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# Mutualist-induced transgenerational polyphenisms in cotton aphid populations

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## Summary

**1.** In defensive mutualistic associations, reduced risk of predation should permit defended organisms to produce phenotypes with higher offspring production than non-mutualistic, unprotected conspecifics which require costly defensive traits.

**2.** Here, we show that cotton aphids, *Aphis gossypii*, which produce any combination of dwarf apterae (low intrinsic rate of increase), light green apterae (medium intrinsic rate of increase), dark green apterae (high intrinsic rate of increase) and alatae (winged dispersal morphs), alter offspring phenotypes when tended by predatory ants.

**3.** Aphids tended by the Argentine ant, *Linepithema humile*, have similar numbers of dwarf, dark green and alate offspring, but greater numbers of light green offspring, compared to untended colonies.

**4.** Because light green morphs have a higher intrinsic rate of increase than dwarf morphs but a decreased risk of parasitism compared to dark green morphs, increased production of the light green phenotype may optimize offspring production in order to maximize clone fitness.

**5.** Since many organisms have high levels of plasticity and mutualistic interactions are ubiquitous, mutualist-induced polyphenisms may be pervasive.

**Key-words:** ant–aphid interaction, inducible defence, mutualism, phenotypic plasticity, predation risk

## Introduction

Plants and animals frequently produce offspring with behavioural or morphological adaptations to reduce risk of predation in response to adverse conditions, such as an increased risk of attack from parasitoids, predators or pathogens (Agrawal, Laforsch & Tollrian 1999; Weisser 2001; Elliot *et al.* 2003). Plants fed upon by herbivores, for example, produce seedlings with higher levels of defensive compounds (Agrawal 2001, 2002). Daphnia exposed to predator kairomones develop defensive crests and spines to reduce the chances of being depredated (Agrawal *et al.* 1999). Similarly, natural enemies (Weisser, Braendle & Minoretti 1999; Sloggett & Weisser 2002; Kunert & Weisser 2003) or their cues alone (Dixon & Agarwala 1999; Mondor, Tremblay & Lindroth 2004; Mondor, Rosenheim & Addicott 2005; Podjasek *et al.* 2005) are capable of inducing a transgenerational wing polyphenism in aphids. Winged aphids are believed to be an adaptive phenotype, capable of dispersing to new habitats in relative enemy-free space (Dixon 1998; Weisser *et al.* 1999).

On the other hand, if organisms experience better than average conditions, such as increased host plant quality or reduced conspecific density, offspring phenotypes should reflect these changes as well (Dixon 1998; Müller, Williams & Hardie 2001). A reduced risk of attack from natural enemies would also be hypothesized to result in altered phenotypic expression. As behavioural and morphological adaptations to increased predation risk are believed to be costly (Fyda & Wiackowski 1998; Tollrian & Harvell 1998; Dahl & Peckarsky 2002), decreased predation risk would allow organisms to forego the cost of producing these augmented defensive traits, and produce phenotypes that optimize offspring production in order to maximize fitness, as would occur under relative enemy-free conditions.

Defensive mutualistic associations, whereby organisms receive protection from natural enemies in exchange for nutritive substances, are common in nature (Fiedler, Hölldobler & Seufert 1996; Moya-Raygoza & Nault 2000; Pierce *et al.* 2002). In ant–aphid mutualistic interactions, ants protect aphids from predators (Nault, Montgomery & Bowers 1976; Katayama & Suzuki 2002) in exchange for nutritive honeydew (Nixon 1951; Way 1963). While the benefits of reduced predation risk are obvious, there may also be fitness costs associated with being ant-tended (Stadler & Dixon 2005). As fitness of the aphid clone is largely phenotype-dependent,

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**Fig. 1.** Photograph showing a parasitized aphid (a mummy), the green 'normal' morph, the yellow 'dwarf' morph, and the alate 'winged' morph of the cotton aphid, *Aphis gossypii*.

that is, some phenotypes have a greater intrinsic rate of increase and/or a greater likelihood of survival than do other phenotypes (Dixon 1998), ants may directly alter aphid fitness. Ant attendance may increase fitness of the aphid clone by allowing individuals to produce morphs with high offspring production and a high likelihood of survival, because of the concomitant reduction in predation risk.

Cotton aphid, *Aphis gossypii* (Glover), exhibits extensive phenotypic plasticity as offspring of a single individual consist of any number of four distinct phenotypes, all with dissimilar intrinsic rates of increase, leading to markedly different population dynamics, that is, dwarf yellow apterae (low intrinsic rate of increase), light green apterae (medium intrinsic rate of increase), dark green apterae (high intrinsic rate of increase) and alatae (winged dispersal morphs) (Fig. 1) (Paddock 1919; Wall 1933; Wilhoit & Rosenheim 1993; Watt & Hales 1996). Like alatae, dwarf apterae are a distinct phenotype (Watt & Hales 1996), having a body size approximately one-half to one-third that of normal apterae, yellow instead of green colouration and five compared to six antennal segments when fully developed (Takahashi 1966; Watt & Hales 1996). Phenotypes of cotton aphid offspring are believed to be determined before birth, with different phenotypes, that is, dwarf, normal, and so on, exhibiting different developmental trajectories (Watt & Hales 1996). Because of these life history differences, stimuli leading to the induction of alternate cotton aphid phenotypes are of great interest from both a basic and applied perspective.

Phenotypic changes in cotton aphids have focused principally on environmental cues such as temperature (Wilhoit & Rosenheim 1993), host plant species (Watt & Hales 1996) and host plant quality (Nevo & Coll 2001). Cotton aphids also alter colony composition in response to increased predation risk, producing more alate offspring in the subsequent generation (Mondor *et al.* 2005). Cotton aphids, however, are facultatively ant-tended, forming mutualistic associations with ant species such as the fire ant, *Solenopsis invicta*, and the Argentine ant, *Linepithema humile* (Kaplan & Eubanks 2005; Mondor *et al.* unpubl. data). The extent to which ant-tending alters cotton aphid transgenerational polyphenisms, however, has not been examined. Furthermore, it is currently unknown whether different aphid phenotypes are equally likely to be depredated. As tending ants are generally very effective at deterring predation on aphid colonies (Kaplan & Eubanks 2005; Altfeld & Stiling 2006), we propose that cotton aphids engaged in a defensive mutualism will produce dark green offspring, with a high intrinsic rate of increase, so as to optimize offspring production and maximize clone fitness under conditions of reduced predation risk.

The response of parasitic Hymenoptera to different cotton aphid phenotypes is also not known, though many parasitoids preferentially attack certain sizes (Frazer & Gill 1981; Chau & Mackauer 2001) and colours (Losey *et al.* 1997; Harmon, Losey & Ives 1998) of aphids. Furthermore, ants are not always successful at preventing cotton aphid parasitism; in fact, parasitism is sometimes much higher in ant-tended than in untended cotton aphid colonies (Kaneko 2003). Resultantly, we propose that cotton aphid phenotypes will be differentially susceptible to parasitism, even when ant-tended. If ants do permit a considerable degree of parasitism, we propose that tended aphids will produce offspring phenotypes that have a decreased risk of parasitism.

## Materials and methods

### EXPERIMENT 1 – DO ANTS ALTER APHID PHENOTYPES?

To determine whether ant-attendance alters transgenerational phenotypic expression of herbivore populations, a single cotton aphid, *A. gossypii*, clone that had been reared in the laboratory for *c.* 2 years was used for the experiment. Aphids were reared as a synchronous colony under low density conditions (< 10 apterous adults per plant) to minimize the numbers of dwarf and alate individuals developing. For bioassays, individual cotton plants, *Gossypium hirsutum* L. cv. Maxxa, were raised in 4″ pots in a 1 : 1 : 1 (topsoil : peat : perlite) soil mixture under summer greenhouse conditions; 21 °C–38 °C, 39%–81% relative humidity, and a 16 : 8 photoperiod. Plants were watered daily and fertilized once a week with Schultz Liquid Plant Food Plus 10-15-10, (Schultz Company, St Louis, MO). Plants were maintained aphid-free throughout their growth, and were raised to the true leaf stage of two to three, at which time they were used for experiments.

Five newly moulted, dark green apterous aphids were placed on a cotton plant. By starting with a known number of aphids of a particular phenotype, we could ensure that all offspring were born after the treatments commenced, that is, that our effects are truly transgenerational responses. Plants were placed in an outdoor setting far removed from any agricultural or horticultural crops but containing a large population of Argentine ants, *L. humile*. Plants were situated in an area *c.* 30 m$^2$, and individual plants were separated by *c.* 1 m, to help eliminate any possible movement of apterae between plants. Ants were allowed free access to some plants (tending treatment, $n = 6$). Tree Tanglefoot (The Tanglefoot Company, Grand Rapids, MI) was applied to the bottom stems of the remainder of the plants to restrict ant tending (no tending control, $n = 5$). Tree Tanglefoot functions as an adhesive, physical barrier, rather than a chemical barrier, to restrict ant foraging. All plants were checked daily to ensure that ants were present and absent on the treatment and control plants, respectively. Aphid colonies were allowed to develop for 2 weeks.

After 2 weeks, plant and aphid colony characteristics were assessed. Plant height, number of true leaves and total leaf area were measured. Concurrently, numbers and phenotypes of cotton aphids colonizing the plants were recorded. Apterous aphids were sorted into categories based on standardized colour plates (Kornerup & Wanscher 1967). Dwarf yellow, light green and dark green phenotypes most closely match; Plate 2 – A4 (Munsell renotation: 8·5Y, 9·0/4·5), Plate 1 – B8 (Munsell renotation: 1GY, 7·9/10·6), and Plate 28 – F6 (Munsell renotation: 7GY, 3·3/2·5), respectively, in the Methuen Handbook of Colour (Kornerup & Wanscher 1967). Alates were easily separated by the presence of wings or wing buds.

### EXPERIMENT 2 – DO PARASITOIDS ATTACK CERTAIN APHID PHENOTYPES?

To determine whether parasitoids preferentially attack certain aphid phenotypes, we took advantage of a semi-natural experiment in a greenhouse at UC Davis. Plants were raised under similar greenhouse conditions as Experiment 1. After 3 weeks, however, it was discovered that cotton aphids had opportunistically colonized a large number of the plants. Simultaneously, it was observed that these aphids were being tended by Argentine ants. Parasitic Hymenoptera were also seen flying from plant to plant, but the screening on the greenhouse was sufficient to deny access to predators. As mummies were not yet visible in the aphid colonies, we allowed this interaction to proceed for an additional 7 days at which time we collected, at random, one leaf from each plant ($n = 30$). At the time of leaf collection, we recorded the number of worker ants actively foraging on each leaf. Leaves were bagged and immediately returned to the laboratory so plant and aphid traits could be recorded.

Plant height and leaf area were measured. The total numbers of mummies on each sampled leaf were recorded and collected, so that adult specimens could be reared and identified. Numbers of each cotton aphid phenotype colonizing each leaf were recorded. Apterous and alate aphids were sorted into categories as in the previous experiment.

### STATISTICAL ANALYSES

#### *Experiment 1 – do ants alter aphid phenotypes?*

Data were analysed with MANOVA (Repeated Measures) using JMP IN 5·1 (SAS Institute 2005). By conducting this analysis as a REM ANOVA, we could account for the dependence in the data directly, that is, aphid phenotypes, being part of a single clone, are not truly independent. The main factor in the analysis was degree of ant tending (tended vs. not tended). Plant characteristics (plant height, number of true leaves and total leaf area) were initially entered into our analysis as covariates. Only the number of true leaves on a cotton plant was subsequently included in the analysis, however, as plant height and total leaf area were both found to be non-significant. Our dependent variables, numbers of dwarf apterae, light green apterae, dark green apterae and alatae were transformed $[x' = (\sqrt{x}) + (\sqrt{x} + 1)]$ prior to analysis to control for increasing variance as the treatment means increased (Zar 1984). As the sphericity test was not significant, significance was determined using the univariate unadjusted epsilon values (SAS Institute 2005).

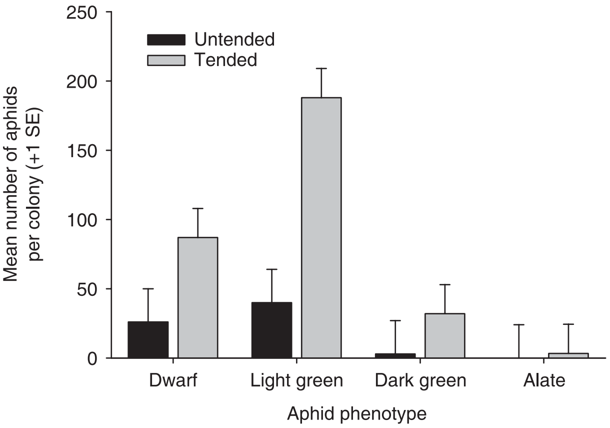

**Fig. 2.** Offspring phenotypes produced by dark green, apterous cotton aphids over 14 days when tended or not tended by Argentine ants. Tending treatment × offspring phenotype interaction; $F_{3,24} = 4·76$, $P = 0·0096$.

#### *Experiment 2 – do parasitoids attack certain aphid phenotypes?*

Data were analysed using multiple regression (JMP IN 5·1; SAS Institute 2005). Initial variables entered into the model were plant height, size of sampled leaf, number of ants on leaf, number of dwarf apterae, number of light green apterae, number of dark green apterae and number of alatae. As plant characters were not significant, plant height and size of sampled leaf were removed prior to running the final analysis. The dependent variable was the total number of mummies per leaf. As the data were normally distributed, with evenly distributed residuals, the data were not transformed prior to analysis (Zar 1984).

## Results

### EXPERIMENT 1 – DO ANTS ALTER APHID PHENOTYPES?

When cotton aphid colonies were ant tended, they were significantly larger than when untended ($F_{1,8} = 10·60$, $P = 0·012$). Aphid colonies were also larger on plants with fewer leaves ($F_{1,8} = 7·74$, $P = 0·024$), indicating that increased colony sizes may form on developmentally younger plants. Across treatments (i.e. tended vs. untended), there were differences in the number of phenotypes produced ($F_{3,24} = 6·52$, $P < 0·0022$); more dwarf and light green apterae were produced than dark green apterae or winged morphs. Most surprisingly, however, aphid colonies consisted of different numbers of phenotypes, when tended vs. not tended ($F_{3,24} = 4·76$, $P = 0·0096$) (Fig. 2). When aphids were tended by ants, increased numbers of light green apterae were produced. Similar numbers of dwarfs, dark green apterae and alatae were produced by both tended and untended colonies. Thus, ant-attendance resulted in altered transgenerational phenotypic expression in cotton aphid colonies.

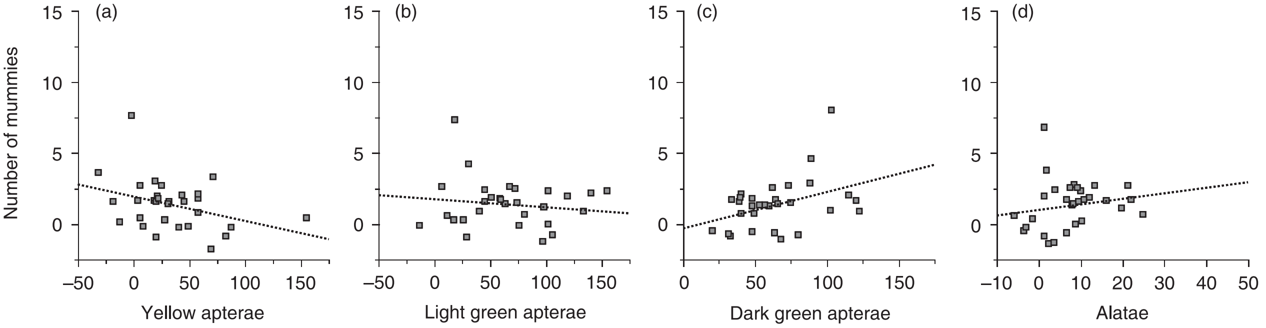

**Fig. 3.** Multiple regression leverage (partial residual) plots representing parasitism of: (a) dwarf apterae ($F_{1,24}$ = 3·52, $P$ = 0·073), (b) light green apterae ($F_{1,24}$ = 1·37, $P$ = 0·25), (c) dark green apterae ($F_{1,24}$ = 4·50, $P$ = 0·045) and (d) alatae ($F_{1,24}$ = 0·79, $P$ = 0·38), in colonies of mixed phenotypes when tended by Argentine ants. Leverage plots display, by plotting $x$ and $y$ residuals, the relationship between each $x$ and $y$ variable when 'removing' the effect of the other $x$ variables in the model.

### EXPERIMENT 2 — DO NATURAL ENEMIES ATTACK CERTAIN PHENOTYPES?

In the greenhouse, we found aphid mummies to be exclusively that of *Lysephlebus testaceipes*, a common cotton aphid parasitoid throughout California. Interestingly, aphids were more likely to be parasitized when ant-tended, as there was a positive relationship between the number of ants tending aphid colonies and the number of mummies within those colonies ($F_{1,24}$ = 10·71, $P$ = 0·0032). Mummies were less likely to be found in colonies consisting of large numbers of dwarf aphids ($F_{1,24}$ = 3·52, $P$ = 0·073), but more likely to be found in colonies with large numbers of larger, dark green individuals ($F_{1,24}$ = 4·50, $P$ = 0·045). There was, however, no relationship between mummification and numbers of the light green phenotype ($F_{1,24}$ = 1·37, $P$ = 0·25), indicating that this phenotype is neither disregarded nor favoured by *L. testaceipes*. There was also no relationship between numbers of mummies and abundance of winged aphids ($F_{1,24}$ = 0·79, $P$ = 0·38) (Fig. 3), perhaps because of the greater dispersal ability of alates or because there were simply low numbers of alates on the leaves.

## Discussion

Organisms frequently produce progeny with behavioural and/or morphological adaptations in response to increased risk of attack from natural enemies (Agrawal *et al.* 1999; Weisser 2001; Elliot *et al.* 2003). Similarly, if predation risk declines, organisms may produce phenotypes lacking costly defensive adaptations, with resultantly higher offspring production. Here, we have shown that cotton aphids engaged in a defensive mutualism with Argentine ants produce phenotypes with higher offspring production, than aphids in untended colonies. Our hypothesis was not wholly supported, however, as aphids produced greater numbers of light green but not dark green apterae when ant-tended. Since parasitoids preferentially attack dark green apterae, even when ant-tended, production of light green morphs may maximize clone fitness.

Ant tending has been shown to induce intra-generational changes in aphid behaviour and physiology. Tended aphids have reduced dispersal responses to aphid alarm pheromone, E-β-farnesene (Nault *et al.* 1976; Mondor & Addicott 2007). Aphids also alter the amount and composition of their honeydew (Fischer & Shingleton 2001; Yao & Akimoto 2001; Fischer *et al.* 2002) when competing for ant protective services (Cushman & Addicott 1989; Fischer, Hoffmann & Voelkl 2001). Intra-generational mutualist-induced morphological changes in aphids are also not unprecedented. When tended, some aphid taxa have depressed wing-induction responses (El-Ziady & Kennedy 1956; Johnson 1959; Kleinjan & Mittler 1975), perhaps due to compounds from ant mandibular secretions (Kleinjan & Mittler 1975).

Currently, it is uncertain whether transgenerational mutualist-induced phenotypic changes are herbivore or mutualist-driven. Ants may be inducing cotton aphids to produce larger more fecund phenotypes (Wilhoit & Rosenheim 1993), as larger morphs have increased honeydew production. It is also possible, however, that aphids alter the phenotypes of their offspring in response to increased nutrient acquisition (Dixon 1998; Müller *et al.* 2001), as a result of being moved from less nutritious to more nutritious parts of the plant by the ants or from not having to elude predators. We did not observe coccinellid, syrphid, or lacewing larvae/adults on the plants when they were checked daily, indicating that natural enemies were in low numbers or the ants were effective at defending the colony. Further experimentation is required to determine the proximate mechanisms underlying changes in aphid phenotypic expression.

If organisms involved in defensive mutualisms experience decreased predation risk (Nault *et al.* 1976; Katayama & Suzuki 2002), we would anticipate that phenotypes with the greatest fitness, that is, dark green apterae (Rosenheim, Wilhoit & Colfer 1994), would be produced. Thus, why do ant-tended cotton aphid colonies consist of predominantly light green, but not dark green, apterae? We believe that this is directly related to our second hypothesis; aphid phenotypes are not all equally likely to be parasitized. Dark green apterae are subject to the highest parasitism rates, even when ant tended. Thus, as dwarf apterae have the lowest offspring production (Rosenheim *et al.* 1994) but the lowest parasitism rates and dark green apterae have the highest offspring production (Rosenheim *et al.* 1994) but also the highest parasitism rates, light green apterae with intermediate offspring production (Rosenheim *et al.* 1994) and intermediate parasitism risk may be the optimal phenotype to produce when tended by Argentine ants. If this explanation is correct, we further hypothesize that cotton aphids may produce predominantly dark green phenotypes when tended by more aggressive ant species, which deter both predators and parasitoids.

It is important to note that the dissimilar numbers of phenotypes in tended vs. non-tended aphid colonies may have resulted from differential predation rates. As noted previously, it is not currently known whether predation rates are phenotype-dependent (Mondor *et al.* 2005); however, we believe that this was a not major factor in our experiment. Though our first experiment was conducted in an outdoor setting, it was a significant distance from any potential host plants harbouring aphid colonies or natural enemies. Furthermore, as stated previously, we did not observe predators on the plants when they were checked daily. While we cannot entirely discount the effect of differential predation in influencing our cotton aphid phenotypic ratios, we believe that it did not significantly influence the results of our experiment.

The factors underlying changes in herbivore phenotypic expression are complex. Phenotypic plasticity of herbivores can be altered by both biotic and abiotic stimuli (Tollrian & Harvell 1998). Mutualistic interactions, though pervasive in nature, are frequently overlooked as key determinants of phenotypic change. As mutualisms are ubiquitous (Bronstein 1994) and many organisms have high levels of phenotypic plasticity (West-Eberhard 1989), mutualist-induced transgenerational phenotypic plasticity in herbivore populations may be more common than previously realized.

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