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PLANT-MICROBE-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Benefits of gregarious feeding by aposematic caterpillars depend on group age structure

Stuart A. Campbell · Michael Stastny

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Abstract Gregarious feeding is a common feature of herbivorous insects and can range from beneficial (e.g. dilution of predation risk) to costly (e.g. competition). Group age structure should influence these costs and benefits, particularly when old and young larvae differ in their feeding mode or apparency to predators. We investigated the relative value of gregarious feeding by aposematic larvae of *Uresiphita reversalis* that we observed feeding in groups of mixed ages and variable densities on wild *Lupinus diffusus*. In a manipulative field experiment, the survivorship and growth of young larvae were enhanced in the presence of older conspecifics, but not in large groups of similarly aged larvae. Estimates of insect damage and induced plant responses suggest that mixed-age groups enhance plant quality for young larvae while avoiding competition. We conclude that benefits of gregariousness in this species are contingent on group age structure, a finding of significance for the ecology and evolution of gregariousness and other social behaviours.

Keywords Social behaviour · Insect-plant interactions · Facilitation · *Uresiphita reversalis* · *Lupinus diffusus*

Introduction

During host plant colonization, many herbivorous insects engage in a rich array of social behaviours (Costa 2006). Many species improve host quality or reduce predation by cooperatively feeding or attacking gregariously as either adults or larvae. Conifer-colonising bark beetles, for example, attack as adults in pheromone-mediated aggregations that are critical for successful reproduction (Raffa et al. 1993). In many Lepidoptera, gregarious larval feeding groups arise from the deposition of a large clutch of eggs by single females (Costa and Pierce 1997; Sillén-Tullberg 1988). Other species show evidence of preferential oviposition by different females on the same hosts (Francini and Lucci Freitas 2010; Reed 2003; Ulmer et al. 2003) though observations from the wild are extremely rare (Reed 2003). Finally, groups of unrelated larvae may merge on the same host plant (Costa and Ross 2003). Group feeding can have strong fitness benefits by reducing the per capita effects of host defences (or foraging costs in general) (Denno and Benrey 1997; Reader and Hochuli 2003), predation risk (Hunter 2000; Stamp and Bowers 1988; Tullberg et al. 2000) and/or microclimate (Battisti et al. 2005; Casey et al. 1988; Ronnas et al. 2010). These benefits can facilitate host plant adaptation (Fordyce and Nice 2004) and

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S. A. Campbell and M. Stastny have contributed equally to this work.

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S. A. Campbell · M. Stastny
Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA

S. A. Campbell
Department of Entomology, Cornell University, Ithaca, NY 14853, USA

Present Address:
S. A. Campbell (✉)
Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, ON M5S 3B2, Canada
e-mail: sa.campbell@utoronto.ca

Present Address:
M. Stastny
Department of Biology, University of Ottawa, 30 Marie-Curie, Ottawa, ON K1N 6N5, Canada

may provide a selective pathway for the evolution of highly social life histories from simpler social behaviours (Costa and Pierce 1997). Costs of gregariousness, such as competition, might constrain such transitions under certain conditions (e.g. high group densities) (Prokopy and Roitberg 2001; Wise et al. 2006). Feeding benefits of gregariousness can also differ based on developmental stage, with potential consequences for larval dispersal patterns (Inouye and Johnson 2005). However, relatively few estimates of the net benefits of gregariousness have been based on direct experimental manipulations of group size (Inouye and Johnson 2005; Kawasaki et al. 2009; Krause and Ruxton 2002; Reader and Hochuli 2003).

Additional costs and benefits may arise from the natural history of the particular organism. Some species gregariously feed at the same life history stage (e.g. early instar larvae), usually as a by-product of a single oviposition event. However, if several adult females oviposit asynchronously on the same host, or groups of differing ages merge, the resulting age structure could alter group dynamics (Costa and Ross 2003; Reed 2003). In these cases, older larvae may harm or outcompete smaller, younger larvae by directly consuming certain host plant parts or by inducing host defences to which the younger larvae have not mounted a response. Asymmetric competition among larvae of different ages is known from parasitoids (Dorn and Beckage 2007) and suggests that repeated oviposition on the same hosts (superparasitism) may represent a ‘better-than-nothing’ strategy in the face of limited host abundance. Alternatively, older larvae could weaken a host more effectively than young larvae, which may then benefit from feeding in mixed-age groups. In aposematic species, older (and larger) larvae could also improve the apparency of the warning signal and provide an additional indirect benefit to younger conspecifics. Optimal oviposition theory (Jaenike 1978) would predict that the occurrence of mixed-age feeding groups in nature should be associated with a fitness benefit to developing offspring; however, there are few previous data to support this hypothesis.

Here, we report observations on the gregarious, aposematic caterpillars of *Uresiphita reversalis* (Guenée), which we found feeding on wild *Lupinus diffusus* Nutt. in groups of mixed ages. Upon observing their feeding behaviour, we conducted a field experiment to test two hypotheses: first, that larvae benefit from feeding in large vs. small groups; and second, that this benefit differs depending on the age structure of the group.

Materials and methods

Natural history observations

This study was conducted at the Archbold Biological Station (ABS) in Lake Placid, Florida (27°08′N; 81°11′W).

Fig. 1 Gregarious feeding group of *Uresiphita reversalis* on wild spreading lupine, *Lupinus diffusus*. *Inset* Close-up showing patterning characteristic of aposematism

The host, spreading lupine, *Lupinus diffusus* (Fabaceae) (Fig. 1), is an endangered, native perennial of the southeast US, where it occurs in sandy, or similarly xeric, disturbed habitats such as roadsides and recently burned areas. It flowers from late February until late May. At ABS, *L. diffusus* occurs at low densities primarily in sandy, elevated sites dominated by slash pine, *Pinus elliottii*. The herbivore, larvae of the genista moth, *Uresiphita reversalis* (Lepidoptera: Crambidae) (Fig. 1), is oligophagous, feeding on species in quinolizidine-alkaloid-containing tribes of the Fabaceae (Leen 1997), though appearing restricted to *L. diffusus* at ABS. Larvae sequester host alkaloids as an anti-predator defence (Montllor et al. 1990) and are aposematically coloured with black, white and chartreuse markings. On *L. diffusus*, younger larvae are found primarily on upper, younger foliage and shoot tips, where they establish weak silk shelters and characteristically chew out leaves, leaving a papery, translucent window; older larvae are found on lower foliage and consume leaf material completely (M. S. and S. A. C., personal observations). Larvae are gregarious feeders (Bernays and Montllor 1989; Leen 1995). The gregariousness appears to result in part from the deposition of large (though variable) clutches of eggs (Leen 1995). Moreover, plants in the field appear to receive sequential clutches of eggs despite the presence of alternative, unattacked hosts (Leen 1998), and females prefer to oviposit on previously preferred hosts in laboratory assays (Leen 1998). While this preference is indirect evidence for an adaptive value of gregariousness (Jaenike 1978), the actual benefit of this behaviour has not been tested in a manipulative experiment.

In March 2006, a systematic survey of over 200 *L. diffusus* plants revealed 16 individuals colonized by *U. reversalis*, scattered across the surveyed area (approximately 125 ha). In some cases, the colonized plants were in relatively close proximity to other, uncolonized individuals. We noted the relative frequencies of different larval ages (as determined initially by mass and subsequently by instar) and found these to be highly variable among hosts (Online Resource 1). While some variation in development would be expected among larvae, the highly variable age structure we observed could only have resulted from females ovipositing sequential clutches on the same hosts, as noted by Leen (1998). Based on these observations, and the low overall percentage of colonized plants (ca. 8 %), we hypothesized that *U. reversalis* benefits from creating mixed-age feeding groups, rather than spreading clutches among all available hosts.

Manipulative experiment

We collected larvae of *U. reversalis* and supplied them with fresh *L. diffusus* leaves prior to the experiment. Larvae were classified as 'young' (ca. instars 1–3 and <1.99 mg), and 'old' (ca. instars 5–7 and 30–80 mg); a few larvae that appeared to be in their fourth instar were assigned a category based on mass. Larvae of intermediate mass (between 2 and 30 mg) were not used. Larvae were then allocated randomly to three experimental treatments that manipulated the density and age structure of the feeding groups: high density (ten larvae) with a mix of young and old larvae (five each), high density (13 larvae) of only young larvae, and low density (five larvae) of young larvae. These treatments (1–3) lie within the natural distribution of abundances and age/size classes and had average instars of 4.0 ± 0.1, 2.3 ± 0.07 and 2.4 ± 0.09, respectively (mean instar ± SE). We did not use a single-larva treatment because we did not observe plants with single larvae. We used 13 (rather than ten) young larvae in the high-density groups of young larvae in an attempt to reduce the difference in the initial larval mass of the high-density treatments. On 23 March 2006, we located 27 similarly sized host plants that were of intermediate size for this area (ca. 35–45 cm tall), were not flowering, showed no previous insect damage and were at least 15 m apart. Treatments were dispersed among these plants as nine randomized complete blocks. Larvae were applied onto a single shoot of each plant and all surviving larvae were collected again on 30 March. We determined three components of insect fitness and performance: proportional survivorship (recovery of larvae), larval mass and larval instar (developmental stage). While we collected all remaining larvae, we focused on the young larvae (see "Analyses"). Recovery is likely to be an excellent measure of young larval survivorship in this habitat, in which plants are separated by wide stretches of bare sand.

Plant traits often explain variation in herbivore performance, and thus on each host plant we recorded stem diameter, height, and numbers of the following: vegetative shoots, shoots with fruits, inflorescences, inflorescences in bud stage, damaged inflorescences, leaves with feeding damage (including damage other than by *U. reversalis*, though this was minor), leaves fed on by young larvae (recognized by the characteristic scars), and total leaves. We did not observe any eggs or ovipositing moths during the experiment, ensuring that each experimental plant only contained our larvae.

Analyses

For each plant (the experimental unit), we calculated the mean trait values for young larvae collected at the end of the experiment. The majority of young larvae had not grown enough to be mistaken for old larvae; however, we excluded larvae above the fifth instar from our analyses to ensure that we did not inflate our performance estimates for the mixed-age treatment by inadvertently including slow-growing larvae that had been part of the initial pool of older (i.e. larger) larvae; one plant in the mixed-age treatment was excluded entirely in this way (results were similar with the inclusion of these data). Thus, our results are based on the common cohort of young larvae that was found in all treatments. Treatment effects on per capita mass and instar, feeding damage, fruiting shoot and inflorescence number were analysed by ANOVA in SAS® (PROC GLM) followed by the Ryan–Einot–Gabriel–Welsch multiple-range test (REGWQ test) (Day and Quinn 1989); survivorship among treatments was compared with the likelihood-ratio χ^2-statistic (PROC FREQ). Block was included as a random model effect by specifying a random statement. Bivariate correlations among larval and plant traits were analysed using Pearson correlation coefficients (PROC CORR). Data were $\log_{10}$ transformed when necessary to meet normality and homoscedasticity assumptions.

Results

Young larvae did not perform better when in large compared to small feeding groups, but exhibited dramatically improved growth and survivorship when feeding in the large, mixed-age groups. Young larval mass (Fig. 2a; $F_{2,15} = 8.48$, $P = 0.0034$), survivorship (Fig. 2b; $\chi^2 = 13.31$, $P = 0.0013$) and stage of development (Fig. 2c; $F_{2,15} = 4.24$, $P = 0.0347$)

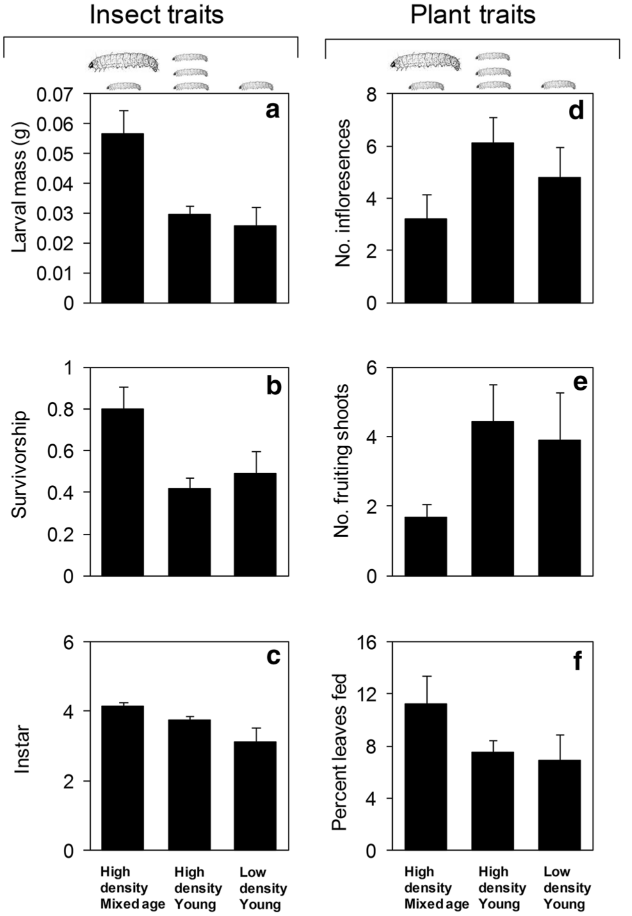

Fig. 2 Variation in larval performance and development (**a**–**c**) and plant traits (**d**–**f**) under three experimental treatments: low density of young larvae, high density of young larvae, and a high-density mixture of old and young larvae. Insect data are for the cohort of young larvae found in all three treatments. *Percent leaves fed* refers to leaves with characteristic feeding scars by young larvae (see text). *Bars* represent the mean + SE

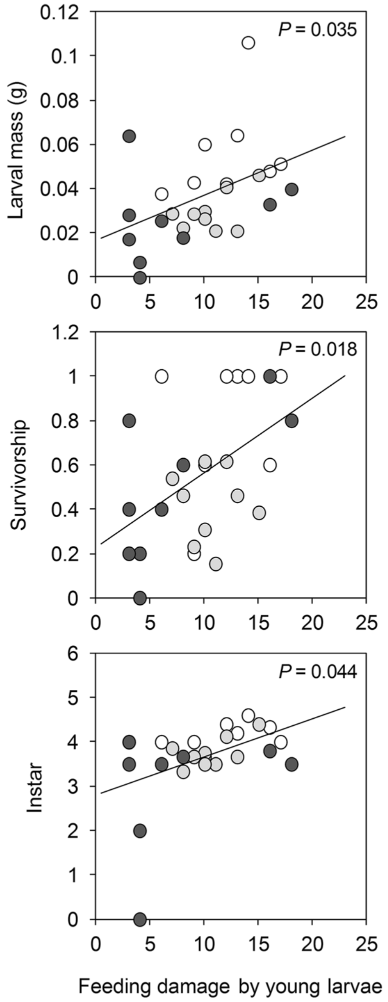

Fig. 3 Relationships between three measures of performance of young *U. reversalis* larvae (final mass, survivorship and developmental stage) and the percentage of leaves exhibiting feeding damage by young *U. reversalis* larvae. Data points are averages for each experimental plant. *White circles* High density, mixed-aged larvae; *light grey circles* high density, young larvae; *dark grey circles* low density, young larvae. *P*-values are for the significance of Pearson correlation coefficients

were, respectively, 118, 34 and 64 % higher in the mixed-age treatment (relative to the low-density, young-larvae treatment). In contrast, these metrics were statistically similar (REGWQ test) in the treatments with large and small groups of only young larvae. Percent feeding damage by young larvae (as indicated by their characteristic damage) also did not differ between plants with large and small groups of similarly aged larvae, but was 62 % higher in the mixed-age treatment ($F_{2,16} = 2.91$, $P = 0.084$; Fig. 2f). In addition, the number of leaves fed upon by younger larvae was positively correlated with larval mass ($r = 0.41$, $P = 0.035$), development ($r = 0.40$, $P = 0.044$) and survival ($r = 0.46$, $P = 0.018$) of the young larvae, confirming that variation in consumption accounted for larval performance (Fig. 3).

Insect feeding negatively affected components of plant reproduction over the course of the experiment. Compared to the high-density groups of young larvae, inflorescence (Fig. 2d) and fruiting shoot production (Fig. 2e) were reduced by 48 and 61 %, respectively, in the mixed-age treatment, with the sum of these fitness components ('reproductive effort') differing among treatments ($F_{2,16} = 3.30$, $P = 0.063$). These differences corresponded to the increased feeding damage by young larvae (Fig. 2f) and there were overall negative correlations between the percentage of leaves that had been fed upon by young larvae and both fruiting shoot number ($r = -0.44$, $P = 0.0207$) and reproductive effort ($r = -0.45$, $P = 0.0176$).

Discussion

Theoretical and empirical studies on gregariousness in social species have focused almost exclusively on the numerical advantages, comparing individual benefits in large or small groups, or when solitary (Costa and Ross 2003; Krause and Ruxton 2002). However, when groups are formed asynchronously, e.g. by repeated oviposition on a single host, the resulting mix of ages, and age-specific behaviours, should influence the costs and benefits of group living. Our finding that young *U. reversalis* caterpillars perform equally well when in large vs. small groups, but perform significantly better when feeding with late-instar larvae, supports the hypothesis that benefits of gregariousness in this species are contingent on group age structure. This experimental result supports an adaptive explanation for the observed field pattern (Jaenike 1978). It is likely that many lepidopteran herbivores exhibit natural variation in the distribution of larval ages and stages on hosts, and to our knowledge this study is the first confirmation of an adaptive value of this variation.

We propose two likely mechanisms underlying the benefits of gregarious feeding with older conspecifics. First, older larvae may improve plant quality for younger larvae (facilitation). Older larvae feed primarily on entire lower leaves, while younger larvae chew out fenestrations in the younger, upper leaves (S. A. C. and M. S., personal observations). This segregation would avoid direct competition, and could also improve food quality for younger larvae by altering source-sink relationships within the plant, by lowering overall plant resistance, and/or by causing induction of defences in lower leaves at the expense of upper leaf tissue. Higher plant quality may have led to greater survival in mixed-age groups if quinolizidine resistance traits were sufficiently toxic (Montllor et al. 1990). These mechanisms have been suggested for other gregarious larval herbivores in the Lepidoptera, but only in the context of the numerical benefits of group feeding (Clark and Faeth 1997; Denno and Benrey 1997; Fordyce 2003; Reader and Hochuli 2003). In our study, the interpretation that older larvae altered host quality is directly supported by two results. First, feeding by young larvae was greater in the mixed-age treatment, suggesting that the palatability and/or nutritional quality of upper leaves was improved, leading to the observed covariation of our damage estimate with insect performance (Fig. 3). The similar number of leaves damaged by high- and low-density groups of only young larvae also rules out competition among young larvae and resource limitation as factors in this system. Second, the rapid and striking impacts on plant reproduction seen in the mixed-age treatment over the 8 days of this study strongly suggest that older larvae were able to alter plant resource allocation at the phenologically sensitive time of flowering in this species. These results lead us to conclude that age-specific facilitation underlies the stronger performance of young larvae on the mixed-age plants, with older larvae potentially inducing allocation of plant resources to storage (Schwachtje et al. 2006) at the expense of both vegetative defence and reproduction. While it is possible that greater numbers (>13) of young larvae could have provided per capita facilitation benefits comparable to feeding with older larvae, it is clear that for the average size of *U. reversalis* feeding groups in our study area, a mixed composition of age classes has significant fitness benefits to young larvae. It remains unknown whether the older larvae accrue any benefit or cost from feeding with younger conspecifics.

A second mechanism for benefits of mixed-age groups could involve a reduction in predation risk. Subject to significant predation risk in other habitats (Bernays 1997), *Uresiphita reversalis* is warningly coloured, particularly in later instars, and is known to sequester alkaloids for defence against predators (Bernays and Montllor 1989; Montllor et al. 1990). Anti-predation benefits of gregariousness in aposematic species are well known (Hunter 2000), with one proposed mechanism of these benefits being increased signal repellence in larger groups (Gamberale and Tullberg 1998). We speculate that the larger size of late-instar larvae, and their observed preference for feeding in more exposed locations (S. A. C. and M. S., personal observations), could provide a more visible aposematic warning that indirectly benefits the younger cohort by more effectively deterring predators or accelerating their learning process. While an intriguing hypothesis, we saw no evidence of predation during our experiment. In spite of the relatively short duration of our experiment, which likely underestimated any effects of parasitoids (Stamp 1981), our results are similar to those from a 7-year study of predation on *U. reversalis* at the same location, in which only a single natural predation event was observed (Carrell 2001). Therefore, any putative benefits of reduced predation risk, when present, would be over and above the facilitation benefits described above. Finally, thermal regulation can represent an additional benefit to feeding in groups (Battisti et al. 2005; Stamp and Bowers 1990) but is an unlikely mechanism in this system since old and young larvae remain at least partially segregated on the host.

The range of naturally occurring stages on some plants (e.g. first and sixth instars; Online Resource 1) suggests that repeated oviposition is the proximate cause of mixed-age gregariousness, an hypothesis supported by laboratory experiments with this species (Leen 1998). Several other species of lepidopteran herbivores also show preferential or gregarious oviposition on hosts with eggs or larvae already present (Francini and Lucci Freitas 2010; Reed 2003; Ulmer et al. 2003), while some species avoid previously attacked plants (Vasconcellos-Neto and Monteiro 1993). Ovipositing females can also adjust the size of clutches based on host traits (Pilson and Rausher 1988) or presence of conspecifics (Shapiro 1981; Ulmer et al. 2003; Vasconcellos-Neto and Monteiro 1993), and the size of additional clutches may influence the benefits of gregariousness (Fordyce 2006). Our results suggest that such variation in oviposition behaviours may be explained in part by the social context of any benefits or costs to gregariousness.

The correlations between feeding damage and plant performance suggest that fitness impacts in this system may be reciprocal; that is, *U. reversalis* may impose fitness costs to the plant, which may in turn depend on the composition of the feeding group. Older larvae could have affected plant reproduction directly through their own feeding, but also indirectly by facilitating young larval feeding, an hypothesis supported by the fact that the correlation between plant reproductive effort and damage remains significant ($r = -0.55$, $P = 0.0185$) after excluding the mixed-age treatment. That is, young larvae alone had a negative effect on plant reproduction, but the magnitude of their effect may be mediated by the presence of older conspecifics. The significant reduction in flower and fruit production in the mixed-age treatment is surprising given the short duration of this experiment, and our results may in fact underestimate the cumulative impact of this herbivore on resource allocation and fitness. From the plant's perspective, herbivory by *U. reversalis* in this study may have coincided with a critical point in the phenology of *L. diffusus*, specifically the onset of flowering at the end of the dry season. Alternatively, the effects of herbivory on floral traits in the mixed-age treatment may have caused herbivory-induced pollination limitation, leading to reduced fruit production (Kessler et al. 2011). Young larvae feed on shoot tips, and also fed on developing flowers (personal observations), though most feeding occurred prior to flowering. While the significant effects over such a short-term experiment are compelling, a longer-term experiment is required to confirm the effects on plant fitness, and to determine whether mixed-cohort social feeding imposes natural selection on host plants relative to undamaged plants.

In conclusion, we find that *U. reversalis* feeds gregariously in mixed groups of different developmental stages, and that this age structure has significant fitness benefits for developing young larvae in the absence of a strict numerical benefit to group living. These results raise several interesting questions as to the mechanisms of group formation in gregarious species, particularly in terms of whether females use herbivory-induced cues when choosing hosts, and whether they are able to quantitatively assess the number or age of conspecific larvae and optimally adjust their clutches to maximise the fitness benefits of group feeding. Our data suggest that mixed-cohort gregariousness represents a strategy to cope with plant resistance while possibly avoiding intraspecific competition and predation. While the numerical advantages of group feeding are well known, our results suggest that a careful dissection of other features of gregariousness may prove useful to understanding the ecology and evolution of a variety of social behaviours.

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Conflict of interest The authors declare that they have no conflict of interest.

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