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ON THE EVOLUTION OF DISPERSAL AND ALTRUISM IN APHIDS

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How competitive interactions and population structure promote or inhibit cooperation in animal groups remains a key challenge in social evolution. In eusocial aphids, there is no single explanation for what predisposes some lineages of aphids to sociality, and not others. Because the assumption has been that most aphid species occur in essentially clonal groups, the roles of intra- and interspecific competition and population structure in aphid sociality have been given little consideration. Here, I used microsatellites to evaluate the patterns of variation in the clonal group structure of both social and nonsocial aphid species. Multiclonal groups are consistent features across sites and host plants, and all species—social or not—can be found in groups composed of large fractions of multiple clones, and even multiple species. Between-group dispersal in gall-forming aphids is ubiquitous, implying that factors acting ultimately to increase between-clone interactions and decrease within-group relatedness were present in aphids prior to the origins of sociality. By demonstrating that between-group dispersal is common in aphids, and thus interactions between clones are also common, these results suggest that understanding the ecological dynamics of dispersal and competition may offer unique insights into the evolutionary puzzle of sociality in aphids.

KEY WORDS: Aphids, dispersal, plant–insect interaction, population structure, sociality.

Beyond the fundamental dilemma posed by the evolution of cooperative behaviors that seem to bear no net benefit to individuals, interest in complex sociality stems from the curious observation that it is both taxonomically rare and often ecologically successful (Wilson 1990). Determining the factors that explain this pattern, and in particular why certain taxa have made the transition to complex sociality while most have not, has motivated a long history of broadly comparative approaches to sociobiology (Michener 1969; Wilson 1971; Choe and Crespi 1997). Consequently, there is increasing interest in a diversity of nontraditional social taxa, because these may offer unique insights and novel approaches (Costa 2006; West et al. 2007). Many, such as the halictine and allodapine bees or gall-forming thrips, provide sufficient phylogenetic variation for comparative analyses of hypotheses that test broad themes in social evolution (Schwarz et al. 2007; Chapman et al. 2008). And social microbes such as *Dictyostelium* and *Myxococcus*, although not normally employed in explicit comparative analyses (but see Schaap et al. 2006), offer powerful tools, de-

rived from bacterial genetics and developmental biology, for testing explicit hypotheses in frameworks derived from experimental microbial evolution (Fiegna et al. 2006; Gilbert et al. 2007).

Aphids are one such group. Although not traditionally associated with complex social organization, a small fraction expresses social traits similar to those found in more familiar social insects (see reviews in Aoki 2003 and Pike and Foster 2008 and references therein). Like termites or thrips, social aphids live in family groups and produce castes of wingless and often morphologically or developmentally specialized altruistic “soldiers.” The evolutionary puzzle with aphids is a microcosm of broader puzzles in sociality: it is phylogenetically rare and evolutionarily labile, often varying between related species with nearly indistinguishable ecological habits. At the moment, there is no simple explanation for this pattern. Galls—tumor-like structures aphids induce on plants—are clearly important (Wool 2004). Sociality is almost entirely confined to two small subfamilies within the family Aphididae (the Pemphiginae and Hormaphidinae) in

which complex life cycles and galls are common, and it is in association with these that most examples of aphid altruism are found. Galls are thought to provide a proximate basis for social acts, due to their role as “live-in-food” resources (as with wood-feeding termites; Korb 2008), garrison-like defensibility, requirements for maintenance or repair, and physical constraints they impose on clonal growth rates. More generally, by spatially sequestering clones, they enforce a degree of clonal cohesion and population viscosity otherwise uncommon in aphids. Galls, thus, foster the opportunity for interactions among kin and thereby the conditions for the evolution of altruistic traits (Dawkins 1979; Hamilton 1987). However, most species that form galls—despite nearly indistinguishable biological attributes—do not produce highly aggressive soldiers, hence the “puzzle” of sociality.

Recent work has turned to delineating the ecological factors, such as predation or protective mutualisms with ants, that may vary in subtle ways between social and nonsocial lineages (Pike and Foster 2008). A long-standing question in this regard has centered on the role of between-clone dispersal in promoting fusion and admixture between clones (Aoki 1979; Stern and Foster 1996). Multiclonal groups have been described in social species from both the Pemphiginae and the Hormaphidinae; in these, individuals from foreign clones sometimes outnumber the nats themselves (Abbot et al. 2001; Johnson et al. 2002; Wang et al. 2008). Not unlike some unicolonial ants (Chapuisat et al. 2005; Holzer et al. 2006), these mixed groups apparently form in the absence of behavioral responses from resident aphids (Shibao 1999), although this is not always the case (Wang et al. 2008). (A note on terminology: by dispersal, I mean movement by aphid offspring between clones within a host plant. However, all aphids have quite intricate life cycles involving winged morphs specialized for long-distance dispersal between host plants.)

From an ecological perspective, genetic group structure in eusocial aphids is of interest because of the implications it has for factors such as intra- and interspecific resource competition that may affect the costs and benefits of group-living (Bilde et al. 2007; Ronce 2007). More generally, the fact that there is within-group genetic structure in aphids (as opposed to uniclonality) may offer opportunities for utilizing aphids for empirical inquiry into the role of spatial processes in social evolution (El Mouden and Gardner 2008; Hochberg et al. 2008; Lion and van Baalen 2008; Kümmerli et al. 2009), an area in which theory far outpaces empirical work (Moore et al. 2006; Ronce 2007). Important unknowns in aphids relate to the broad ecological and phylogenetic patterns of between-group dispersal and genetic structure, which have never been systematically evaluated.

Working with the North American species in the Pemphiginae, I address these unknowns by first characterizing geographic variation in the clonal composition of gall-dwelling groups in

the social aphid *Pemphigus obesinymphae* (Moran 1993), including patterns of heterospecific group composition due to the co-occurrence and close proximity of multiple species on the same host plants. I then extend the perspective, and by using multilocus genotyping across the subfamily simply ask how between-clone dispersal has evolved in the North American members of the Pemphiginae, with respect to sociality (keeping in mind that the subfamily contains both social and nonsocial species). Currently, four species occur in North America are known to produce first instar larvae with soldier-like phenotypes (*P. obesinymphae*, *P. monophagus*, *P. bursarius*, and *P. spyrothecae*; the latter two have broad global distributions [Blackman and Eastop 2006]). Although a few species produce galls that appear completely sealed during the early phase of gall development, most rapidly develop apertures of various shapes and sizes, potentially allowing the entry or exit of aphids (P. Abbot, pers. obs.).

Based on what is known currently, there are two general evolutionary scenarios for the relationship between cooperation and dispersal in aphids. The first (“dispersal is rare”) is that the tendency to invade conspecific clones is largely a property of social species, and therefore generally rare (because sociality is generally rare in aphids). The relevance of this hypothesis is that it suggests a positive correlation between sociality and dispersal/competition in aphids, perhaps because the factors associated with sociality may also ultimately favor dispersal. Or, the existence of altruistic groups may have simply provided conditions for intraspecific competition and the evolution of “cheaters.” The second and contrasting scenario (“dispersal is common”) is that clonal admixture is not unique to social species and, by virtue of being widespread, possibly ancestral to the more phylogenetically episodic evolution of sociality. Here, in addition to the obvious implication that soldiers would have evolved out of ancestral groups that were not uniformly clonal, this hypothesis also suggests the possibility of trait correlations between dispersal (or “intruder”) phenotypes and those of soldiers, but acting in the opposite direction. Indeed, Aoki (1979; see also Aoki 2003) and Hamilton (1987) suggested that the factors that favored intraspecific competition and clonal admixture (a gall that is not completely sealed, heightened mobility beyond the safety of galls, changes in larval developmental rates that favor the retention of mobile early larval instars, etc.) may also have acted to predispose lineages to soldier production, given ecological conditions that subsequently favored defensive castes. Hamilton (1987) paraphrased this idea as “. . . not so much a case of swords being beaten out of ploughshares as of swords being beaten out of burglars’ jemmies.” The relevance of the dispersal is common hypothesis is that it suggests that understanding the ecological and life-history factors that underlie variation in dispersal and competition may shed light on why closely related aphid species differ so distinctly in the expression of sociality.

Thus, there are two alternative hypotheses that bear on our understanding of the origins of sociality and social complexity in the aphids. These differ principally in assumptions about the timing of the evolution of clonal admixture in aphids with respect to sociality. I tested these two hypotheses and describe intraspecific variation in clonal admixture by using microsatellite loci and diagnostic DNA sequences to evaluate the clonal composition of gall-dwelling groups in eight members of the North American genus *Pemphigus*, and reconstructing the ancestry of clonal admixture therein.

Methods

GENERAL METHODS

Molecular methods and primer sequences followed those described in (Abbot and Chhatre (2007), except for *P. bursarius*, for which the original published primer sequences were used (Miller et al. 2000). From two to eight microsatellite markers were used to generate multilocus genotypes following DNA extraction, PCR, slab gel electrophoresis, and visualization via the incorporation of fluorescently labeled primers (Abbot and Chhatre 2007). Fragment sizes were called manually in Cartographer DNA fragment analysis software version 1.2.6 (BIO-RAD, Hercules, CA). Consistency of scoring was tested by a researcher uninvolved in the study, who blindly rescored randomly selected gels. No genotyping differences occurred between the two, except for some systematic 1 bp differences in establishing initial allele sizes. All statistical analyses were performed in JMP 4.0 (SAS Institute Inc., Cary, NC). (A note on terminology: I use “intruders” to identify aphids dispersing between and entering other clones, and “chimerism” to mean nonclonality—the condition of having groups composed of more than one clone).

THE CLONAL COMPOSITION OF APHID GROUPS

Geographic, host-associated, and species specific variation in clonal admixture

The primary diagnostic methods involved the use of multilocus genotypes to estimate the fraction of unrelated aphids in galls. I did not derive standard estimators of average relatedness within galls. My interest was in the diversity of multilocus genotypes within groups, as in Johnson et al. (2002). *Pemphigus* galls were collected over a period of 20 years by the author and colleagues (see Supporting information), and either frozen or preserved in ethanol individually. Included in these is at least one species with weakly aggressive larvae (*P. bursarius*; Pike et al. 2007), and various species not evincing soldier-like traits (P. Abbot, pers. obs.). The social species *P. obesinymphae* occurs commonly throughout North America on two cottonwoods, *Populus fremontii* and *P. deltoides* (Abbot and Withgott 2004). To determine if clonal admixture varies by host plant across sites, populations in Tennessee

and Kentucky (from *P. deltoides*) and a population in southern Arizona (from *P. fremontii*) were sampled intensively. (In general features, all trees were densely galled, and sites in Tennessee were a single large cottonwood in an urban environment in Nashville, and a cottonwood from a riparian area about 80 miles east of Nashville. In Kentucky, several immature cottonwoods were sampled from a dense cluster at a single site, near the southern bank of the Ohio River at Warsaw, Kentucky. In Arizona, a single large cottonwood was sampled near the San Raphael grasslands, on the eastern border of the Patagonia Mountains, south of Tucson, Arizona.)

Multilocus genotypes were compiled and analyzed in GENALEX software version 6.1 (Peakall and Smouse 2006) using the “Find clones” submenu. Normally, nonnatal aphids can be detected by comparison to the genotype of the single gall foundress, which is essentially immobile and cannot move between galls. However, the natal clone was defined as the most common multilocus nymphal genotype because the foundress was missing or dead in some galls (those collected toward the end of the season) and because a single scoring error in the foundress could result in misidentification of all subsequently tested nymphs. To reduce the influence of artifactual variation, singleton individuals with unique multilocus genotypes differing from the natal genotype at only a single locus were excluded from the analysis, unless this genotype was “confirmed” by other nymphs with the identical single-locus difference.

Finally, estimates of heterospecific admixture between *P. obesinymphae* and its sister taxon (which does not produce highly aggressive soldiers) were obtained using a fast-evolving fragment *atp synthase* operon from the aphid primary endosymbiont, *Buchnera aphidicola*. The fragment was generated from aphids identified as migrants in microsatellite analysis, using methods and primers identical to those described in Abbot and Moran (2002). Sequencing was performed directly on the PCR fragments at the Vanderbilt University Medical Center Sequencing Core Facility.

PHYLOGENETIC AND ANCESTRAL STATE

RECONSTRUCTION OF CLONAL ADMIXTURE

Reconstruction of ancestral states was performed in Mesquite version 2.5. (Maddison and Maddison 2008). First, a parsimony search was conducted in PAUP version 4.1 (Swofford 1998) with the concatenated mitochondrial and *Buchnera* dataset from Abbot and Withgott (2004; GenBank numbers reported therein) and the addition of two previously unincluded species (*Pemphigus nortonii* and *P. monophagus*; GenBank nos. DQ779155, AY182341, AY182300, AY182291, AY182281, GQ284568, GQ284569, GQ284570, GQ284571). I used the branch and bound search option with default settings, characters unweighted, branch swapping set to tree bisection reconnection, and accelerated

transformation character optimization. Species with and without soldiers were coded as 1 or 0, respectively, based on published literature (see Supporting information). Species with and without dispersal (“chimeric” vs. clonal groups) were coded in a similarly discrete fashion, as determined by data from this study (see Supporting information). With sufficient sampling, the average degree of clonal admixture between species could be treated as a continuous variable, but was not done so here. Species not evaluated for clonal admixture, including the outgroup species, were coded as lacking it (clonal). Binary character states were then mapped using parsimony and assuming equal rates of gains and losses of both soldiers and dispersal.

There are two principle uncertainties in reconstructing the ancestral character states in *Pemphigus*. The first is that more species may in fact be social than the current coding indicates. Sociality in *Pemphigus* is probably best thought of as a life-history syndrome, such that there are grades of differences between highly social and nonsocial species, some quite subtle (Pike et al. 2007). Perhaps other social species remain to be identified in the North American members of the genus. Both *P. obesinymphae* and *P. monophagus*, which are only described from North America, almost certainly represent independent origins of soldiers. Beyond that, any serious effort to count the number of origins of soldiers in the subfamily is severely hampered by the fact that most species worldwide have not been studied (the majority of diversity is found in central Asia), and there is no well-sampled phylogeny of the genus. A more serious concern is uncertainty in the phylogenetic reconstruction of the North American members of the genus. *Pemphigus* has probably radiated on poplars in North America, and seems to have done so rapidly, such that species sharing the same or related host poplars tend to be themselves related. Relationships between species on different, distantly related poplars are more difficult to reconstruct (Abbot and Withgott 2004). To account for phylogenetic uncertainty in character reconstruction (Pagel et al. 2004), I also used Markov chain Monte Carlo and maximum-likelihood methods on the same dataset, using BayesTraits version 1.0. (<http://www.evolution.rdg.ac.uk/index.html>). First, a tree was constructed in BayesPhylogenies version 1.0 (<http://www.evolution.rdg.ac.uk/index.html>) using species in the genus *Thecabius* and *Mordvilkoja* as outgroups, a GTR model of base evolution, base frequencies estimated, and rate heterogeneity using a discrete gamma model with four rate categories. A single chain was then run for 1,000,000 iterations, and trees were sampled every 1000 iteration. The evolution of clonal admixture was then reconstructed over the resulting 1000 trees in BayesTraits. Those taxa were coded which have not been assayed for chimerism as having uniformly clonal groups (i.e., not chimeric). I used the “fossil” command to reconstruct the basal node of the ingroup for the alternative states, clonal or not clonal, using a burn-in of 50,000, a rate dev parameter of 20.0 and

an exponential prior (using the RJ hyperprior command) were drawn from a uniform distribution on an interval of 0 to 8. I ran 5,000,000 iterations, sampling every 100th iteration, and repeated this analysis five times. Convergence appeared to be reached by 5,000,000 iterations, based on the inspection of the likelihoods.

Results

THE CLONAL COMPOSITION OF APHID GROUPS *Geographic and host-associated variation in clonal admixture*

Estimates of clonal admixture are probably rough approximations at best, as galls can typically number in the thousands and aphids in the millions on a single tree (Whitham 1998). However, in the eusocial *P. obesinymphae*, which was sampled intensely, the fraction of nonnatal aphids in galls does not vary markedly by geography (single-factor ANOVA on the log-transformed fractions of natal aphids within galls, across three sites in Ohio and Tennessee on the host *P. deltooides*; $N = 50$ galls, $F_{2,47} = 1.53$, $P = 0.22$) or between plant host plants (single-factor ANOVA, on the log-transformed fractions of natal aphids within galls, from 50 galls on the hosts *P. deltooides* in the eastern United States and 11 galls on *P. fremontii* in Arizona; $F_{1,59} = 0.7$, $P = 0.43$).

Variation in clonal admixture across aphid species

Clonal admixture occurs in all species surveyed, and multiclonal or “chimeric” groups are typically composed of more than two clones (Table 1; Fig. 1). Across all species, between 20% and 50% of individuals are “intruders” on average, and in some, nearly 50% are. Although sample sizes are small, the species with the lowest overall rate of clonal admixture (*P. populicaulis*) lacks soldiers and is not social. Multiple aphid species typically co-occur on single trees, and some fraction of migrants are likely interspecific in origin. In particular, the social aphid *P. obesinymphae* and its sister taxon, *P. populitransversus*, which does not produce highly aggressive soldiers, commonly co-occur on *P. deltooides* throughout eastern North America (Abbot and Withgott 2004). Eighteen percent of migrants in *P. obesinymphae* galls (15 of 86 nymphs diagnosed as migrants by microsatellite analysis, from a sample of ten galls) were nymphs belonging to the nonsocial *P. populitransversus* species (Fig. 1; Supporting information). Surprisingly, the reverse was not true for *P. populitransversus* galls. None of the 29 migrant nymphs tested across eight *P. populitransversus* galls were from co-occurring *P. obesinymphae* clones, although rare events may have been undetected because of the smaller size of the survey.

PHYLOGENETIC AND ANCESTRAL STATE RECONSTRUCTION OF CLONAL ADMIXTURE

Finally, both parsimony and likelihood-based ancestral state reconstructions of sociality and nonclonality (chimerism) in

Table 1. Summary of clonal variation within galls of North American aphids in the genus *Pemphigus*, only some of which are social.

Species	Soldiers?	No. of loci	No. of galls sampled	No. of individuals sampled	Average percentage of nonnatal aphids per gall (SE)	Range percentage nonnatal aphids per gall	Fraction galls with at least one nonnatal aphid	Average no. of genotypes per gall ¹
<i>P. betae</i>	No	2	7	74	30.7 (±8.96)	0–61	0.86	3.0
<i>P. bursarius</i>	Yes	8	12	167	26.0 (±6.10)	0–60	0.92	3.1
<i>P. obesinymphae</i>								
<i>deltoides</i>	Yes	5–8	50	1011	22.7 (±3.20)	0–77	0.84	4.2
<i>fremontii</i>	Yes	5–8	11	197	28.6 (±8.49)	0–82	0.91	5.9
<i>P. p. caulis</i>	No	6	8	95	7.2 (±5.88)	0–42	0.25	1.3
<i>P. p. ramulorum</i>	No	7	8	84	21.4 (±7.1)	0–45	0.75	2.8
<i>P. spyrothecae</i> ²	Yes	2	13	277	9.8 (±4.41)	0–59	0.58	–
<i>P. p. transversus</i>	No	4–7	14	141	25.4 (±7.90)	0–60	0.67	3.0
<i>P. p. venae</i> NR	No	6	5	95	37.5 (±7.53)	10–55	1.0	4.2

¹Including the natal genotype²Data from Johnson et al. (2002).

Pemphigus place chimerism at the root of the extant North American group (Fig. 2). Unsurprisingly, maximum parsimony yielded a single tree with essentially the same topology as that of Abbot and Withgott (2004). For the Bayesian reconstruction of ancestral

states, the harmonic means for the likelihoods for the ingroup basal node were -14.00445 for clonality, and -11.879915 for chimerism, which at two log units, can be taken as a “significant” improvement in likelihood using the Bayes Factor test (Pagel 1999) and thus confirms the results from the parsimony analysis. The difference is not dramatic, however, reflecting both the conservative coding (undetermined species may not turn out to be uniformly clonal, after all) and the difficulty in reconstructing the deeper and apparently rapid radiations of the various host-associated *Pemphigus* clades. However, assuming that the highly aggressive soldiers of *P. obesinymphae* and *P. spyrothecae* represent a distinct advance in the development of sociality in the genus (Pike et al. 2007), *Pemphigus* did not express sociality ancestrally, and these origins are independent and recent, evolving after the tendency to invade one another’s clones.

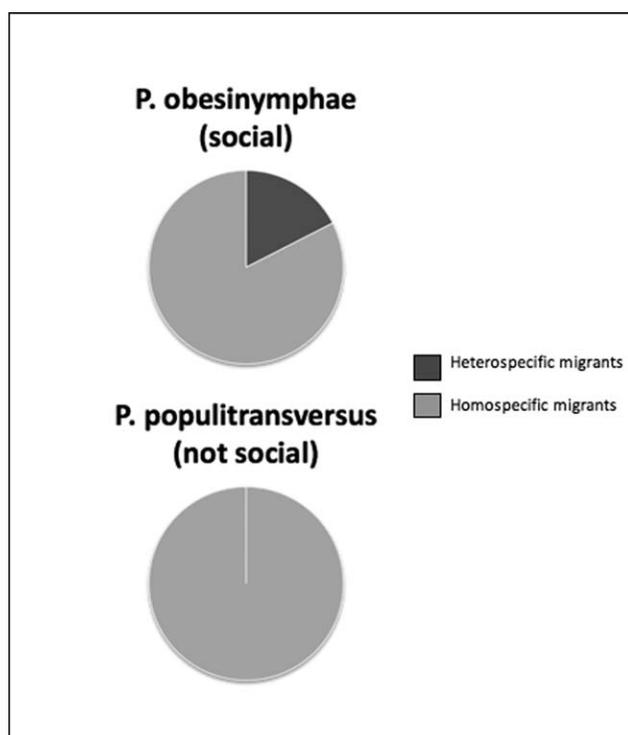


Figure 1. Of the aphids in galls identified as heterotypic by microsatellite analysis, the fraction in which subsequent sequence analysis identified as interspecific migrants. None of the heterotypic aphids in *P. populitransversus* galls were interspecific migrants, whereas nearly 20% of the heterotypic aphids in *P. obesinymphae* galls were *P. populitransversus* migrants (dark gray shading).

Discussion

Sociality in aphids is almost entirely restricted to the two subfamilies Pemphiginae and Hormaphidinae. In these, plant galls are initiated by a lone asexual female and, barring rare mutations, aphid groups begin as single clones. A matter of long-standing interest in the study of social aphids has been whether clonal variation develops seasonally as aphids disperse between groups (Stern and Foster 1996). The general interest is not precisely whether aphid social groups are clonal or not (a clone is still a clone, regardless of the presence of other clones), but what the presence or absence of such dispersal implies about resource allocation strategies in social aphids (which may differ depending on the presence or absence of unrelated aphids; Stern and Foster 1996; Foster 2002), and the spatial and demographic contexts out of which altruism evolves (West et al. 2002; Lehmann et al.

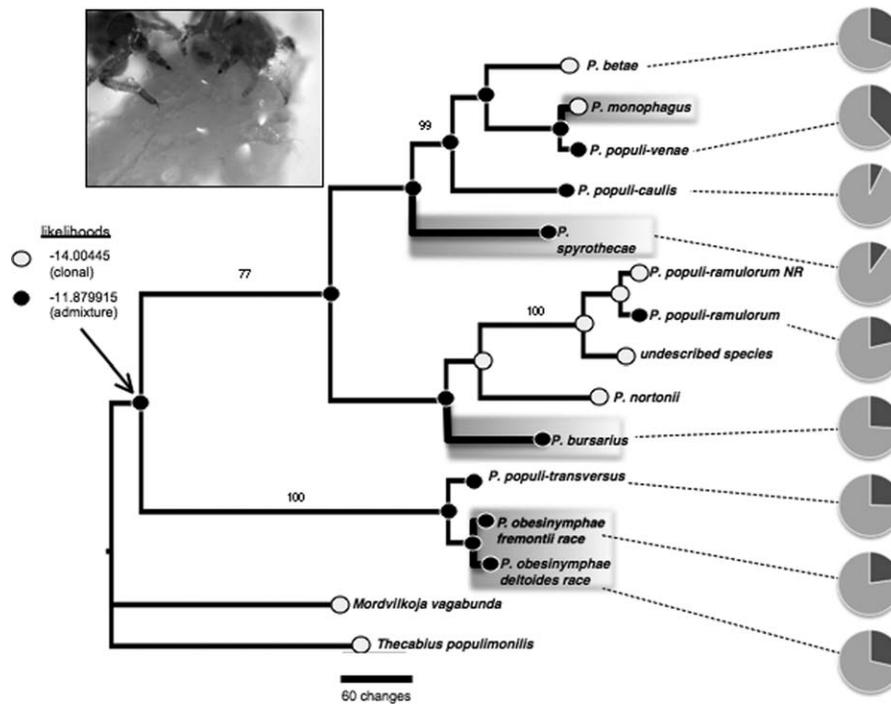


Figure 2. Parsimony reconstruction of soldiers (gray background shading) and clonal admixture (black circles admixture present, white circles admixture absent) on a maximum parsimony phylogeny that includes the majority of North American aphids in the genus *Pemphigus*. Numbers above lines indicate bootstrap proportions based on 1000 branch and bound searches. Bootstrap support for all other nonterminal branches were >50 but <75. For the purpose of analysis, species not surveyed for admixture were coded as having uniformly clonal groups (white circles). The parsimony reconstruction of admixture is basal and consistent with a Bayesian ancestral reconstruction indicating the early evolution of dispersal in the genus, indicated by the arrow and likelihoods of alternative reconstructions. Pie charts show the fraction of heterotypic aphids averaged across galls, as determined by multilocus microsatellite analysis (light gray = homotypic fraction; dark gray = heterotypic fraction).

2006; El Mouden and Gardner 2008). Although prior descriptions of social species indicates that multiclonal groups might be common, the larger patterns of genetic structure and dispersal in gall-dwelling aphid groups have not been broadly evaluated. These results are the first to do so.

ROUTES TO SOCIALITY IN APHIDS

Aoki (1979) noted that some larvae of *Pachypappa marsupialis* leave their maternal gall and invade those of conspecifics. Using this observation as a cue, Hamilton (1987) later proposed an evolutionary route to sociality in aphids via dispersal, the idea being that some soldier-like traits may have been expressed ancestrally for the purpose of dispersal (e.g., delayed maturation of the highly mobile first-instar larvae, the tendency to exit galls, the formation of galls that are not completely sealed, sclerotization and specialized morphology, etc.). Because it is just as easy to imagine the opposite—of dispersal and “cheating” as a consequence of sociality, and not a cause (Foster 2002)—this hypothesis lends itself to a test of the ancestry of dispersal and sociality in the genus. Multilocus genotyping of individuals in galls from a large fraction of the extant members of the Pemphiginae in North America

indicates that multiclonal groups are common in this subfamily, in both social and nonsocial species. When multiple species co-occur on their host plants, interspecific dispersal can occur as well, producing menageries of aphids in heterotypic groups. It is worth noting that the reconstruction of sociality itself reveals little not already evident in the fact that sociality is rare in the genus in North America (Moran 1993). Rather, the value lies in relation to the ubiquity of dispersal, as it appears that sociality evolved out of ancestral conditions characterized by within-group relatedness asymmetries and clonal interactions, including resource competition within groups (P. Abbot, K. Grogan, and V. Chhatre, unpubl. ms.). These results do not explicitly address the genetic and developmental mechanisms underlying soldier and dispersal morphology, and further work on the genus may reveal more nuanced descriptions of sociality in the genus, including descriptions of transitional species with weakly aggressive soldiers (Pike et al. 2007). But the highly aggressive soldiers exemplified by *P. obesinymphae* are clearly derived with respect to the tendency to disperse between clones and, coupled with the ubiquity of dispersal in the genus, lends credence to the hypothesis that Hamilton coyly paraphrased (Aoki 1979; Hamilton 1987): that the tendency

for clones to intrude and compete fostered traits that may have been coopted for defense, like beating swords out of burglars' jemmies.

GEOGRAPHIC PATTERNS IN DISPERSAL

With more than 70 species described worldwide, the present study only captures a small fraction of the full diversity in the genus (Blackman and Eastop 2006). However, it is not surprising that gall-forming aphids express cryptic within-host dispersal mechanisms, possibly acting to alleviate intraclonal competition within galls, or to guard against clonal failure by exporting offspring to nearby galls (Moore et al. 2006; Ronce 2007). Specializations for within-host dispersal are common in parasitic insects, and especially so in hemimetabolous insects (Summers et al. 1996; Gullan and Kosztarab 1997; Cook et al. 2000). Aphids themselves are specialized for rapid growth and seasonal migrations, and for those associated with food crops (i.e., not living in galls), adaptive movement at fine spatial scales can be common (Hodgson 1991; Hazell et al. 2005; Lombaert et al. 2006). As well, there is considerable behavioral evidence of dispersal specializations in both social aphid families (Aoki 1979; Stern et al. 1997; Aoki 2003; Wang et al. 2008). If so, an important question with regard to understanding the development of alternative strategies for reproduction and defense in aphid groups is how dispersal itself varies and how it is regulated. The geographic data from *P. obesinymphae* suggests that dispersal morphs may not be environmentally induced polyphenisms, as can be common in other aphid species (Loxdale and Lushai 1999): average fractions of nonclonal aphids across sites are similar (15–30% of aphids on average are unrelated), and most of over 60 galls evaluated across three geographical regions and two host plants contain migrants. Assuming it is reasonable to expect environmentally induced dispersal polymorphisms to result in greater variation between sites or host plants, the general consistency provides indirect evidence that dispersal may have attributes akin to those of the developmentally specialized soldier castes in aphids (Withgott et al. 1997; Ijichi et al. 2005). A caveat is that I only measured the receipt of dispersal, and not the production of migrants themselves, nor the degree to which different aphid clones invest in either dispersal or philopatric strategies. However, previous work along these lines did not reveal a great deal of covariation between measures of gall status and dispersal (Abbot et al. 2001). Indeed, the species with the lowest rates of dispersal (*P. populicaulis*) commonly overlaps in dense assemblages on the same host plant with two other species (the social *P. obesinymphae* and nonsocial *P. populitransversus*; pers. obs.; also see Bird et al. 1979), suggesting species-specific patterns. Using allozymes, Setzer (1980) reports remarkably similar overall rates of clonal variation in some *Pemphigus* galls, and also lower rates in *P. populicaulis*. (Note: Setzer (1980) evaluated the clonal composition of two nonsocial species (*P. populicaulis*

and *P. populitransversus*), and found variation within galls in both. However, there is some uncertainty about this result, because of subsequent phylogenetic work that clarified taxonomic identities unknown at the time (Sokal and Riska 1981; Abbot and Withgott 2004).

DISPERSAL AND THE EVOLUTION OF SOCIALITY IN APHIDS

Judging by the volume of recent literature, understanding the role of spatial structure in the evolution of cooperation is an area of burgeoning interest (e.g., Gardner and West 2006; Lehmann et al. 2006; Taylor et al. 2007; El Mouden and Gardner 2008; Grafen and Archetti 2008; Johnstone 2008; Lehmann et al. 2008; Kümmerli et al. 2009; see reviews by Hochberg et al. 2008 and Lion and van Baalen 2008). Hamilton (1971) diagnosed that a central problem in the evolution of cooperation is that population viscosity establishes conditions for both cooperative and competitive interactions among kin groups, such that the fecundity benefits of cooperation may also incur costly competitive interactions between relatives (Queller 1992; Taylor 1992). Empirical studies remain limited (Moore et al. 2006), and to the degree that they conform to demographic assumptions (El Mouden and Gardner 2008), aphids and other “nontraditional” social species could provide useful insights (West et al. 2007).

A key point, often repeated within the modest literature on social aphids but potentially lost in translation, is the fundamental importance of clonality itself in aphids—in particular, the importance of defining the appropriate measure of fitness (Stern and Foster 1996). For a galling aphid clone, probably the most relevant measure of success is the number of winged reproductives it produces. Growth in aphids is not unlike that of clonal plants and other modular organisms (Harper and White 1974), in which dispersal and competition govern patterns of aggregation and distribution (Schmid and Harper 1985; de Kroon and van Groenendael 1997; Pineda-Krch and Lehtila 2004; Pineda-Krch and Poore 2004; Lenssen et al. 2005). The extremes of movement between clones of aphids (no dispersal or much) clearly have different ecological and demographic consequences in this regard, because one implies no clonal interactions and strong intraclonal and density-dependent regulation of clone size, whereas the other implies clonal interactions and the regulation of clone size at least partially mediated by extrinsic factors (interspecific competition, the density and availability of nearby galls, predators, abiotic conditions, the presence or absence of recognition mechanisms that prevent intrusion, etc.).

Because the latter seems to be likely the case for *Pemphigus*, and may well be the case for social aphids in general (Wang et al. 2008), ecological theories of social evolution in this group must account for the factors that govern the competitive success of aphid clones, and the role of dispersal in exporting the fecundity

benefits of altruistic traits (Aoki 1982; Foster and Xavier 2007; Gardner and Foster 2008). An important unknown is what fraction of total clone productivity, in terms of winged clonal reproductives that migrate to other host plants, is ultimately generated beyond the natal clone itself, from within neighboring groups. If this fraction is not trivial, then the inclusive fitness of soldiers depends on a component that is realized beyond the corporate group in which defense-based altruism is expressed (Lehmann et al. 2006; El Mouden and Gardner 2008). The origins of soldiers in aphids therefore may be closely tied to their role in fostering clonal growth and expansion, by virtue of the positive effect they have on the longevity of the reproductive gall foundress (Le Galliard et al. 2005; Lehmann et al. 2006; Hochberg et al. 2008; also see Stern and Foster 1996 and Pineda-Krch and Poore 2004).

This view suggests a slight rephrasing of the line of reasoning about why galls may be so important in the larger puzzle of sociality in aphids: it may not be their role precisely in, say, maintaining clonal cohesion or defensibility, as much as they correspond to a spatial, network-like framework conducive to the coevolution of dispersal and altruism in aphids in the first place. In particular, galls represent the spatial fixation of a sessile reproductive in a neighborhood of such reproductives. Galling therefore seasonally reestablishes the population conditions for extinction–expansion dynamics in clonal aphids, and thus the potential for ecologically mediated associations between density, dispersal, and strategies for clonal productivity, of which defense is simply one of several (Harper and White 1974)—galling as a recurrent state of early successional dynamics (Lenssen et al. 2005; Brockhurst et al. 2007). It is the existence of a structured neighborhood that is indispensable, and need not be limited to galls (there are cases of aphid soldiers not associated with galls, for example; Pike and Foster 2008). This structured network may vary in spatial and temporal properties between different species, and therefore may alter the relationship between dispersal, clonal growth rates, and altruism in social and nonsocial lineages (e.g., Agrawal et al. 2004).

Conclusions

In some respect, the emergence of sociality in aphids is a transition in evolution in miniature, in which more derived units of organization emerged out of ancestral conditions favorable to within-group defection (Grosberg and Strathmann 2007). The aggregation of multiclonal groups is common in gall-forming aphids, whether they are social or not. Understanding the evolution of dispersal and aggregation may be a key to deciphering social evolution in aphids, because traits favorable to both may have laid the groundwork to routes to sociality. In terms of ecological theories, unless sociality is expressed in entirely clonal groups (in which case the relevant unit of selection is the gall-dwelling clone; Stern and

Foster 1996), empirical efforts to understand the ecology of aphid social evolution must account for the need to weight the relative costs and benefits of sociality with the appropriate measure of fractional relatedness, and to define the appropriate spatial scale at which aphid clones are regulated. In particular, dispersal introduces interactions both within and between aphid groups that may alter the conditions for the evolution of altruistic traits. How sociality and dispersal have coevolved may be a fruitful area for further inquiry into the puzzle of sociality in aphids.

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LITERATURE CITED

- Abbot, P., and V. Chhatre. 2007. Kin structure provides no explanation for intruders in social aphids. *Mol. Ecol.* 16:3659–3670.
- Abbot, P., and N. A. Moran. 2002. Extremely low levels of genetic polymorphism in endosymbionts (Buchnera) of aphids (*Pemphigus*). *Mol. Ecol.* 11:2649–2660.
- Abbot, P., and J. H. Withgott. 2004. Phylogenetic and molecular evidence for allochronic speciation in gall-forming aphids (*Pemphigus*). *Evolution* 58:539–553.
- Abbot, P., J. H. Withgott, and N. A. Moran. 2001. Genetic conflict and conditional altruism in social aphid colonies. *Proc. Natl. Acad. Sci. USA* 98:12068–12071.
- Agrawal, A. A., N. Underwood, and J. R. Stinchcombe. 2004. Intraspecific variation in the strength of density dependence in aphid populations. *Ecol. Entomol.* 29:521–526.
- Aoki, S. 1979. Dimorphic first instar larvae produced by the fundatrix of *Pachypappa marsupialis* (Homoptera: Aphidoidea). *Kontyû* 47:390–398.
- . 1982. Soldiers and altruistic dispersal in aphids. Pp. 154–158 in M. D. Breed, C. D. Michener, and H. E. Evans, eds. *The biology of social insects*. Westview Press, Boulder, CO.
- . 2003. Soldiers, altruistic dispersal and its consequences for aphid societies. Pp. 201–215 in T. Kikuchi, N. Azuma and S. Higashi, eds. *Genes, behaviors and evolution of social insects*. Hokkaido Univ. Press, Sapporo.
- Bilde, T., K. S. Coates, K. Birkhofer, T. Bird, A. A. Maklakov, Y. Lubin, and L. Aviles. 2007. Survival benefits select for group living in a social spider despite reproductive costs. *J. Evol. Biol.* 20:2412–2426.
- Bird, J., D. P. Faith, L. Rhomberg, B. Riska, and R. R. Sokal. 1979. Morphs of *Pemphigus populitransversus*—allocation methods, morphometrics, and distribution patterns. *Ann. Entomol. Soc. Am.* 72:767–774.
- Blackman, E. L. and V. F. Eastop. 2006. *Aphids on the world's herbaceous plants and shrubs*. Vol. 2. John Wiley & Sons, West Sussex, England.
- Brockhurst, M. A., A. Buckling, and A. Gardner. 2007. Cooperation peaks at intermediate disturbance. *Curr. Biol.* 17:761–765.
- Chapman, T. W., B. J. Crespi, and S. P. Perry. 2008. The evolutionary ecology of eusociality in Australian gall thrips: a 'model clades' approach. *Ecol. Social Evol.*:57–83.
- Chapuisat, M., C. Bernasconi, S. Hoehn, and M. Reuter. 2005. Nestmate recognition in the unicolonial ant *Formica parolugubris*. *Behav. Ecol.* 16:15–19.

- Choe, J. C., and B. J. Crespi. 1997. The evolution of social behavior in insects and arachnids. Cambridge Univ. Press, Cambridge.
- Cook, L. G., P. J. Gullan, and A. C. Stewart. 2000. First-instar morphology and sexual dimorphism in the gall-inducing scale insect *Apiomorpha rubsaamen* (Hemiptera : Coccoidea: Eriococcidae). *J. Nat. His.* 34:879–894.
- Costa, J. T. 2006. The other social insect societies. Harvard Univ. Press, Cambridge.
- Dawkins, R. 1979. 12 misunderstandings of kin selection. *Zeitschrift Fur Tierpsychologie-Journal of Comparative Ethology* 51:184–200.
- de Kroon, H., and J. Van Groenendael. 1997. The ecology and evolution of clonal plants. Backhuys, Leiden
- El Mouden, C., and A. Gardner. 2008. Nice natives and mean migrants: the evolution of dispersal-dependent social behaviour in viscous populations. *J. Evol. Biol.* 21:1480–1491.
- Fiegna, F., Y. T. N. Yu, S. V. Kadam, and G. J. Velicer. 2006. Evolution of an obligate social cheater to a superior cooperator. *Nature* 441:310–314.
- Foster, W. A. 2002. Soldier aphids go cuckoo. *Trends Ecol. Evol.* 17:199–200.
- Foster, K. R., and J. B. Xavier. 2007. Cooperation: bridging ecology and sociobiology. *Curr. Biol.* 17:R319–R321.
- Gardner, A., and K. R. Foster. 2008. The evolution and ecology of cooperation—history and concepts. Pp. 1–36 in J. Korb and J. Heinze, eds. *Ecology of social evolution*. Springer-Verlag, Berlin.
- Gardner, A., and S. A. West. 2006. Demography, altruism, and the benefits of budding. *J. Evol. Biol.* 19:1707–1716.
- Gilbert, O. M., K. R. Foster, N. J. Mehdiabadi, J. E. Strassmann, and D. C. Queller. 2007. High relatedness maintains multicellular cooperation in a social amoeba by controlling cheater mutants. *Proc. Natl. Acad. Sci. USA* 104:8913–8917.
- Grafen, A., and M. Archetti. 2008. Natural selection of altruism in inelastic viscous homogeneous populations. *J. Theor. Biol.* 252:694–710.
- Grosberg, R. K., and R. R. Strathmann. 2007. The evolution of multicellularity: a minor major transition? *Annu. Rev. Ecol. Evol. Syst.* 38:621–654.
- Gullan, P. J., and M. Kosztarab. 1997. Adaptations in scale insects. *Annu. Rev. Entomol.* 42:23–50.
- Hamilton, W. D. 1971. Selection of selfish and altruistic behaviour in some extreme models. Pp. 59–91 in J. Eisenberg and W. Dillon, eds. *Man and beast: comparative social behaviour*. Smithsonian Institution Press, Washington, D.C.
- . 1987. Kinship, recognition, disease, and intelligence: constraints of social evolution. Pp. 81–102 in Y. Ito, J. L. Brown and J. Kikkawa, eds. *Animal societies: theories and facts*. Japan Scientific Societies Press, Tokyo.
- Harper, J. L., and J. White. 1974. The demography of plants. *Annu. Rev. Ecol. Syst.* 5:419–463.
- Hazell, S. P., D. M. Gwynn, S. Ceccarelli, and M. D. E. Fellowes. 2005. Competition and dispersal in the pea aphid: clonal variation and correlations across traits. *Ecol. Entomol.* 30:293–298.
- Hochberg, M. E., D. J. Rankin, and M. Taborsky. 2008. The coevolution of cooperation and dispersal in social groups and its implications for the emergence of multicellularity. *BMC Evol. Biol.* 8:article 238.
- Hodgson, C. 1991. Dispersal of apterous aphids (Homoptera, Aphididae) from their host plant and its significance. *Bull. Entomol. Res.* 81:417–427.
- Holzer, B., R. Kummerli, L. Keller, and M. Chapuisat. 2006. Sham nepotism as a result of intrinsic differences in brood viability in ants. *Proc. R. Soc. Lond. B* 273:2049–2052.
- Ijichi, N., H. Shibao, T. Miura, T. Matsumoto, and T. Fukatsu. 2005. Comparative analysis of caste differentiation during embryogenesis of social aphids whose soldier castes evolved independently. *Insectes Sociaux* 52:177–185.
- Johnson, P. C. D., J. A. Whitfield, W. A. Foster, and W. Amos. 2002. Clonal mixing in the soldier-producing aphid *Pemphigus spyrothecae* (Hemiptera : Aphididae). *Mol. Ecol.* 11:1525–1531.
- Johnstone, R. A. 2008. Kin selection, local competition, and reproductive skew. *Evolution* 62:2592–2599.
- Kummerli, R., A. Gardner, S. A. West, and A. S. Griffin. 2009. Limited dispersal, budding dispersal, and cooperation: an experimental study. *Evolution* 63:939–949.
- Korb, J. 2008. Termites, hemimetabolous diploid white ants?. *Frontiers in Zool.* 5:15 (Available at <http://www.frontiersinzoology.com/content/5/1/15>).
- Le Galliard, J. F., R. Ferriere, and U. Dieckmann. 2005. Adaptive evolution of social traits: origin, trajectories, and correlations of altruism and mobility. *Am. Nat.* 165:206–224.
- Lehmann, L., N. Perrin, and F. Rousset. 2006. Population demography and the evolution of helping behaviors. *Evolution* 60:1137–1151.
- Lehmann, L., V. Ravigne, and L. Keller. 2008. Population viscosity can promote the evolution of altruistic sterile helpers and eusociality. *Proc. R. Soc. Lond. B* 275:1887–1895.
- Lenzen, J. P. M., C. Shock, T. Speek, H. J. During, and H. de Kroon. 2005. Experimental ramet aggregation in the clonal plant *Agrostis stolonifera* reduces its competitive ability. *Ecology* 86:1358–1365.
- Lion, S., and M. van Baalen. 2008. Self-structuring in spatial evolutionary ecology. *Ecol. Lett.* 11:277–295.
- Lombaert, E., R. Boll, and L. Lapchin. 2006. Dispersal strategies of phytophagous insects at a local scale: adaptive potential of aphids in an agricultural environment. *BMC Evol. Biol.* 6:13.
- Loxdale, H. D., and G. Lushai. 1999. Slaves of the environment: the movement of herbivorous insects in relation to their ecology and genotype. *Philos. Trans. R. Soc. Lond. B* 354:1479–1495.
- Maddison, W. P., and D. R. Maddison. 2008. Mesquite: a modular system for evolutionary analysis. Version 2.5 <http://mesquiteproject.org>.
- Michener, C. D. 1969. Comparative social behavior of bees. *Annu. Rev. Entomol.* 14:299–342.
- Miller, N. J., A. J. Birley, and G. M. Tatchell. 2000. Polymorphic microsatellite loci from the lettuce root aphid, *Pemphigus bursarius*. *Mol. Ecol.* 9:1951–1952.
- Moore, J. C., A. Loggenberg, and J. M. Greeff. 2006. Kin competition promotes dispersal in a male pollinating fig wasp. *Biol. Lett.* 2:17–19.
- Moran, N. A. 1993. Defenders in the North American aphid *Pemphigus obesinymphae*. *Insectes Sociaux* 40:391–402.
- Ozaki, K. 1995. Intergall migration in aphids—a model and a test of ESS dispersal rate. *Evol. Ecol.* 9:542–549.
- Pagel, M. 1999. The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. *Syst. Biol.* 48:612–622.
- Pagel, M., Meade, A., and Barker, D. 2004. Bayesian estimation of ancestral character states on phylogenies. *Syst. Biol.* 53:673–684.
- Peakall, R., and P. E. Smouse. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Mol. Ecol. Notes* 6:288–295.
- Pike, N., and W. A. Foster. 2008. The ecology of altruism in a clonal insect. *Ecol. Social Evol.* 1:37–56.
- Pike, N., J. A. Whitfield, and W. A. Foster. 2007. Ecological correlates of sociality in Pemphigus aphids, with a partial phylogeny of the genus. *BMC Evol. Biol.* 7:Article No.: 185.
- Pineda-Krch, M., and K. Lehtila. 2004. Costs and benefits of genetic heterogeneity within organisms. *J. Evol. Biol.* 17:1167–1177.
- Pineda-Krch M., and A. G. B. Poore. 2004. Spatial interactions within modular organisms: genetic heterogeneity and organism fitness. *Theor. Pop. Biol.* 66:25–36.

- Queller, D. C. 1992. Does population viscosity promote kin selection? *Trends Ecol. Evol.* 7:322–324.
- Ronce, O. 2007. Like a rolling stone? Ten questions about dispersal. *Annu. Rev. Ecol. Evol. Syst.* 38:231–253.
- Schaap, P., T. Winckler, M. Nelson, E. Alvarez-Curto, B. Elgie, H. Hagiwara, J. Cavender, A. Milano-Curto, D. E. Rozen, T. Dingermann, et al. 2006. Molecular phylogeny and evolution of morphology in social amoebas. *Science* 314:661–663.
- Schmid, B., and J. L. Harper. 1985. Clonal growth in grassland perennials. I. Density and pattern-dependent competition between plants with different growth forms. *J. Ecol.* 73:793–808.
- Schwarz, M. P., M. H. Richards, and B. N. Danforth. 2007. Changing paradigms in insect social evolution: insights from halictine and alodapine bees. *Annu. Rev. Entomol.* 52:127–150.
- Setzer, R. W. 1980. Intergall migration in the aphid genus *Pemphigus*. *Ann. Entomol. Soc. Am.* 73:327–331.
- Shibao, H. 1999. Lack of kin discrimination in the eusocial aphid *Pseudoregma bambucicola* (Homoptera: Aphididae). *J. Ethol.* 17:17–24.
- Sokal, R. R., and B. Riska. 1981. Geographic variation in *Pemphigus populi-transversus* (Insecta: Aphididae). *Biol. J. Linn. Soc.* 15:201–233.
- Stern, D. L., and W. A. Foster. 1996. The evolution of soldiers in aphids. *Biol. Rev. Camb. Philos. Soc.* 71:27–79.
- Summers, C. G., A. S. Newton, and D. Estrada. 1996. Intraplant and interplant movement of *Bemisia argentifolii* (Homoptera: Aleyrodidae) crawlers. *Environ. Entomol.* 25:1360–1364.
- Swofford, D. L. 1998. PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4.1. Sinauer Associates, Sunderland, MA.
- Taylor, P. D. 1992. Altruism in viscous populations – an inclusive fitness model. *Evol. Ecol.* 6:352–356.
- Taylor, P. D., T. Day, and G. Wild. 2007. Evolution of cooperation in a finite homogeneous graph. *Nature* 447:469–472.
- Wang, C. C., S. C. Tsaur, U. Kurosu, S. Aoki, and H. J. Lee. 2008. Social parasitism and behavioral interactions between two gall-forming social aphids. *Insectes Sociaux* 55:147–152.
- West, S. A., I. Pen, and A. S. Griffin. 2002. Conflict and cooperation—cooperation and competition between relatives. *Science* 296:72–75.
- West, S. A., A. S. Griffin, and A. Gardner. 2007. Evolutionary explanations for cooperation. *Curr. Biol.* 17:R661–R672.
- Whitham, T. G. 1998. Ecology of *Pemphigus* gall aphids. Pp. 225–237 in J. D. Shorthouse and O. Rohfritsch, eds. *Biology of insect-induced galls*. Oxford Univ. Press, Oxford.
- Wilson, E. O. 1971. *The insect societies*. Harvard Univ. Press, Cambridge.
- . 1990. *Success and dominance in ecosystems: the case of the social insects*. Ecology Institute, Oldendorf/Luhe, Germany.
- Withgott, J. H., D. K. Abbot, and N. A. Moran. 1997. Maternal death relaxes developmental inhibition in nymphal aphid defenders. *Proc. R. Soc. Lond. B* 264:1197–1202.
- Wool, D. 2004. Galling aphids: specialization, biological complexity, and variation. *Annu. Rev. Entomol.* 49:175–192.

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Supporting Information

The following supporting information is available for this article:

Table S1. Collection localities, dates, and collector names for species included in this study.

Table S2. Character coding for the ancestral state reconstruction.

Table S3. Data table showing fixed differences in a 400-bp region of the *Buchnera atp synthase* operon used to diagnose interspecific migrants between *P. obesinymphae* and *P. populi-transversus* intergall migrants, identified by microsatellite genotyping.

Supporting Information may be found in the online version of this article.

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