ and $B > D$. See text for the equations representing the payoffs and further details.

by several aphids. However, it seems likely that clones entering a colony later might adopt different investment strategies. For example, a migrant into a large colony would probably find it advantageous to withhold soldier investment relative to other clones in the colony. We do not explore these asymmetric conditions here. Secondly, we assume that the ecological conditions affect all clones equally. Finally, we assume that each clone is able to assess the extent of clonal mixing and adjust investment decisions accordingly.

Figure 16 presents the predicament faced by a focal clone deciding whether or not to

invest in soldiers. A clone's investment decisions are clearly dependent on the investment decisions of other clones. The problem therefore falls under the rubric of game theory (Maynard Smith, 1982). We can first examine the boundary conditions and ask when it pays for Clone 2 to invest in soldiers when the population is made up of non-soldier-producing clones (i.e. when is $B > D$). From equation (4) the payoff for producing soldiers (B) can be represented as

$$r_B = b*(1-c) - d_o - d_p * \left(1 - \frac{y*c^x}{N}\right), \quad (6)$$

where the benefit due to soldiers $y*c^x$ is diluted N times by the N clones (the focal clone plus $N-1$ other clones). The payoff for a clone not producing soldiers (D) is the same as equation (1). By setting B greater than D we find that soldier production will spread when

$$\frac{d*y}{N*b} < \frac{c}{c^x}. \quad (7)$$

This condition is clearly more difficult to satisfy as the number of clones in a colony increases and it will therefore be more difficult for a soldier-producing mutant to invade a population of non-soldier-producing clones as the level of clonal mixing increases.

We are particularly interested in knowing under what conditions both clones will produce soldiers. That is, when is soldier production by both clones an 'evolutionarily stable strategy'? Soldier production by both clones is evolutionarily stable either when $A > C$ or when both $A = C$ and $B > D$ (Maynard Smith, 1982). If we assume that each clone invests equally in soldiers then the payoff for A is

$$r_A = b*(1-c) - d_o - d_p * \left(1 - \frac{N*y*c^x}{N}\right) \quad (8)$$

and the N s cancel. That is, each clone invests the same amount but because all clones are the same size the net effect per aphid is identical to the investment strategy of a single clone alone. The payoff for a non-soldier-producing clone (C) in a population of soldier-producing clones is

$$r_C = b - d_o - d_p * \left(1 - \frac{(N-1)*y*c^x}{N}\right) \quad (9)$$

because $N-1$ clones invest in soldiers but this investment is spread over N clones. In addition, the focal clone does not pay the cost of producing soldiers. By setting $A > C$ we find that soldier production is evolutionarily stable when

$$\frac{d*y}{b} * \left(1 - \frac{N-1}{N}\right) > \frac{c}{c^x}. \quad (10)$$

Again, we find that colonies of mixed clones are more likely to invest in soldiers as the amount of mixing declines. Alternatively, soldier production in mixed colonies is stable when $A = C$ and when $B > D$ (equation 7). In both cases, as N increases the inequality becomes increasingly more difficult to satisfy.

(2) *Predictions of the soldier investment model*

The model presented above provides five qualitative predictions for soldier investment strategies. Below we discuss these predictions, published data bearing on them, and how they might be tested in the future. These predictions can also be expanded for use in interspecific comparisons to elucidate the origins of soldier production. In each section we discuss these interspecific predictions although it should be noted that these predictions cannot be tested simply by comparing soldier-producing species with non-soldier-producing species, without reference to their phylogenetic affinities (Felsenstein, 1985; Harvey & Pagel, 1991).

(a) *Clonal mixing*

Low levels of clonal mixing should favour the evolution of soldiers. As we discussed earlier, in aphids (and other clonal but separately mobile organisms) the source of intracolony genetic variation is very different from the situation in colonies of sexually reproducing organisms. Asexual reproduction in aphids assures genetic identity among the offspring of a single mother and intracolony genetic variation can only arise through the mixing of clones (Carvalho *et al.*, 1991; Shufran, Black & Margolis, 1991). In contrast, in sexually reproducing animals most or all genetic heterogeneity within a colony arises among related individuals (e.g. Strassman, 1989; Strassman *et al.*, 1989).

There is currently very little data on the extent of intraspecific clonal mixing in natural colonies of soldier-producing aphids. This fact is undoubtedly due to the difficulty of collecting genetic information from individual small insects. However, several recent studies indicate that such efforts will be extremely worthwhile. In the only published survey of clonal mixing in a soldier-producing species, Fukatsu & Ishikawa (1994) used the polymerase chain reaction with arbitrary primers to survey mixing in galls of *Ceratovacuna nekoashi*. These authors demonstrated that their method was sensitive and reproducible and may be a useful tool for surveying for natural mixing. There are two time windows when intruders might enter subgalls: each gall of *C. nekoashi* is composed of more than ten subgalls that are open early in gall development when the offspring of the foundress enter each subgall (Kurosu & Aoki, 1990b), the subgalls then close, but later in the season they open again. Fukatsu and Ishikawa performed a preliminary survey by sampling an aphid from each of three subgalls from five separate galls. They found no evidence for mixing (all the samples within a gall were identical but all samples among galls were different), but it is difficult to draw firm conclusions about the extent of natural mixing from this small sample. Shufran *et al.* (1991) used DNA fingerprinting of individual aphids to examine genetic variation within natural populations of *Schizaphis graminum*, a non-soldier-producing aphid attacking wheat. They found surprisingly high levels of genetic variation on very small spatial scales and very low levels of population differentiation. Setzer (1980) found high levels of inter-gall migration in two non-soldier-producing species of *Pemphigus*. Kurosu & Aoki (1990a) found evidence of interspecific inter-gall migration between the two soldier-producing aphid species *Astegopteryx bambucifoliae* and *Ceratoglyphina bambusae*. Finally, colonies of many species of cerataphidine aphids are often found in inter-specific assemblages on both their primary and secondary host plants (Aoki & Kurosu, 1985; Stern, personal observations), suggesting that mixing of

different clones of the same species may be common. All of these observations make it imperative to obtain better estimates of clonal mixing for soldier-producing species and their non-soldier-producing relatives. Recent advances in molecular biology, including the polymerase chain reaction (e.g. Fukatsu & Ishikawa, 1994), hold great potential in assisting in this task, although a considerable amount of information can still be gleaned from field experiments on natural populations (Setzer, 1980).

There is currently no evidence that soldier-producing aphids can discriminate between clonemates and non-clonemates (Foster 1990; Aoki *et al.*, 1991) so it seems likely that soldier investment strategies will be tuned to the average degree of clonal mixing in natural populations. If soldier-producing colonies are often comprised of several clones then, in addition to the theoretical considerations discussed above, a number of other questions must be addressed. For example, how does this mixing come about? Do all clones contribute equally to soldier production? Do soldiers of one clone defend all clones within the colony?

(b) *Birth rate*

The model predicts that soldier investment should increase with declining birth rate. This effect is easy to intuit; if predation remains constant then there is more need for defence as the birth rate declines. Coley, Bryant & Chapin's (1985) model for plant chemical defences also implicates the growth rate as a major factor in defence investment decisions. More importantly, Coley *et al.* presented comparative data showing that slow-growing plants tend to invest more in defence.

There are no published data on birth rates of soldier-producing aphid colonies. The most pertinent data come from Akimoto's (1992) study of defence investment in the gall forming aphid, *Hemipodaphis persimilis*. This species produces galls on *Zelkova serrata* in late May and the colony then passes through several generations during which alates are continuously produced and exit the gall. Monomorphic first instar larvae defend the gall against a number of predators and the duration of the first instar can be lengthened, resulting in an increase in defence investment, by delaying moulting. Akimoto found that first instars throughout the season progressively increased the duration of the first instar and thus effectively increased defence investment, while the duration of all other instars remained constant. This increase is correlated with a decline in the birth rate, measured as the number of mature embryos in adults, of the colony through the summer. This observation is consistent with the prediction from the model but it is possible that several important unmeasured variables, including predation pressure, may also change during the course of the summer. In addition, as Akimoto points out, larvae produced late in the season may have little chance of maturing to adulthood, making them effectively sterile. They may thus lengthen the duration of the first instar to boost defence since they have no possibility of reproduction. However, this scenario predicts a drastic shift in moulting rate late in the season, whereas Akimoto observed a gradual decline in moulting rate.

(c) *Predation*

The model predicts that soldier investment should increase as the predation rate increases. This increase can take the form of a facultative response to predation or an obligate increase in soldier investment in response to a predictable periodical cue

correlated with a periodical increase in predation. In the only published study with data bearing on this question, Sunose *et al.* (1991) measured the population dynamics of colonies of *P. bambucicola* and two of their predators monthly over the course of 2–4 yr. They found that the percentage of soldiers in colonies fluctuated widely and seasonally. These fluctuations appear to be generally related to fluctuations in population densities, predator numbers, and the percentage of alate larvae in the colony. The authors did not provide statistics of the correlations among these variables so it is difficult to interpret these patterns. Nonetheless, it appears that colonies are not anticipating predator outbreaks but, if anything, they are producing soldiers just after predator outbreaks. We anticipate that these results will be considerably easier to interpret if data on predation and soldier defence are collected on a finer temporal and spatial scale in combination with measures of colony success after experimental manipulations.

It is more difficult to translate the model's results on predation into interspecific predictions. Imagine that the true cause of the origin of soldiers in a lineage was an increase in predation pressure. This would lead to an expected interspecific positive correlation between predation pressure and presence of soldiers. However, there are two reasons to believe this correlation would quickly be destroyed by subsequent evolutionary events. First, the evolution of soldiers will probably lead to the evolution of predators capable of overcoming soldier defences (see above). These predators might inflict the same predation pressure on the soldier-producing species as other predators inflict on the ancestral non-soldier-producing species. In addition, as the predators evolved to overcome soldier defences, the aphids would become locked into an arms race. The aphids would be required to produce soldiers to counteract the specialized predators.

Secondly, the community of predators attacking soldier-producing and non-soldier-producing species is often different, and soldiers will have differential efficiencies against different types of predators. As soon as one aphid species in a community evolves soldiers it will select for predators capable of successfully attacking soldier species and these predators will then be available to switch to other aphid species producing soldiers. As above, the aphids will lock themselves into soldier-production to deal with the specialized predators.

The above arguments rest on a number of important assumptions concerning the effects of predation, the evolutionary lability of predator species, and the nature of the predator and aphid communities. We are currently in a state of near total ignorance concerning these factors. Some observations have been reported on the types of predators attacking soldier-producing aphids and the nature of the specializations they have evolved to overcome soldier defence (see above). However, there are no quantitative measures of predation under natural conditions and no estimates of the relative effects of different predators. In addition, there is no information on predators attacking non-soldier-producing species closely related to soldier-producing species. This information is critical to unravelling the evolutionary events leading to the evolution of soldiers and their guild of predators. Only once this information has begun to be collected will it be possible to assess the likelihood that soldiers have evolved in response to differential predation pressure.

We wish not to be misinterpreted on this point. We are not suggesting that predation might not have been important in the evolution of soldiers. In one sense, there is no

other possible cause for the evolution of soldiers. Soldiers defend against predators. However, by taking a phylogenetic perspective it becomes clear that the relevant question is: 'What happened in the lineage leading to soldiers that did not happen in the sister lineage that never evolved soldiers.' This event might have been an increase in predation pressure, but also might have been a decrease in the growth rate of the colony, or some other event.

(d) *Soldier Efficiency*

Soldier investment strategies should be qualitatively different depending on soldier efficiencies, and the small amount of data available suggest this might be a particularly fruitful avenue for future research. For example, temporal patterns of soldier investment seem highly variable among species. Colonies of *Pseudoregma bambucicola* produce soldiers primarily at one time of the year (Sunose *et al.*, 1991) and then only when colonies become very large (Sakata *et al.*, 1991). In colonies of *Pseudoregma sundanica* the number of soldiers is strongly correlated with colony size, and it appears that the proportion of soldiers to the total number of individuals may be roughly constant (Schütze & Maschwitz, 1991). In contrast, *Cerataphis fransseni*, which produces soldiers in galls, appears to scale the number of soldiers to either the surface area of the gall or the circumference of the colony, and not to the total number of individuals in the colony (Stern, Aoki & Kurosu, 1994).

Soldier efficiency is simply the return (the number of aphids protected) on a certain investment in soldiers. It depends on factors both intrinsic and extrinsic to soldiers. For example, soldier morphology is an intrinsic factor and the evidence reviewed above suggests that soldiers of different species have both differing morphologies and differing fighting abilities.

There are two kinds of extrinsic factors that will influence soldier efficiency: factors beyond the control of the aphids, such as predation, and factors that can be controlled by the aphid colony, such as gall morphology (Stern, 1995). There is mounting evidence that soldiers are only able to successfully attack some predators, and then only certain larval instars (see above). This suggests that the nature of soldier efficiency will change depending on the predators encountered: large, well defended predators (e.g. adult coccinellids) will lower soldier efficiency relative to small defenceless predators (e.g. syrphid eggs).

With regards to gall morphology, a relatively enclosed gall with a small entrance should be easier to defend than a blister or leaf-roll gall, and this will provide greater soldier efficiency. Furthermore, as the surface area to volume ratio of a gall decreases, a soldier is protecting relatively more aphids for the same defensive act, thereby increasing its efficiency. This might help explain why the most aggressive soldiers yet discovered are produced in galls of *Ceratoglyphina styracicola* which have highly convoluted tissues that greatly increase the feeding surface within the gall (see photographs in Moffett, 1989).

(3) *Future directions for modelling*

The model discussed above is based on a highly simplified view of aphid colonies. Below we discuss some of the most obvious deficiencies in the model.

(1) The model assumes the colony is growing at an exponential rate. This is probably approximately true for only part of the life cycle. In particular, many of the gall producing species do not appear to grow in an exponential fashion and do not reach a stable age distribution. We need models that examine cycles similar to gall cycles with a fixed beginning and end and constraints of host alternation (see Stern & Foster, 1996).

(2) Soldier efficiency is too generally defined. Soldiers certainly vary in effectiveness against different predators and it would be valuable to model this explicitly.

(3) Predation is not a constant factor, as assumed in the above model, but varies both spatially and temporally. More importantly, predation on phytophagous insects is often density dependent (Strong, Lawton & Southwood, 1984). This is perhaps the most important problem requiring modelling because soldier investment varies with colony size in all species where this has been examined (Sakata *et al.*, 1991; Schütze & Maschwitz, 1991; Stern *et al.*, 1994).

(4) Many soldier-producing species are tended by ants (Stern, unpublished observations), some obligately (Schütze & Maschwitz, 1992) and ant tending typically has important effects, usually positive, on homopteran colonies (Buckley, 1987). Ants and soldiers therefore play very similar roles. Models of the costs and benefits of the interaction between ants and soldier-producing aphids will provide a theoretical framework for field work.

VI. FURTHER WORK

Considerable work remains to be done at many levels to gain a clearer understanding of the causes for the evolution of soldiers in aphids. The multiple gains and losses of soldiers in aphids presents an ideal setting for testing general hypotheses for the evolution of soldiers. Several hypotheses are suggested by the models presented above and we have discussed the information required to test these hypotheses. Below we emphasize four general areas of inquiry that we believe are crucially important at this early stage in the development of soldier aphid studies.

First, we require surveys for the presence and absence of soldiers in many aphid taxa. Soldier-producing species are currently confined to the Pemphigidae and Hormaphididae and some theories concerning soldier evolution are specific to these taxa (see above and Foster & Northcott, 1994). It is possible that this taxonomic bias is due to incomplete investigation of other aphid taxa and information from more diverse taxa would be extremely useful. We predict that soldiers outside of the Hormaphididae and Pemphigidae are most likely to be found in the species of Aphididae producing pseudogalls.

Secondly, we need further phylogenetic analyses of clades containing soldier-producing aphid species both to better estimate the evolutionary patterns of soldier evolution and to provide the framework for comparative studies. Species level phylogenies are most useful for these purposes, but at this stage even further information on generic relationships will be useful for guiding field studies.

Thirdly, it would be extremely useful to know the mechanism of production of morphologically specialized soldiers both to corroborate phylogenetic hypotheses for convergence and to offer tools for manipulating colonies for functional studies. For example, it will be interesting to learn the external cues, if any, that trigger soldier production and the hormonal changes that accompany and trigger soldier production.

Fourthly, we need considerably more information on the precise function of soldiers in natural colonies. It is now clear that soldiers can kill some predators and can increase the growth rate of colonies in nature. It will be useful to have more detail on the types of predators that soldiers are effective against and the types of predators that attack both soldier-producing and non-soldier-producing species.

VII. SUMMARY

1. Defensive individuals, termed soldiers, have recently been discovered in aphids. Soldiers are typically early instar larvae, and in many species the soldiers are reproductively sterile and morphologically and behaviourally specialized.

2. Since aphids reproduce parthenogenetically, we might expect soldier production to be more widespread in aphids than it is. We suggest that a more useful way to think about these problems is to attempt to understand how a clone (rather than an individual) should invest in defence and reproduction.

3. Known soldiers are currently restricted to two families of aphids, the Pemphigidae and Hormaphididae, although they are distributed widely among genera within these families. We discuss the use of a phylogenetic perspective to aid comparative studies of soldier production and we demonstrate this approach using current estimates of phylogenetic affinities among aphids. We show that the distribution of soldier production requires a minimum of six to nine evolutionary origins plus at least one loss.

4. At least four main types of soldiers exist and we present and discuss this diversity of soldiers.

5. Most soldier-producing species produce soldiers within plant galls and we discuss the importance of galls for the evolution of soldiers.

6. We summarize the evidence on the interactions between soldiers and predators and between soldier-producing aphids and ants.

7. We present an optimality model for soldier investment strategies to help guide investigations of the ecological factors selecting for soldiers.

8. The proximate mechanisms of soldier production are currently very poorly understood and we suggest several avenues for further research.

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