

## Chapter 2

# The Ecology of Altruism in a Clonal Insect

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**Abstract** Social aphids are an ideal animal group in which to demonstrate the relative importance of ecological versus genetic factors in the evolution of sociality for several reasons: (1) Since aphids are clonal, the genetics of a colony is starkly simple (the aphids are either from the same clone or they are not) and, in principle, easy to measure; (2) Because good phylogenies are available for several aphid taxa and there is clear evidence that there have been more independent origins of sociality in aphids than in any other social clade, it is possible to test for associations between ecological factors and the evolution of sociality; (3) Recent developments, in the understanding of the mechanism of the proximate control of soldier development, in the genetic basis of sociality, and in models of social evolution, make the social aphids an ideal group for experimental work on the evolution of social behavior; (4) The social aphids are of special ecological interest because they include the only organisms that have evolved sterile castes in societies that do not occupy some kind of nest (the secondary-host generations of the Hormaphidinae).

The ecological context of altruism in social aphids has been shown to be quite intricate since it is now clear that colony defense is not the only costly behavior that they perform: they also have vital roles in keeping the colony clean, migrating to new colonies, and repairing their nest. Numerous ecological factors are highly pertinent in aphid social evolution including (1) the fact that all social aphids have at some stage in their life cycle a valuable and defensive fortress in the form of a plant gall, (2) population size and density, (3) birth rate, (4) the level of exposure to specialized predation, and (5) variation in the level of tending provided by ants. Kin selection in social aphids has given rise not only to a range of elaborate adaptations in behavior and morphology but also to impressive short-term flexibility in social investment. For example, in species that have specialized defenders that can mature to make a direct contribution to their colony's fitness, defense investment can be increased both through heightened production of defenders at birth and prolongation of the defender stage.

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We demonstrate that ecological factors are essential in any attempt to understand the role of kin selection in the evolution of social behavior in a group of organisms: ecology determines the extent to which groups consist of related individuals and the context in which these individuals can give and receive help.

## 2.1 Introduction

Social aphids provide an excellent system in which to study the role of ecology in the evolution of altruism. This is primarily because the other essential component of kin-selected explanations of altruism – relatedness – is straightforward and in principle easy to measure: the aphids in a colony are either from the same clone or they are not. Ecology determines the extent to which colony members are a pure clone and whether social behavior will be selectively advantageous. Aphids are, of course, not the only clonal organisms that are social, and there has recently been an upsurge of interest in the evolutionary biology of these organisms, especially microorganisms (e.g., Crespi 2001; Griffin et al. 2004; Queller 2004), such as bacteria, myxobacteria, and cellular slime moulds, and also higher organisms, such as marine invertebrates and polyembryonic wasps (Cruz et al. 1990; Duffy et al. 2002). The social aphids stand out from these other clonal organisms because they consist of clones whose members are highly mobile and independent of each other and also because we have far more reliable information about their phylogeny, their ecology and their genetic structure. However, the general ideas that we are discussing here are relevant to our understanding of the evolutionary biology of a very wide range of events from the origins of multicellularity to social interactions in bacteria. In this chapter, after a very brief introduction to the biology of social aphids, we will discuss developments in our understanding of their social evolution since the reviews of Stern and Foster (1996, 1997).

Hamilton (1964) was the first to point out the paradox of the rarity of altruism in clonal organisms in general and in aphids in particular. In these organisms, any helping behavior that reaps more rewards than it costs will be selected for. The paradox is more apparent than real: altruism is in fact quite common in clonal organisms, if we relax the definition to include multicellularity. Even in aphids, social behaviors have evolved independently on many occasions: possibly as many as 17 times (Fukatsu, pers. comm.), considerably more than in any of the other major taxa of eusocial insects. In addition, the conditions favoring the evolution of altruism remain quite stringent, even in clonal organisms. An individual's critical cost/benefit ratio (i.e., direct offspring lost through altruism/indirect offspring gained through altruism) of unity is no lower than in societies of diploids or haplodiploids ruled by a singly mated queen, and the issue of the maintenance of clonal purity is crucial. The chief reason given by Hamilton (1972) for the absence of social aphids is almost certainly wrong, namely that

there is little scope for providing help if you are a specialized sedentary sapfeeder. Recent work has demonstrated the inexhaustible inventiveness of natural selection in providing ways in which these small sapsuckers can help each other (see Sect. 2.4).

## 2.2 Basic Biology of Aphid Soldiers

Aphids are small, phloem-feeding bugs (Order Hemiptera; Suborder Sternorrhyncha), which, for most generations, are parthenogenetic and bear live young. In most species, a series of parthenogenetic generations alternates with a single generation of sexual reproduction. A minority of aphid species (about 10%, but including almost all the social species) alternate between two plant species: the primary host, where sex occurs and several parthenogenetic generations are produced, and a secondary host where successive entirely parthenogenetic generations of females develop.

The most widespread feature of aphid sociality is the presence of soldiers that defend the clone against predators. These soldiers are almost always early instars, although there is one example of an adult aphid showing defensive behavior (Inbar 1998). The soldiers are impressively diverse, both in morphology and physiology. The commonest weapons are highly sclerotized stylets, legs and horns, and some soldiers are known to inject venomous proteases. The only way to study the behavioral subtleties of caste in aphids, as for all social insects, is by detailed observations, and recent studies have suggested that aphids might have unexpectedly complex caste systems to rival those of the social Hymenoptera. Rhoden and Foster (2002) studied six species of *Pemphigus* and showed that defensive behavior was widespread not only among the different *Pemphigus* species, including those without any morphological specialization, but also among the different developmental stages. First instars were always the most aggressive, but later instars in all the soldier-producing species showed some degree of anti-predator behavior. These observations suggest that defensive behavior might be quite widespread and generalized in this genus, and can be adapted flexibly in response to the ecology of a particular species. In two sibling species of *Pseudoregma* that produce dimorphic first-instar larvae of soldiers and non-soldiers, Shingleton and Foster (2001) showed that the division of labor in these larvae could be very flexible, with non-soldiers frequently being recruited into defensive roles.

There are essentially two axes along which aphid soldiers can be aligned: sterility and morphological specialization. At one extreme are highly specialized, obligately sterile first instars, which never moult to the next instar. These would include *Pseudoregma alexanderi* soldiers on the secondary host (Aoki and Miyazaki 1978). At the other extreme are those soldiers, for example early instar gall-generations of *Pemphigus bursarius*, that are not morphologically specialized

and all have the potential to develop into winged individuals that fly from the gall. The intermediate phenomenon of facultative sterility is also well known. Some soldiers have the potential to mature to adulthood despite also being physically specialized, but their development may be delayed to such an extent that they do not, in practice, have much chance of reproducing. This is the case for the third-generation soldiers of *Pemphigus spyrothecae* (Pike et al. 2004; Rhoden and Foster 2002). We follow Stern and Foster (1997) in classing all the defensive aphid morphs as “soldiers” and not restricting the term just to those morphs that are obligately sterile.

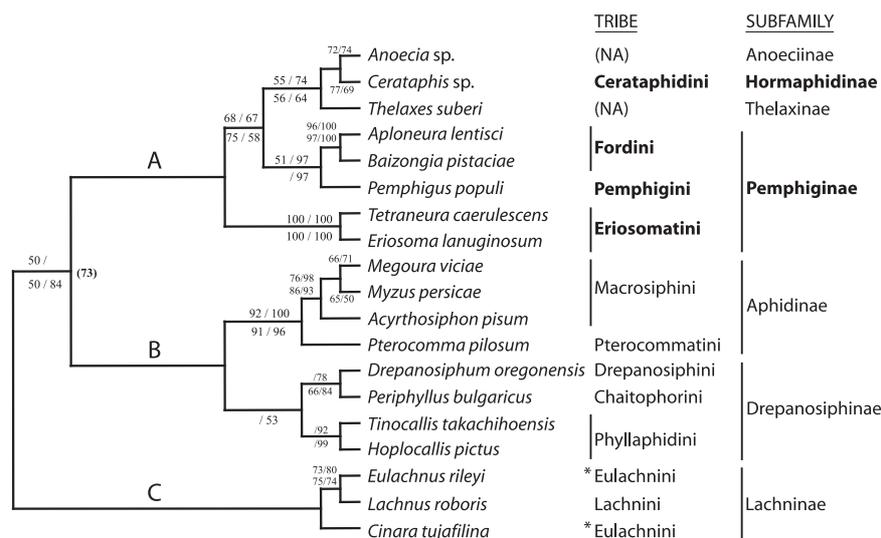
### 2.3 The Phylogenetic Distribution of Aphid Soldiers

Of the approximately 4,700 species of aphids described (Remaudière and Remaudière 1997), around 60 are known to be social. These social species are found in six tribes: the Pemphigini, Eriosomatini and Fordini of the Pemphiginae and the Hormaphidini, Certataphidini and Nipponaphidini of the Hormaphidinae (Fig. 2.1). The fact that aphid sociality is evolutionarily labile is evident even from examination of phylogenies providing only subfamily/tribe resolution. For example, the asocial Thelaxinae and Anoeciinae occur deep amongst the lineages in which some of the most social species occur (Ortiz-Rivas et al. 2004). More significantly, because the degree and, in many cases the presence, of sociality varies within each of the soldier-producing tribes, it is clear that soldiers have evolved and been lost a number of times. For example, in the Cerataphidini, while soldiers are always present in primary-host colonies, Stern's (1998) examination of secondary-host soldiers indicates that these specialized horned defenders have evolved once and been lost once or twice. At the level encompassing all taxa known to contain social species, Stern and Foster (1996) gave a highly conservative early estimate of six to nine origins but Fukatsu (pers. comm.) has good evidence that the soldiering trait has evolved at least 17 times. These figures dwarf the number of independent origins of sociality found in other taxa such as the wasps, bees and termites. Of the 17 evolutionary origins estimated by Fukatsu, four or five have produced extreme cases in which there is absolute division of labor between reproductives and sterile soldiers. The number of losses of aphid sociality is more difficult to estimate accurately because detailed behavioral observations are lacking for many pemphigine and hormaphidine species. It is nevertheless clear that these evolutionary losses are also numerous.

The six aphid tribes named above provide biologists with one of the few social clades for which a good phylogeny is available (see also Chap. 3 for thrips). By also being a unique clade for having had multiple losses of social traits in diverse lineages, these aphids provide a unique opportunity for understanding the determining influence of ecology on sociality.

## 2.4 Are Aphids Eusocial?

It has not been universally accepted that the soldier-producing aphids are eusocial (e.g., Gullan and Cranston 1994; Hölldobler and Wilson 1990). This seems unreasonable, since many species readily fulfill the three traditional criteria of eusociality. All aphids routinely show overlap of generations and those with sterile soldiers clearly have reproductive division of labor. The sticking point would seem to be cooperative brood care, but recent work has clearly shown that many species show an intricate range of cooperative behavior, principally to do with the care and maintenance of the “fortress” (the plant gall). We discuss these behaviors here, not primarily in defense of the aphids’ eusociality, which is largely a matter of semantics, but because of the light they throw on the complex ecological context of altruism in these animals.



**Fig. 2.1** A molecular phylogeny for selected species from family Aphididae based on variation of the DNA sequence of the long-wavelength opsin gene. Species names are given along with tribes (where possible) and subfamilies. Tribes and subfamilies known to contain social species are indicated in bold. Vertical lines (or, in the case of the apparently polyphyletic Eulachnini, asterisks) indicate multiple members of a higher taxon. Bootstrap support for maximum likelihood analysis is indicated above branches and, for values of 50 and greater, bootstrap support for maximum parsimony analysis is indicated below branches. Bootstrap values derived from analysis of first-plus-second positions only are given to the left of the slash and those derived from analysis of all positions are given to the right. Three main clades are apparent (indicated by the letters A–C), with all known social aphids occurring in clade A. The value in parentheses indicates the bootstrap value obtained in a maximum parsimony combined analysis of the long-wavelength opsin sequences and mitochondrial ARP-6 sequences (modified from Ortiz-Rivas et al. 2004, with permission)

### 2.4.1 Colony Defense

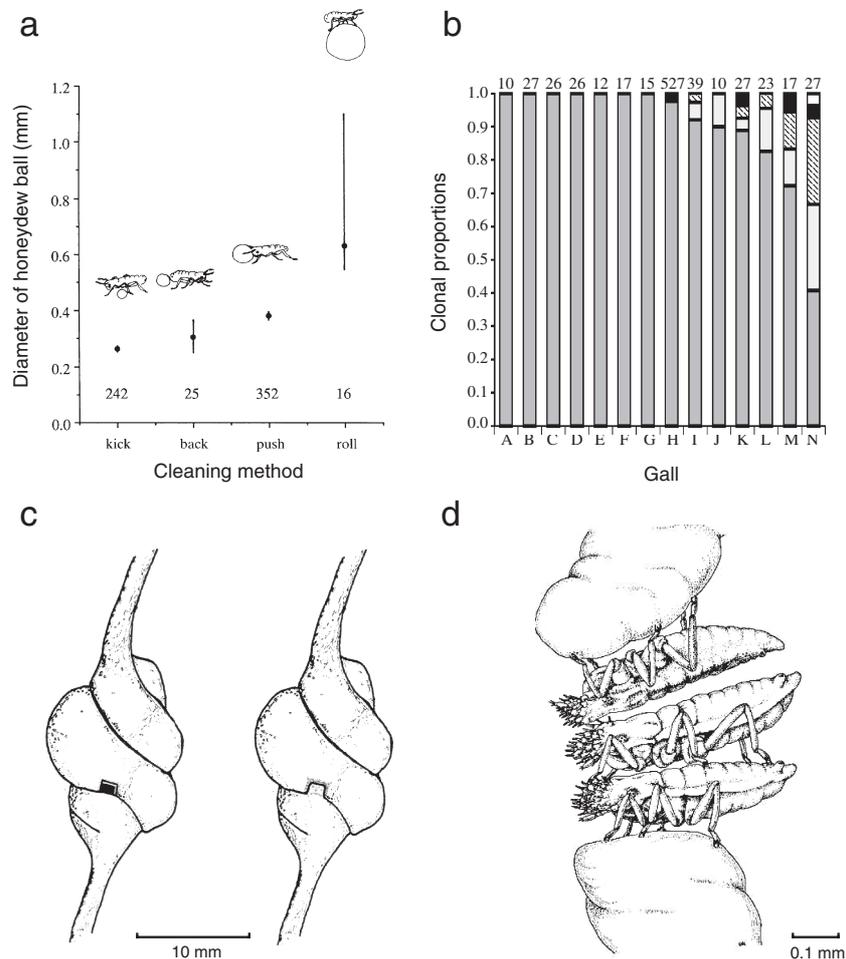
The unique behavioral, morphological, and physiological adaptations associated with defense are perhaps the best evidence of advanced social specialization (Stern and Foster 1996, 1997). The weaponry used by aphid soldiers against their predators is hugely diverse, including the following combinations: stylet with hindlegs (e.g., *Pemphigus spyrothecae*, Foster 1990), stylet with fore and mid legs (e.g., *Colophina clematis*, Aoki 1977), stylet alone (e.g., the primary host soldiers of *Pseudoregma bambicicola*, Aoki and Kurosu 1992a), horns and forelegs (e.g., *Pseudoregma alexanderi* Aoki et al. 1981). The soldiers of *Tuberaphis styraci* manufacture a highly toxic protease that is injected through their stylets into predators (Kutsukake et al. 2004) and it is likely that a number of other aphid soldiers use venom in a similar fashion. Although adult and larval predators that are attacking the colonies are the usual targets for soldier defense, eggs are sometimes attacked preemptively (e.g., *Ceratovacuna lanigera*, Aoki et al. 1984), just as preemptive patrolling of the exterior of the gall is also known (e.g., *Ceratovacuna nekoashi*, Kurosu and Aoki 1988). Although defense usually falls to the first instars (e.g., *Hamamelistes cristifoliae*, Akimoto et al. 1996) or second instars (*Tuberaphis styraci* Aoki and Kurosu 1989a), this is not prescriptive and defense is also known in the third instar (e.g., *Eriosoma moriokense*, Akimoto 1983; some *Pemphigus* spp., Rhoden and Foster 2002), the fourth instar (*Grylloprociphilus imbricator*, Aoki et al. 2001) and even in adults (*Smynthuroides betae*, Inbar 1998).

### 2.4.2 Gall-Cleaning

Soldiers take on a cleaning role by removing honeydew, exuviae and other detritus from the gall in a number of species including *Pemphigus dorocola* (Aoki 1980), *T. styraci* (Aoki and Kurosu 1989a) and *P. spyrothecae* (Benton and Foster 1992; Pike et al. 2002; Fig. 2.2a). It is clear that cleaning can evolve in the absence of any defensive role, as the first instars of *Hormaphis betulae*, a species without soldiers, cooperate to push large masses of honeydew out of their galls (Kurosu and Aoki 1991). Such cleaning behaviors are costly both in terms of time and energy expenditure but also because it places the individuals near to the gall opening, the site most susceptible to predation. The critical benefits of cleaning are that the potentially devastating microbial and fungal pathogens are deprived of the honeydew on which they thrive and the full volume of the gall can be used by the aphids.

### 2.4.3 Intergall Migration

Because survival outside of a colony is exceedingly poor, altruistic migration by soldiers away from the native clone to invade an alien colony is a high-risk behavior. Nevertheless, it is also a behavior that can pay huge dividends in terms of reproductive



**Fig. 2.2** Some lesser-known altruistic behaviors of social aphids. **a** The diversity of cleaning behaviors seen in *P. spyrothecae*. The method of removal of wax-coated balls of liquid honeydew is modified according to the size of ball to be removed, with the possible exception of the ‘kick’ and ‘back’ behaviors, which were both used for the smallest balls. The number of observations of each behavior is given above the *x*-axis (from Benton and Foster 1992, with permission). **b** Clonal mixing, the outcome of migration, in *P. spyrothecae*. Microsatellite genotyping of the number of individuals given above each bar was used to identify the proportion of different clones in 14 discrete galling colonies (marked *A-N*). These results are discussed in an earlier section. (modified from Johnson et al. 2002, with permission). **c** Gall repair in *P. spyrothecae*. A square hole has been cut in the gall on the *left*. The full repair seen in the gall on the *right* is achieved over several days during which the aphids induce compensatory growth into the hole from an undamaged portion of the gall. **d** Soldiers of *Astegopteryx spinocephala* cooperating to seal the opening of their subgall with their spinous heads (from Kurosu et al. 2006b, with permission)

success. Alien individuals certainly occur in apparently closed colonies (Johnson et al. 2002, Fig. 2.2b) and there is good reason to expect that migration is widespread (Aoki 1982). It has been documented for *Pemphigus obesinymphae* that these payoffs can be maximized because the migrating soldiers ‘cheat’ by hastening development and abandoning defensive behavior once they have successfully colonized a gall established by an alien clone (Abbot et al. 2001; and see Sect. 2.6).

#### **2.4.4 Gall-Repair**

As the gall represents a resource-rich fortress that protects the colony from predators (Sect. 2.7.1), prompt repair of any breach in the fortress’s walls will be under strong selection. In *P. spyrothecae*, the aphids induce this repair by stimulating the host plant to create complementary regrowth in the gall to fill the damaged area (Pike and Foster 2004, Fig. 2.2c) and, more remarkably, in *Nipponaphis monzeni*, soldiers rapidly seal over holes in their gall by exploding their bodies to release a viscous fluid in which they fatally entrap themselves (Kurosu et al. 2003). Although it has not been studied in detail, highly effective gall repair is also known to occur in *Ceratoglyphina bambusae* (Aoki and Kurosu 1991). As in *P. spyrothecae*, this repair apparently occurs relatively slowly, relying on the aphids’ manipulation of the plant tissue of their damaged gall.

#### **2.4.5 Blocking Behavior**

In *Astegopteryx spinocephala*, a less extreme but equally effective method of filling gall openings is employed: soldiers form a group and protrude their specialized spinous heads into the hole to block it entirely (Kurosu et al. 2006a, 2006b, Fig. 2.2d).

### **2.5 Proximate Factors in the Determination of Soldier Aphids**

While investment in defense is known to vary greatly both within and among species, the proximate causes of this variation are, in general, poorly known. Predation (Shibao 1998), population size (Shibao 1999a), seasonal change (Sunose et al. 1982), condition of the host plant (Sakata et al. 1991), and size of the interior surface area of the gall (Stern et al. 1994) have all been proposed, but not substantiated in conclusive manipulative experiments, as proximate cues.

One of the first proximate cues for increased investment in soldiers was discovered by deduction. Withgott et al. (1997) found that, in *Pemphigus obesinymphae*, the death of the founding female of the gall (the fundatrix) resulted in accelerated development of the first instar soldiers into reproductives. Maternal presence, for at least one species, is thus a proximate cue to continued defense investment.

The difficulty in identifying proximate cues for defense is partly due to the problem that observations and experiments must mostly be done in uncontrolled natural conditions. Shibao et al. (2002) solved this problem for *T. styraci* by establishing an artificial diet on which the species could be reared in continuous laboratory culture. Shibao et al. (2004a) went on to demonstrate that increased density of aphids in the gall (as distinct from high population size) is the major proximate factor causing an increase in soldier number. This finding was consolidated by examination of soldier proportions in field-collected colonies at high population density. The timing of this density-induced defense investment has also been investigated (Shibao et al. 2003). High aphid density was found to have a prenatal influence on embryos still within the ovarioles of their mothers, which resulted in increased soldier production. Furthermore, the flexibility inherent in having second-instar soldiers was also demonstrated in the finding that postnatal exposure (during the first instar) to high aphid density was also sufficient to induce soldiers. The combination of both pre- and postnatal exposure had a synergistic effect, which resulted in soldier production that was approximately four times greater than high-density exposure at just one of the two periods. These findings seem to agree with the report of Ijichi et al. (2004) that showed that for *Pseudoregma bambucicola*, the path to becoming a soldier has two distinct phases: differentiation as an embryo followed by rapid growth after birth. Because the increase in soldier proportion with aphid density tends to reach a plateau in *T. styraci* colonies under natural conditions, Shibao et al. (2004b) also sought a further regulating mechanism for soldier production. They were able to demonstrate conclusively that soldier number was up-regulated when a low proportion of soldiers is present but down-regulated when the proportion of soldiers is already high (i.e., at around 50%). Caste ratio is thus another proximate factor that can influence defense investment.

Clonal mixing (Abbot et al. 2001) and ant tending (Shingleton and Foster 2000) are also documented influences on soldier production but these are dealt with in detail in Sects (2.)6 and (2.)7.3.

## **2.6 A Genetic Factor in the Evolution of Social Aphids: Clonal Mixing**

Clonality is often cited as a fundamental pillar of the evolution of the extreme aphid altruism that is sometimes observed (e.g., Krebs and Davies 1993) and it has been claimed that that the relatedness value of 1 often seen in aphids is the ultimate predisposition to altruism. However, the rarity of social aphid species (which represent just 1% of aphids) provides a clear demonstration that clonality alone is not sufficient to produce altruism (Stern and Foster 1996). The co-requisite ecological factors that encourage altruism by assisting the preservation of monoclonal colonies are discussed in later sections. Clonal mixing, a genetic consideration that can undermine the benefits of altruism, is discussed here.

Hamilton (1987) recognized the potential for aphids from one clone to invade and steal the altruism of another clone, calling the invaders “self-propelled cuckoo eggs”. The benefits of invading a social aphid colony are clear: the invader gains from its host’s food and protection and is relieved of the genetic obligation to perform altruistic duties. The major gain for the invader’s clone is that the clonal genotype is destined to propagate safely in a second location and thus serve as a hedged bet in the event of a calamity befalling the home colony. The only risk incurred when seeking this benefit from invasion is that the invaders may not find a host colony, but this risk can be somewhat alleviated if the invaders are individuals with relatively low reproductive value.

As early as 1980, Setzer used allozyme analysis to demonstrate that colonies of *Pemphigus populitransversus* routinely contain up to 25% invaders. Perhaps tellingly, this species is not known to be social although it is closely related to numerous species that are. In *P. spyrothecae*, a species which is highly social, microsatellite genotyping has been used to demonstrate that the average level of clonal contamination was 10%, albeit with a great range that varied from 0–59% (Johnson et al. 2002). In around 2% of colonies, this contamination was due to multiple alien clones. In one case, nine alien clones were found in a colony that was only 2% contaminated. This detailed information on clonal mixing may indicate that a very low level of mixing is required to take advantage of the bet-hedging mentioned above. In the case of *P. spyrothecae*, the scarcity of would-be immigrant cheats associated with low clonal mixing may have played an important part in maintaining the selective advantages of altruistic traits and facilitating the evolution of sociality. In another *Pemphigus* species, which is highly social, *P. obesinymphae*, the average level of clonal mixing is 41% with a range of 21–71% (Abbot et al. 2001). Abbot et al. were also able to confirm theoretical predictions by demonstrating that the invaders had (1) a vastly reduced propensity to defend and (2) developmental rates that were accelerated such that they reached the reproductive stage more quickly than individuals of the host clone.

At high levels of clonal mixing such as those reported for *P. obesinymphae*, it becomes reasonable to ask why social behavior persists. Certainly, cheating such as that described might be expected to rapidly erode the evolutionary advantages of altruistic behavior when more than 50% of a colony’s population routinely comes from alien clones. Because natural selection has required similar characteristics from invaders and defenders (e.g., low reproductive value to minimize the loss incurred through risky activities, high cuticular sclerotization as armor or protection against desiccation), the invading individuals may be the same individuals that would be defending were they still in their native clone. The effect of this binding social behavior and invasive behavior in positive feedback may be that higher levels of invasion can be tolerated by native clones (see also Foster 2003).

Because clonal mixing has the potential to undermine the benefits conveyed by social behavior, the possibility of social policing to prevent invasion by alien clones has been propounded. A prerequisite to such policing, the ability to distinguish between kin and non-kin, has been assessed in a number of aphid species. Kin recognition was sought, but not found, in *C. bambusae* (Aoki et al. 1991; Aoki and Kurosu 1991). Instead, it was found that, at the beginning of the galling season, the

obligately sterile soldiers defended the exterior of their native gall against non-soldier conspecifics, regardless of whether these conspecifics were from the native or an alien clone. By the end of the galling season, this attacking behavior, based on the ability to discriminate soldiers from non-soldiers had disappeared, presumably because the threat of exploitation by fecund individuals was assuaged by the fact that the reproductives were about to disperse. As in *C. bambusae*, no evidence for kin recognition was found in *Ceratovacuna japonica* (Carlin et al. 1994) or *Pseudoregma bambucicola* (Shibao 1999b). Prevention of invasion by alien clones through behavioral means has thus not been found to date. In contrast, the physical barriers to clonal mixing are obvious and effective. These are described in the next section.

## 2.7 Ecological Factors in the Evolution of Social Aphids

By way of preface to this section in particular, it is worth mentioning that studies of ecological (and genetic) influences upon aphid sociality have focused on defense. Although this focus may sometimes have meant that other social traits were neglected, we hasten to point out that defense is certainly the central social trait that may commonly have been a necessary precursor to the evolution of the others discussed above. In addition, one might reasonably expect that trends in defensive characteristics may often serve at least as qualitative indicators for trends in other social characteristics. For these reasons, the latter parts of this section are mostly devoted to observed and predicted strategies of defense investment. A clear statement of the routes to increased defense investment may thus be subsequently useful: an aphid colony can increase defense by (1) producing a greater number of defenders, (2) lengthening the duration of the defensive stage, (3) improving the efficacy of defense, and/or (4) increasing the plasticity of defensive behavior.

We also note that, for reasons which include social aphids' relatively recent discovery and limited economic importance, direct observations and ecological experiments are entirely lacking for the vast majority of species. Much of the research that relates generally to environmental, life-history and host-related factors is theoretical. Of course, we look forward to a time when empirical evidence to support or refute these predictions becomes available.

### 2.7.1 Galls

One of the key correlates of aphid sociality is the galling habit. Whereas not all gall-forming aphids are social, all of the approximately 60 aphid species that are known to be social do form galls on a host plant at some point in their life cycle (Foster and Northcott 1994). It thus follows that galling life must convey crucial selective predispositions to sociality, over and above its more general selective advantages (described in detail by Price et al. 1987). The implications that the galling habit holds for the evolution of sociality have been reviewed in detail by Foster and Northcott (1994) and are discussed here only in brief:

### **Fortress Defense**

Queller and Strassman (1998) use the term ‘fortress defense’ to describe the evolution of sociality through selection for group cooperation in exploiting and protecting a rare and valuable habitat. Because galls are a rich and truly invaluable resource to the aphids which create and inhabit them, they are ideal examples of defense-worthy fortresses.

### **Facilitating Anti-Predatory Behavior**

Besides providing an environment that is worthy of defense, the gall also serves as a readily defensible fortress in that, for the vast majority of its surface area, it represents a physical barrier to predation. If only the points of entry require active monitoring and defense, the behavioral effort and increased morphological specialization requisite to effective social defense may be reduced to a level that is not only selectively tenable but, indeed, favorable. Specialized placement of morphs within the gall has been demonstrated in *P. spyrothecae*. Soldiers tend to inhabit the area of the gall closest to the opening whereas reproductives (sexuparae) tend to inhabit the area of the gall furthest from the opening (Pike 2007).

### **Encouraging Clonal Integrity**

If defense and other altruistic traits are to produce fitness benefits for the genotypes that invest in them, it is paramount that the individual beneficiaries belong to the same clone. The possibilities for cheating through clonal mixing were discussed in section 0. Such cheating, if sufficiently common, would certainly result in the total breakdown of altruism. However, galls also provide barriers to invasion by alien aphids and, in doing so, preserve the intense potential for intra-clonal selection to promote altruism.

The pivotal role the gall has in encouraging defense is also manifest in comparisons among species (Pike 2002; Rhoden and Foster 2002) and in theoretical findings (Akimoto 1996; Pike and Manica 2006a) which indicate that, as duration of the galling stage increases, so too does the degree to which soldier production is favored.

## ***2.7.2 Life-History and Host Variables***

### **Birth Rate**

Numerous theoretical studies have set out to elucidate the conditions that encourage increased investment in defense. One of the notable conclusions from the earlier studies (Akimoto 1996; Stern and Foster 1996) was that low colony birth rate would favor soldier production. The biological rationale for this mathematical conclusion is that defense is most important for populations that are least able to replace individuals lost

to predation. Increasing the number of soldiers born is perhaps the most obvious way to increase defense. We know that in species with dimorphic nymphs soldiers are certainly distinguishable from non-soldiers immediately from birth, and recent studies of embryology and ontogeny confirm that the allocation decision can be made considerably earlier (Ijichi et al. 2004). In both *Colophina arma* and *P. bambucicola*, soldier differentiation is initiated during embryogenesis (Ijichi et al. 2005). However, in *C. arma* (the species with more specialized soldiers), this differentiation occurs much earlier than it does in *P. bambucicola*.

### Colony Size, Growth Rate, and Carrying Capacity of Host

A series of investigations has assessed the basis of the tendency for larger colonies to have greater proportions of soldiers. This tendency has been empirically sought in a number of species with obligately sterile soldiers and there is evidence for its occurrence in *P. bambucicola* (Itô et al. 1995; Shibao 1998) and *P. sundanica* (Schütze and Maschwitz 1991; Shingleton and Foster 2001). Aoki and Kurosu (2003) created a logistic population model which is consistent with the density-dependent declining growth rate that is expected to differing degrees in both gall-dwelling and free-living aphid colonies. The model of Aoki and Kurosu (2003) indicated that production of soldiers should be more easily favored in large colonies than in small ones. The reason for this effect was that because the fitness impact of a soldier's defensive efforts is greatest in populations near carrying capacity, its indirect fitness contribution to its colony was most likely to outweigh the limited direct contribution that the presence of another reproductive would produce. The authors were quick to point out that the rate of colony growth was also predicted to have a marked effect on propensity to soldier production, with faster-growing colonies likely to have less impetus to produce soldiers.

Expanding on their previous model, Aoki and Kurosu (2004) pointed out that because defense by soldiers increases the intrinsic growth rate of an aphid population, the presence of soldiers allows for a larger optimal colony size than would otherwise be expected. They were also able to determine that the optimal number of soldiers could be calculated by determining up until what point the defensive efficacy resulting from the production of another soldier ceases to exceed  $r_m/K$ , the ratio of the colony's intrinsic growth rate and the theoretical carrying capacity. Interestingly, they predicted that this optimal number was the same regardless of whether the aphid colony was monoclonal or polyclonal. A colony made up of multiple genotypes was, however, expected to conform to Hamilton's Rule by having a larger overall population size and, consequently, a lower proportion of soldiers and a lower productivity than a pure clone.

In the most recent model, Aoki and Imai (2005) sought to clarify whether, in larger colonies, there is a demographic expectation of higher proportions of soldiers (in addition to the greater ease of soldier production which had already been demonstrated). Perhaps obviously, soldier proportion was predicted to increase with predation pressure but, beyond this effect and even when the number of predators per

aphid was constant, the proportion of soldiers increased with increasing colony size. It was also demonstrated that the proportion of soldiers in a mature colony with a small carrying capacity would be greater than the proportion of soldiers in an identically sized developing colony with a high carrying capacity. An elaboration on this finding was the conclusion that under the right conditions (of sufficient limitation by very small carrying capacities), soldierless colonies (such as those recorded by Itô et al. 1995) are the natural outcome of internal population regulation and are not due to external influences such as predation. The positive effect that the aforementioned population parameters had on soldier production was further enhanced under the credible assumption that soldiers incur fewer energetic and material costs than non-soldiers.

The state-dependent dynamic model of Tyerman and Roitberg (2004) concurred with earlier authors that defense investment should have an inverse relationship with productivity. In contrast to previous findings, the model was said to predict a negative correlation between soldier proportion and colony size. This contrary prediction was attributed to the expectation that, whereas predators were able to gauge the colony size of the free-living species, they were not able to do so in the case of the galling aphid species. It deserves to be noted, however, that the high proportion of soldiers expected in small colonies dipped only for colonies of intermediate size before rising again for large colonies which had reduced productivity due to reproductive constraints imposed by a looming carrying capacity. The predictions of this model are thus not actually dissimilar from those of other models. In any case, although the link between colony size and soldier proportion may be common, it is probably not a universal rule: for example, empirical evidence collected by Stern et al. (1994) for *Cerataphis fransseni* suggests that soldier proportion scales with the physical dimensions of the gall.

### **Aphid Density**

Section 0 has detailed how aphid density is the major colony-determined proximate cue for soldier production. High density and not large colony size is the trigger for production of more soldiers in *T. styraci* and (bearing in mind the absence of any obvious mechanisms for an aphid to estimate population size directly) is also a likely trigger for many other species (Shibao et al. 2004a). High density, in the case of galling aphids, effectively means crowding, and this crowding may be the most reliable indicator a colony has when deciding whether increased production of soldiers is necessary and sufficiently cheap.

### **Colony Lifetime**

In addition to increasing the proportion of soldiers produced at birth, other forms of defense investment have been examined through models. Pike and Manica (2006b) suggested that soldier behavior may become more risk-averse when

reproductive rates are low and colony lifetimes are long (i.e., at a time when soldiers are especially costly to replace). Perhaps unexpectedly, this strategy, which amounts to “living to fight another day”, was most favored when predation was high.

Lengthening of the defensive instar has been demonstrated in natural populations of both monomorphic *Hemipodaphis persimilis* (Akimoto 1992) and dimorphic *Pemphigus spyrothecae* (Pike et al. 2004). This phenomenon, termed instar extension, is thought to be most likely to occur in colonies with long lifetimes (Akimoto 1996) and at times (usually the terminal colony stages) when birth rate is at its lowest. Pike and Manica (2006a) predict that both period and level of exposure to predation are important critical factors which, in conjunction with birth rate, may set the optimal level of defense investment. A further conclusion is that increased soldier production at birth is most likely to be favored when soldiers have a markedly higher rate of mortality compared to non-soldiers. However, these authors' model also highlighted that flexibility in birth allocation of soldiers was usually not crucial when other methods of increasing defense investment were available.

### 2.7.3 External Effects

#### Predation

Defense is the aphid's main answer to predation. Because defense is costly to an aphid colony, variation in predation will exert a selective effect on defensive behavior and morphological traits. Nevertheless, the presence of a plastic response to variation in predation has been neither directly observed in nature nor empirically demonstrated. This lack of demonstrable causality is mostly due to difficulties in assessing predation pressure and is not evidence that an effect is absent. Theoretical approaches that are subject to no such practical constraint have clarified the conditions under which predation may have markedly different effects. The most obvious effect of predation is that, as it increases, so too will the degree to which investment in defense is favored (Akimoto 1996; Aoki and Kurosu 2003; Stern and Foster 1996; see also Chap. 6 on ants). However, if a colony is faced by a “non-gluttonous” predator that eats only a set number of aphids in a given period, one can expect the proportion of soldiers to reach a peak at intermediate colony size and subsequently decrease as the population increases further (Aoki and Imai 2005). The state-dependent model of Tyerman and Roitberg (2004) even predicts that for galling aphids, soldier allocation may sometimes be lower when a predator is present in their gall. This prediction was based on the implicit assumption that the predator could serve as a culling influence, which would release the aphids from their density-dependent reproductive constraints. Once thus released, the best strategy for a colony may be to out-reproduce a predator's limited appetite rather than opting for stubborn and costly defense. The above predictions, which require conservative predation, do not concur with observations that some predators routinely decimate galling colonies (Foster 1990).

### Ant Tending

The first demonstration of social aphids' adjusting their defense investment in response to the environmental change dealt with the case of ant tending (Shingleton and Foster 2000). The authors demonstrated that in the obligatorily ant-tended species *Pseudoregma sundanica*, the proportion of soldiers increased in colonies that were deprived of ants. It is known that ants actively remove predators from the colonies that they tend (Schütze and Maschwitz 1991) and, because of this, ant tending is likely to serve to some degree as a substitute for defense investment. A subsequent comparative study of *P. sundanica* and the closely related *Pseudoregma nicolaiiae* supported this conclusion (Shingleton and Foster 2001). It was found that *P. nicolaiiae*, which is rarely ant-tended, had less morphological specialization between soldiers and non-soldiers but that both of these castes were more aggressive than their *P. sundanica* counterparts. The soldiers of *P. nicolaiiae* were also found to be significantly bigger than the soldiers of *P. sundanica*. One would expect that the absence of ant defenders might require *P. nicolaiiae* to have a defensive strategy, which involves a stronger first line of specialized defenders as well as non-specialized reinforcements that could defend when sudden changes in circumstances demanded it. The above observations are consistent with this expectation.

## 2.8 Conclusions

It is clear that the importance of relatedness has been overemphasized in many studies of social evolution – especially in the social insects. This is partly because relatedness is relatively easy both to define and to measure but also because of the seductive complexity inherent in the reproductive asymmetries of the social Hymenoptera. However, although relatedness is clearly an essential component of any kin-selected explanation of sociality, it would be foolish to suggest, as some have done, that there should be any simple relationship between levels of relatedness and eusociality. In essence, relatedness merely sets the threshold that must be overcome by the ecological determinants of the costs and benefits of helping. In probably all social animals, it is the ecological context that drives the evolution of altruism. The social aphids make this point rather clearly. All aphids have what seems like a strong genetic predisposition to help, since they are potentially interacting within a single clone, but yet social aphids are rare. The critical factors that determine whether sociality evolves are to do with the ecological context that affects both the level of clonal purity and the costs and benefits of helping.

In conclusion, we would like to point out a gap in our knowledge of aphid soldiers. Although far from comprehensive, our understanding of the biology of gall-dwelling aphid soldiers on the primary host is considerably greater than our understanding of free-living secondary-host soldiers. There is substantial evidence that primary- and secondary-host soldiers are not homologous and that secondary-host soldiers probably evolved more recently (Aoki and Kurosu 1989b; Fukatsu et al. 1994;

Stern 1998). Secondary-host soldiers are also even rarer than primary-host soldiers. Interestingly, cladistic analyses of these secondary-host soldiers have provided us with one of the most tangible correlations we have for the loss of defense. The switch from bamboos to grasses as secondary hosts is associated with the loss of soldiers (Stern 1998). One possible reason for this evolutionary association is, because grasses may provide better, more accessible nutrition, they may permit the aphids they host to shift their life-history strategy away from defense in favor of rapid reproduction. We know that, in the species where they persist, secondary-host soldiers can defend and migrate between their colonies, but these aphids are the only social animals that have no nest, no home, no fortress. Who knows what novel adaptations, what entirely new behavior, this unique ecological circumstance might have engendered?

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