Maternal death relaxes developmental inhibition in nymphal aphid defenders

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SUMMARY

In certain aphids, first-instar nymphs defend their gall by attacking intruding arthropod predators. One correlate of such defensive behaviour is a lengthened duration of the first nymphal stadium during the galling phase of the life cycle. A prolonged first stadium allows a large army of first-instar defenders to accumulate, which may be advantageous for gall defence. The factors determining developmental delay have been unclear, however. Our field experiment with *Pemphigus obesinymphae*, a North American gall-forming aphid with defensive first-instar nymphs, tests whether first-stadium duration is influenced by the death of the colony's fundatrix (mother). We killed fundatrices in certain galls, left those in control galls alive, and counted aphids in each stadium in each gall. Galls in which fundatrices were killed contained a lower proportion of first-instar defenders and more late-instar nymphs than did galls with living fundatrices, indicating that maternal death dramatically increased developmental rate of nymphs. Possibly nymphal aphids respond adaptively to environmental cues that signal a threat to the colony's welfare. Alternatively, the fundatrix actively suppresses offspring development in order to maintain a large army of soldiers to protect her gall. The results add a new layer of complexity to our understanding of social aphid systems.

1. INTRODUCTION

Although galls are generally thought to protect insects from predation, aphids living in galls that feature an exit hole large enough for predators to enter may be quite vulnerable. Certain aphids have evolved defensive behaviour, in which nymphs protect their colony by attacking predatory arthropods attempting to enter (Aoki 1987; Ito 1989; Foster 1990; Stern & Foster 1996). In some aphids, a caste of sterile soldiers defends the colony, while in other species the work is done by monomorphic defenders—often first-instar nymphs—that retain reproductive potential. Defenders are known to occur in roughly 50 of the world's 4400 described aphid species, and defensive behaviour is thought to have evolved independently at least six times in aphids (Stern & Foster 1997).

A key correlate of defensive behaviour in aphids with monomorphic first-instar defenders appears to be a lengthened duration of the first stadium (Akimoto 1992, 1996a,b; Foster & Rhoden 1996). A prolonged period before first moult may result in an accumulation of first-instar defenders in galls, creating a large 'army' to repel predators. However, the proximate cause of a lengthy first stadium is unknown, and little previous work has addressed plasticity of first stadium duration.

We describe an experiment using the North American aphid *Pemphigus obesinymphae* designed to test whether duration of the first stadium is plastic. We

then generate and discuss two possible explanations for the observed prolongation and plasticity of first-stadium duration.

First-instar nymphs of *P. obesinymphae* defend their galls, and gall populations are heavily biased toward first-instar nymphs, indicating a prolonged first stadium relative to congeneric species that do not show defensive behaviour. In earlier fieldwork, Moran (1993) observed that *P. obesinymphae* galls in which the fundatrix (the inducer of the gall and mother of its inhabitants) was dead or missing contained many non-defending late-instar nymphs. Moran hypothesized that the fundatrix somehow inhibits development of her offspring in order to maintain a large number of defending nymphs to protect her gall, and that nymphs hasten their development in the absence of their fundatrix. To address this idea experimentally, we compared development of nymphal aphids in galls in which fundatrices were purposely killed with those of control galls.

2. STUDY SYSTEM

The annual life cycle of *P. obesinymphae* includes cyclical parthenogenesis and seasonal alternation of host plants (Moran 1993). Females hatched from eggs on Fremont's cottonwood (*Populus fremontii*) induce galls on petioles in the spring. At our study sites, the galling phase of the life cycle lasts from April–October, during which time the fundatrix lives inside the gall and parthenogenetically produces hundreds

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of offspring. First-instar nymphs are heavily sclerotized and defend the gall against predation by attacking intruding arthropods *en masse* (Moran 1993; Aoki & Moran 1994). Successful gall defence depends on maintaining a sizeable army of defenders throughout the gall phase, and during this time the clone consists of nearly all first instars. First-instar defenders are not sterile castes, however, and can reach reproductive maturity if they survive their soldiering duties. Once these nymphs mature past the first stadium, they no longer show defensive behaviour. During a brief period in the fall, nymphal aphids quickly mature through the remaining three juvenile stadia into winged adults. These migrate to herbaceous secondary host plants and deposit nymphs which initiate parthenogenetic reproduction on roots where overwintering occurs.

The unusual preponderance of first-instar nymphs in galls of *P. obesinymphae* indicates a lengthened first stadium and appears to function in gall defence. This contrasts with a more even distribution of instars in galls of closely related species (e.g. *P. populi-transversus*) that do not show pronounced defensive behaviour.

3. METHODS

We conducted our experiment at four field sites in southeastern Arizona, USA, in August and September 1995. Sites were separated by at least 25 km, and each was located in a different drainage. At each site, we located *P. obesinymphae* galls on petioles of cottonwood leaves. Since sites varied greatly in gall density, we were unable to sample a constant number of galls or trees across sites. We divided galls on each tree as evenly as possible among the three treatments and assigned galls to treatments randomly.

Each gall received one of three treatments: (1) removal galls: the fundatrix was killed by carefully inserting a pin into the gall; (2) control galls: handled identically to removal galls, but the fundatrix was not killed; or (3) untouched galls: not handled or manipulated in any way.

We treated a total of 518 galls, of which we were able to use 335 in our main analyses. Number of galls used in analyses from each site for removal, control and untouched categories, respectively, were as follows: Mt Lemmon, 5, 13, 14; Patagonia, 17, 28, 36; Portal, 44, 54, 47; Tumacacori, 9, 22, 46. Sample sizes were uneven due to differential gall mortality among sites and exclusion of some galls from analyses, as addressed below.

After ten days, we collected all galls and placed each gall in a separate vial. In the laboratory we preserved gall contents in alcohol and examined them under a microscope. All aphids were sorted according to stadium and counted. Since it was impossible to count aphids without destroying the gall, we could not measure effects of treatments on developmental rate directly, as we did not know the number of aphids within each gall at the start of the ten-day period. Thus, we had to infer effects by comparing instar ratios among treatments at the end of the ten-day period. Our design ensured that differences in instar ratios between removal and control galls would reflect an effect of fundatrix death, while differences in instar ratios between control and untouched galls would reflect effects of handling. Handling entailed slightly squeezing each gall in order to widen the exit hole so that we could

see the fundatrix inside and insert a pin.

It was necessary to leave the dead fundatrix inside the gall because her intact body was larger than the enlarged exit hole and removing her would have caused severe gall damage. Dead fundatrices were nearly always absent from removal galls upon collection. First-instar nymphs of *P. obesinymphae* most likely perform gall-cleaning behaviour as in some congeners (Aoki 1980; Benton & Foster 1992), and presumably removed the shrivelled and desiccated bodies of dead fundatrices.

Before analysing the data, we lumped instars 2–4 and alate adults into a category of ‘late instars’. We performed a two-way analysis of variance to determine whether the proportion of first-instar nymphs varied with treatment or site. We then performed an identical ANOVA using absolute number of late-instar nymphs as our dependent variable. We felt it important to analyse both of these dependent variables separately, since a decreased proportion of first-instar nymphs in removal galls could result partly from the lack of births following fundatrix death rather than from an accelerated developmental rate. So, while differences in the proportion of defending nymphs is the result of interest, the fact that we also measured differences in numbers of late-instar nymphs assured that differences in proportion of defenders actually resulted from developmental acceleration.

Non-parametric methods were necessary since data were not normally distributed and could not be successfully transformed. Thus we ranked our two dependent variables across all sites and treatments, and performed our ANOVAs on the ranks, following the Scheirer–Ray–Hare extension of the Kruskal–Wallis test (Sokal & Rohlf 1995, p. 446). Non-parametric one-way ANOVAs were also run for each of the four sites separately, testing for differences among treatments with Tukey–Kramer multiple comparison tests. Galls empty due to predation and those with severely depleted populations (less than 25 aphids) were excluded from analysis.

Patterns of gall availability in the field allowed us to test for effects of tree quality on instar ratios at two of the four sites. Rates of gall intrusion by predators and other arthropods during the ten-day period were compared between removal and control galls by χ^2 analysis. Insects, eggs, frass or other insect remains found inside collected galls provided evidence of known predation or intrusion, while empty galls and those with severely depleted populations were considered possible instances of predation or intrusion.

4. RESULTS

Removal galls contained a much higher absolute number of late-instar nymphs and a much lower proportion of first-instar nymphs than control and untouched galls (figure 1). This pattern was consistent across all four sites (figure 2). Our ANOVAs showed highly significant treatment effects for both dependent variables measured, and no significant site effects (table 1). Multiple comparison tests of differences among treatments in four within-site ANOVAs showed that at every site removal galls contained significantly more late-instar nymphs and a significantly lower proportion of first-instar nymphs than control and untouched galls.

Control galls had significantly more late-instar nymphs and a significantly lower proportion of first-

Figure 1. Mean ($\pm$ s.e.) number of first-instar and late-instar aphids per gall, for each of the three gall treatments, pooled across the four study sites. All three gall treatments differ significantly, both in proportion of first instars and absolute number of late instars.

Table 1. *Non-parametric analyses of variance*

(a) For proportion of first instars			
source	d.f.	<i>F</i>	<i>p</i>
treatment	2	142.13	< 0.0001
site	3	6.07	> 0.1
interaction	6	5.49	> 0.4

(b) For number of late instars			
source	d.f.	<i>F</i>	<i>p</i>
treatment	2	96.01	< 0.0001
site	3	1.60	> 0.6
interaction	6	4.25	> 0.6

instar nymphs than untouched galls at only one of the four sites (Portal), but these two treatments differed significantly in this manner when data were pooled across sites (Scheffe multiple comparison test, $p = 0.017$). Thus, our data showed a slight handling effect.

At the two sites (Patagonia and Tumacacori) for which we were able to test for treatment-by-tree interaction effects, we found no significant effects (all $F < 0.63$, d.f. = 2, all $p > 0.5$).

Fundatrix death resulted in greater rates of predation and gall intrusion by various arthropods during the ten-day test period. The rate of known predation and/or gall intrusion in removal galls was 25.5% while that for control galls was 9.6% ($\chi^2 = 15.13$, d.f. = 1, $p < 0.001$). The rate of severe population depletion (to sizes below 25 aphids)—presumably often the result of predation or gall intrusion—was 49.7% in removal galls and 27.8% in control galls ($\chi^2 = 16.85$, d.f. = 1, $p < 0.001$). Intruding arthropods included predaceous fly larvae (Diptera: Chamaemyi-

Figure 2. (a) Mean ($\pm$ s.e.) proportion of aphids per gall from the first instar, for each of the three types of gall treatments, across the four study sites. Removal galls (♦) show a significantly lower proportion of first instars than control (●) and untouched (■) galls at each of the four sites. Control galls show a significantly lower proportion of first instars than untouched galls only at the Portal site. (b) Mean ($\pm$ s.e.) number of aphids per gall that are 'late-instar' (second, third, fourth instar, and alate), for each of the three types of gall treatments, across the four study sites. Removal galls show a significantly higher number of late instars than control and untouched galls at each of the four sites. Control galls show a significantly higher number of late instars than untouched galls only at the Portal site.

idae), predaceous bugs (Hemiptera: Anthocoridae), various lepidopteran larvae, several species of ants and ant-tended *Chaitophorus* aphids.

Not all of our gall manipulations worked as planned. Across treatments, roughly 20% of galls were devoid of aphids when collected, and so were not included in analyses. In addition, some other

Table 2. *Instar ratios for galls in relation to intended treatment category and actual fundatrix status*

(For each treatment category, data are shown for galls with: (1) fundatrix alive; (2) fundatrix dead and removed; and (3) fundatrix dead and inside gall. Removal galls containing living fundatrices were galls in which we inadvertently failed to kill fundatrices. Control and untouched galls with dead and removed fundatrices were galls in which fundatrices died of natural causes. Galls with fundatrices dead and inside the gall were galls in which death occurred shortly before gall collection, so that nymphs had not yet removed the body of the fundatrix. The data show that instar ratios followed actual fundatrix status rather than intended experimental treatment, and that instar ratios of the third category are intermediate between those of the first two. Means are accompanied by standard errors.)

chosen treatment	actual fundatrix status	<i>n</i>	mean number first instars	mean number late instars	mean percentage first instars
removal	alive	15	143.7 ± 15.2	6.7 ± 1.6	95.2 ± 1.2
control	alive	117	165.7 ± 6.3	7.1 ± 0.9	95.2 ± 0.8
untouched	alive	143	168.3 ± 6.6	4.4 ± 0.6	97.4 ± 0.3
removal	dead, removed	75	32.4 ± 3.3	50.4 ± 3.8	39.1 ± 2.6
control	dead, removed	11	58.2 ± 21.9	30.9 ± 9.2	57.8 ± 9.3
untouched	dead, removed	1	38.0	93.0	29.0
removal	dead, inside gall	10	68.1 ± 21.7	23.6 ± 5.8	61.3 ± 9.2
control	dead, inside gall	7	76.3 ± 25.6	21.9 ± 7.7	69.1 ± 12.6
untouched	dead, inside gall	2	145.0 ± 11.0	23.5 ± 10.5	86.8 ± 4.3

galls could not be used. These included removal galls in which we accidentally failed to kill the fundatrix ($n = 15$), and control and untouched galls in which fundatrices were missing upon inspection ($n = 11$ and 1, respectively). Ratios of first to late instars in these galls follow the patterns expected based on fundatrix status rather than on intended gall treatment. That is, ‘removal’ galls that retained live fundatrices showed high first-to-late instar ratios similar to normal control and untouched galls, while ‘control’ and ‘untouched’ galls in which fundatrices were missing showed lower first-to-late instar ratios more typical of normal removal galls (table 2). Finally, in some galls ($n = 19$) the fundatrix apparently died during the test period but had not yet been removed by gall-cleaning nymphs. Instar ratios in these galls were variable, and on average intermediate between ratios for typical removal and typical control and untouched galls (table 2).

5. DISCUSSION

The striking difference in instar ratios among galls given different treatments reflects a sharp increase in first-instar moulting rate in removal galls, demonstrating that fundatrix death leads to relatively faster first-stadium development among her clonal offspring. Because the strong bias toward first-instar nymphs normally found in *P. obesinymphae* galls is absent among congeners that lack defenders, our experimental effect apparently represents a relaxation of developmental inhibition in *P. obesinymphae* and a resulting abbreviation of its prolonged first stadium. The conclusions from our main experimental results are reinforced by data shown in table 2; in control galls in which the fundatrix was inadvertently killed and removal galls in which she was not, instar ratios were predicted by fundatrix status rather than intended treatment.

The demonstration of an effect of maternal death on offspring developmental rate is an unusual finding in studies of arthropods. In the context of social evolution, it suggests that interactions within colonies of social aphids may be complex, not unlike the intricate social interactions known from the Hymenoptera and Isoptera. However, aphids differ from other social insects in that colonies are clonal, so that defensive behaviour of individual nymphs may perhaps be best regarded not as reproductive altruism of individuals, but as an adaptation at the level of the clone.

In this light, both the prolongation of the first stadium in social pemphigids and the subsequent release from moult suppression may be viewed as clonal adaptations to predation pressure. As long as a fundatrix is present producing offspring, first-stadium prolongation functions to create a large first-instar army to repel predators. In the absence of a fundatrix continually producing offspring, defender populations can be expected to dwindle due to mortality from repeated confrontations with predators, eventually leaving the gall defenceless. It may therefore be advantageous for all aphids to develop and leave the gall as quickly as possible, thus minimizing their period of risk.

The pattern we found is consistent with two mechanistic explanations of the process producing it. The first is that a fundatrix exerts control over her offspring’s development, inhibiting their moult into the second stadium, and that absence of the fundatrix (through death and subsequent removal) brings a halt to stimuli suppressing nymphal development. Since there is no genetic conflict of interest between mother and daughter, such maternal control of development may best be viewed as a within-clone regulation mechanism. The second explanation is that some aspect of the fundatrix death event itself (e.g. contact with haemolymph or release of alarm pheromones) directly triggers an acceleration of genetically inhibited nymphal development. Under this view, aphid

nymphs have evolved plasticity in first-stadium duration that enables them to respond adaptively to events that threaten the colony's long-term welfare, and fundatrix death is one such event.

These two explanations differ in a proximate but not an ultimate sense; in each, the aphid genome has evolved some mechanism to inhibit first-stadium development and subsequently to release the inhibition. Likewise, they are not mutually exclusive. Nonetheless, it is worth exploring the two scenarios in relation to previous work on aphids and other arthropods. Maternal control has previously been suggested in aphids as a mechanism for regulating ovariole number in offspring, production of alates, production of sexuales and production of sterile soldiers (Dixon 1985; Stern *et al.* 1996). However, the adaptive plasticity argument helps explain the slight handling effect apparent in our data. At one site alone and in all sites together, control galls contained significantly more late-instar nymphs and a significantly lower proportion of first-instar nymphs than untouched galls. Our handling consisted of widening the gall opening, which may increase ventilation and lower humidity within the gall. Desiccation is a serious threat to *P. obesinymphae* in Arizona, where drought may decimate large numbers of gall colonies (personal observation). Perhaps aphids in our control galls accelerated development in response to a threat of desiccation.

We do not think it implausible that these aphids have evolved adaptive plasticity in developmental rate to respond to a variety of potential environmental stresses and ecological threats. Moulting time in insects may be influenced by such variables as temperature, humidity, crowding and food quality and availability (Chapman 1982). In aphids, Akimoto (1992) showed that first-instars' moulting rates became progressively slower with colony age. In addition, recent work on non-insect arthropods (Harvey 1994; Witt & Dill 1996) has shown moult timing to be affected by ecological factors such as predation risk. However, our data suggest that for *P. obesinymphae* such responses, if they exist, are quite limited and much weaker than response to fundatrix death. If developmental rate was free to respond to variables such as phloem quality; exposure to heat, sun or wind; and predation pressure; then we should have found appreciable variation in instar ratios among our untouched galls, and also among trees and sites. The extremely low variance in instar ratio among untouched galls (none of which contained large numbers of late-instar nymphs)—as well as the lack of significant tree or site effects—suggests that only a very strong stimulus or severe threat such as fundatrix death can trigger a marked response in developmental rate.

Either nymphal response to environmental cues or release of maternal control—or both—may regularly occur each autumn, when first-instar nymphs moult and quickly progress through the last three juvenile stadia to reach the alate stage and leave the gall. Fundatrices generally survive throughout this period,

Figure 3. Scatterplots showing proportion of first-instar aphids plotted against two presumed correlates of within-gall competition. Control galls are indicated by closed circles, removal galls by open squares. If decreased competition for food resulting from decreased colony size due to lack of births following fundatrix death was responsible for our results, we would expect to see strong decreasing trends in figure 3a within each treatment, and strong increasing trends in figure 3b within each treatment. Such patterns are not evident, and instead we see clustering of points according to treatment, enabling us to rule out the competition hypothesis. (a) Scatterplot showing proportion of first-instar aphids plotted against gall diameter (in centimetres). (b) Scatterplot showing proportion of first-instar aphids plotted against total number of aphids in the gall.

remaining alive in the gall until after it falls from the tree.

An alternative hypothesis worth considering in our study is that reduced competition for food among first instars may account for the patterns we found. Fundatrix death brings a halt to the birth of new first

instars and, combined with defender mortality, leads to a decrease in colony size. With fewer aphids in the gall, first instars might experience less competition for access to feeding sites, and thus might survive better and moult more quickly, resulting in a higher number of late instars and lower proportion of first instars. To address this idea, we tested the predictions that proportion of first instars would be greater in galls with larger populations and smaller in galls of larger size, and that these trends should be evident *within* each of our three treatments. We found no such patterns, indicating that competition did not significantly influence our results. Figure 3 illustrates data for control and removal galls, showing that differences exist *between* treatments, but that the predicted trends are not apparent *within* treatments. In addition, the extremely low variance in instar ratio among untouched galls, which varied greatly in population and gall diameter, is further evidence against the competition hypothesis.

Because a lengthy first stadium is thought to be an important correlate to defensive behaviour in social aphids (Akimoto 1992, 1996a,b; Foster & Rhoden 1996), our results suggest that prolonged fundatrix survival is one factor facilitating the maintenance of sociality in aphids. The extended duration of the gall phase of the life cycle in *P. obesinymphae* relative to its congeners may have increased predation risk and selected for the evolution of defensive behaviour (Moran 1993). Akimoto (1996a) showed using computer simulations that defensive behaviour is likely to evolve in colonies with long durations, and that in such colonies, a lengthened first-instar defensive stage will be favoured by natural selection.

Our experiment clearly demonstrates developmental plasticity in instar duration and developmental plasticity associated with maternal death—both unusual findings in insects. Further work of a more mechanistic nature will be required to determine the proximate causes of first-stadium prolongation and the influence of various factors on plasticity in nymphal developmental rate in *P. obesinymphae*. In addition, further work on other aphid species is needed to determine the generality of these phenomena. Presently, our results suggest that social aphid systems may be more complex than previously thought, and that within-clone interactions may comprise an important element of social evolution in aphids.

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