Between-clutch interactions affect a benefit of group feeding for pipevine swallowtail larvae

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Abstract. 1. In California, early instar larvae of the pipevine swallowtail (Battus philenor) develop at an accelerated rate when feeding in large groups compared with small groups due to a plant-mediated response to feeding group size. Larvae benefit from accelerated growth because the time larvae remain in early stages, where mortality is highest, is reduced. Occasionally, multiple clutches are laid on the same plant stem. Clutch size modification by females ovipositing on plant with previously laid clutches and the effect of kinship and group size on larval behaviour was examined. The direct and indirect interactions between clutches were investigated to determine if group size and time between clutch establishment affects the performance of early instar larvae.

2. Larger groups consume the young foliage more quickly and develop at an accelerated rate compared with smaller groups. Older foliage available to later clutches is an inferior food resource compared with younger foliage.

3. There was no evidence that females adjust clutch size in response to the presence of conspecific clutches.

4. Second groups of larvae readily joined previously established feeding groups. There were no observed behavioural differences between sibling and mixed-family groups.

5. The effect of a second group on the growth of the initial group was dependent on the size of both groups and the time interval between the arrival of the two groups.

6. Accelerated growth associated with larger feeding aggregations was absent when these groups were introduced to plants with previously established groups.

7. It is beneficial for ovipositing females to avoid plants with previously laid clutches because direct and indirect interactions with established clutches compromises larval performance.

Key words. Behaviour, clutch size, gregariousness, interactions, induced plant response, oviposition, Papilionidae, plant-mediated interaction.

Introduction

Variation in the quality of host plants available to herbivores can be influenced by nutritional value, defensive characteristics, and the presence of competitors (Karban, 1992). These factors are known to vary both spatially and temporally. Many species of insects inspect potential host plants carefully prior to oviposition, and thereby may assess the quality of a particular plant for their offspring. Numerous studies have indicated that females of some species avoid laying eggs on plants with heterospecifics or conspecific herbivores present (Rausher, 1979; Shapiro, 1981; Vasconcellos-Neto & Monteiro, 1993). Avoiding plants with established herbivores reduces the potential detrimental effects of competitive interactions, which can be realised as an insufficient quantity of food for larvae to...
complete development, or delayed development as a consequence of larvae being restricted to feeding on poorer quality plant tissues (Rausher, 1979; Denno et al., 1995). These direct competitive effects are probably strongest among herbivores occupying the same feeding guild, and may explain why many species of Lepidoptera avoid laying eggs on plants with conspecific eggs present.

In addition to direct competitive interactions among herbivores, subsequent plant responses to previous herbivory can similarly affect female oviposition preference and larval performance (Stamp, 1984; Harrison & Karban, 1986; Van Zandt & Agrawal, 2004a). Dynamic plant responses to herbivory have been observed in numerous systems and can be manifested as structural and chemical changes in the plant phenotype (Karban & Baldwin, 1997). Induced resistance and defence exhibited in plants can be generally effective, or specific to particular herbivore guilds or even species (Agrawal, 2000; Van Zandt & Agrawal, 2004b). Thus, herbivore-induced plant responses can potentially mediate important antagonistic indirect interactions among herbivores (Denno et al., 1995; Denno et al., 2000; Tindall & Stout, 2001).

However, these plant-mediated interactions need not be antagonistic to all players in the interaction. Some herbivores may actually benefit from induced plant responses caused by other herbivores (Masters & Brown, 1992; Brown & Weis, 1995). Additionally, herbivore-induced plant responses may not be effective defences; rather, they may actually be beneficial in some cases resulting in increased herbivore performance (Karban & Baldwin, 1997). Induced susceptibility of plants to herbivores has been documented in systems where early season herbivory increases a plant’s susceptibility to attack by later arriving herbivores (Martinse et al., 1998; Underwood, 1998). Induced suitability has similarly been documented in systems where herbivore life-history traits and behaviours effectively manipulate host-plant quality, resulting in enhanced performance for the herbivore. For example, large clutch size and aggregative feeding of some Lepidoptera enhances plant quality for larvae inflicting the initial damage (Benrey & Denno, 1997; Fordyce, 2003).

Aggregative feeding has evolved independently in many groups of Lepidoptera, and many hypotheses have been posited to explain its adaptive function (Stamp, 1980; Reader & Hochuli, 2003). These hypotheses include defence (Hunter, 2000), feeding facilitation (Chew & Robbins, 1984; Clark & Faeth, 1997), thermoregulation (Porter, 1982; Bryant et al., 2000), and host-plant manipulation (Fordyce, 2003). Whereas thermoregulation and defence are a consequence of interactions among larvae, feeding facilitation and host-plant manipulation through aggregative feeding are direct interactions between the plant and the herbivore. For example, the defensive efficacy of trichomes can be effectively circumvented by large feeding aggregations that construct a communal silk mat, or scaffolding, permitting larvae to forage and feed unimpeded by these structures (Rathcke & Poole, 1975; Fordyce & Agrawal, 2001). Similarly, large feeding groups can establish feeding sites more quickly than solitary larvae (Clark & Faeth, 1997). Larger feeding aggregations may also induce dose-dependent responses that enhance plant quality, resulting in increased developmental rate of the larvae (Fordyce, 2003). Each of these plant-related direct consequences of aggregative feeding may accelerate larval developmental rates, especially in earlier instars where larvae are most vulnerable to natural enemies and more susceptible to abiotic factors (Williams, 1999; Zalucki et al., 2002; Fordyce & Shapiro, 2003). Thus, increased growth rate reduces the amount of time larvae spend in these vulnerable stages.

Oviposting females of egg clustering species can compensate for the costs involved with competition among siblings by modifying their clutch size in response to the amount of available foliage for their offspring (Pilson & Rausher, 1988; Lawrence, 1990; Matsumoto et al., 1993; Fordyce, 2005). In addition, between-clutch competition may be avoided if females avoid laying clutches where other clutches are present (Fordyce, 2005). Alternatively, some species add eggs to previously laid clutches, suggesting that the benefits of aggregative feeding may outweigh the potential costs (Ulmer et al., 2003). Modification of clutch size in response to previously laid clutches has not been explored. It is a reasonable assumption that previously laid clutches are more likely to hatch earlier than later clutches. This may be costly for later hatching clutches if superior food resources are consumed prior to their hatching, or if induced plant responses are initiated prior to hatching. However, these adverse effects may be ameliorated if feeding establishment of larvae or induced plant suitability are the important factors favouring aggregative feeding (Chew & Robbins, 1984; Clark & Faeth, 1997). Thus, timing between oviposition and the effects of group size on larval performance may play a central role determining the outcome of the direct and indirect interactions between two or more clutches laid in close proximity on the same plant.

This study addresses the consequences of direct and indirect interactions among clutches of the pipevine swallowtail, Battus philenor L., in California, which is known to benefit from aggregative feeding by group-size-dependent plant responses (Fordyce, 2003; Fordyce & Nice, 2004). Specifically, the following questions were asked: (i) Is there evidence that females adjust their clutch size in response to previously laid clutches? (ii) Do mixed family feeding aggregations behave differently than full sibling groups? (iii) What are the direct consequences for later emerging larvae joining a previously established clutch or being restricted to feeding on older foliage? (iv) Are the plant-mediated benefits of feeding in a large aggregation affected by the presence of another clutch? (v) Does clutch size and time between hatching dates of clutches affect the direct and indirect interactions between groups?

Materials and methods

Study system

The pipevine swallowtail ranges from the south-eastern and central United States to Arizona and south into Central America (Racheli & Pariset, 1992). A disjunct
population in California occupies the northern Central Valley and surrounding foothills of the Coast Range and Sierra Nevada Mountains. *Battus philenor* is a specialist on plants in the genus *Aristolochia* (Aristolochiaceae), commonly called pipevines, which contain toxic alkaloids called aristolochic acids that larvae sequester and use for their own defence (Brower, 1958; Jeffords et al., 1979; Sime et al., 2000; Fordyce, 2000, 2001). The California population has only one available host-plant species, *Aristolochia californica* Torr., an endemic liana characteristic of riparian habitats. *Battus philenor* larvae are the only herbivores consistently observed feeding on the plant. Females lay egg clusters on plant stems and on the underside of leaves. On average, clutch size observed in California is 13 eggs per cluster (Fordyce, 2003). In populations studied elsewhere, average clutch size ranges between two and five eggs (Spade et al., 1988; Rausher, 1995; Fordyce & Nice, 2004).

In California, larvae feed in tight aggregations until the third or fourth instar, at which time they disperse and usually feed solitarily (Fordyce, 2003). The large clutch size and subsequent aggregative feeding observed in California confers the benefit of accelerated larval growth. This accelerated growth is, in part, due to changes in plant quality, which is a function of the size of a feeding aggregation (Fordyce, 2003). This dose-dependent effect of group size is realised irrespective of the population origin of *B. philenor*. It is possible that the large clutch size observed in California is an adaptation to the group-size-dependent benefits associated with feeding on *A. californica* (Fordyce & Nice, 2003). There are also direct benefits of feeding in aggregation on *A. californica*. Unlike most other species of *Aristolochia* that *B. philenor* has been documented to use as a host plant, *A. californica* is densely covered with trichomes, which are densest on the young, nutritious leaves and impede caterpillar feeding. Larger feeding aggregations appear to circumvent trichomes by feeding from communally constructed silk scaffolding (sensu Ratheke & Poole, 1975; Fordyce & Agrawal, 2001). Thus, the advantages of group feeding for individuals in California are both indirect (plant mediated) and direct (feeding facilitation). Previous experiments have failed to detect a direct defensive benefit for aggregative feeding of larvae in California, rather an indirect benefit associated with accelerated development is apparent (Fordyce & Agrawal, 2001). More than 60% of larval mortality occurs during the first instar (J. A. Fordyce, unpublished data), due in part to predation and occasional periods of extended cool temperatures (Fordyce & Agrawal, 2001; Fordyce & Shapiro, 2003). Unless noted otherwise, all experiments and observations reported herein were conducted at Stebbins Cold Canyon, University of California Ecological Reserve, Solano County, California, U.S.A.

**Clutch size adjustment in response to previously laid clutches**

Oviposition on plant stems where previously laid clutches are present has not been directly observed for *B. philenor* in the wild. However, multiple clutches on the same stem are occasionally observed. To test if females adjust clutch size in response to conspecific eggs, a null model approach was used to compare the average difference in clutch size observed on plants with multiple clutches (*n* = 38) to a random expectation. For instances where more than two clutches were present, the difference between the largest and smallest clutch was calculated. Four thousand data sets of 38 clutch pairs were generated by randomly sampling with replacement 526 naturally laid clutches observed in the field. These observed clutches included the multiple clutch data. The average difference in clutch size for each of these data sets was used to construct a null distribution. The re-sampling procedure was conducted using a macro programmed in Microsoft Excel®. The clutch size data were collected in the years 1999–2001 at various locales in Solano Co., located in the inner Coast Range of California. Multiple clutches from separate oviposition events were inferred only when discrete hatching time for each clutch was observed. If females are adjusting clutch size in response to conspecific eggs, the observed difference is expected to be less than or greater than the random expectation. Similarly, to test if the total number of eggs on a plant with multiple clutches was greater or less than a random expectation, the average total number of eggs observed on plants with multiple clutches were compared against 4000 randomly generated data sets using observed clutches. The probability that the observed data were different from a random expectation was calculated using the cumulative probability based on the null distribution (Manly, 1991).

**Group feeding behaviour and clutch relatedness**

To examine if unrelated clutches segregate along family lines, field experiments using mixed-family and single-family clutches were placed on *A. californica*. All larvae used in this experiment were newly hatched from eggs laid by captive, wild-caught females. Groups of 12 siblings, or groups of 12 consisting of two families (six individuals from two different females) were placed on an *A. californica* leaf and permitted to feed and forage on the plant for 48 h. After 48 h, the distribution of larvae was recorded to determine if larvae in mixed family groups were more likely to separate into smaller groups and if these groups segregate along family lines. Sibling larvae were identified using either blue or red fluorescent powder (BioQuip Products, Inc., Rancho Dominguez, CA, U.S.A.). All larvae, including those in all sibling treatments, received powder. In total there were 12 replicates of sibling and mixed family group treatments.

**The effect of leaf age on larval growth**

Exploitation competition may operate between earlier established clutches and later arriving clutches. Groups of larvae consume young foliage at the growing stem tips, and
therefore may restrict later emerging clutches to feeding on older foliage. Nearly all leaves on the plant are formed on newly growing stems, with older, nearly fully expanded leaves occurring distally from the growing tip. To assess if leaf age affects leaf quality for developing larvae, individual neonate larvae were confined in clip cages on leaves of various ages in the field and permitted to feed for 48 h. Larval weights were used to assess leaf quality as a larval food source. The length of the mid-rib through the leaf blade was used as an estimate of relative leaf age. The experiment was conducted in 2001 and 2002 with the initial sample size of 45 larvae per year. In 2002, the leaf area consumed over the 48-h period was also recorded by digitally scanning the experimental leaves and estimating area consumed using the public domain NIH Image program (developed at the U.S. National Institutes of Health and available on the Internet at http://rsb.info.nih.gov/nih-image/). These data were recorded because reduced feeding rate may be associated with older leaves, which become tougher with age (J. A. Fordyce, pers. obs.). By removing variation in larval weights due to the rate of larval feeding, age-related changes in the nutritional quality of the leaves can be more accurately examined. Leaf area removed was square-root transformed prior to analysis and all data were log transformed to meet the assumptions of normality. Simple linear and multiple regressions were used to assess the importance of leaf age and feeding rate on larval growth using JMP Version 5 (SAS Institute Inc, Cary, North Carolina).

**The effect of previously established feeding sites**

To examine the effect of previously established feeding sites on larval growth, a paired experiment was conducted where larvae were confined to previously damaged and undamaged portions of the same leaf. Initial damage was inflicted by groups of either two or 12 newly hatched larvae obtained from captive laid eggs confined to one side of the leaf using a clip cage. The portion of the leaf on the other side of the mid-rib received a clip cage containing no larvae. Each treatment was replicated 10 times and larvae were permitted to feed for 24 h after which they were removed from the leaf. A single newly hatched larva was placed in separate clip cages on the damaged and undamaged portion of the leaf and permitted to feed for 48 h and then weighed as a measure of larval growth rate. To determine if growth differed between larvae feeding on previously damaged and undamaged portions of the leaves, a repeated measure ANOVA was used where the within-subjects factor was the undamaged and previously damaged portions of the leaf, and the between-subject factor was the size of the initial group inflicting damage.

**Multiple clutch interactions**

An experiment was conducted to determine if two clutches established on a plant at different times affected each other’s growth rate. Initial feeding groups of two or 12 neonate larvae were established on *A. californica* in the field 5, 3, or 1 days prior to the establishment of a second group. Second groups of two or 12 larvae were placed on the plants with established groups after the appropriate number of days had passed. Additionally, ‘second’ groups of two or 12 individuals were placed on plants that had not received initial feeding groups (see Fig. 1 for a schematic of the experimental design). Two days after the second groups were added to the plant, all larvae were collected and weighed. Previous work on this system has demonstrated that 2 days is a sufficient amount of time to detect the accelerated growth associated with larger feeding aggregations. Larvae were confined to plants using spun-polyester mesh bags. All plants were bagged at the beginning of the experiment to control for possible bag effects on plant quality and the treatment that each plant received was determined randomly. Larvae of the initial and second groups were identified using either blue or red fluorescent powder. The identifying colour used for each group (initials or seconds) in each replicate was determined using a coin toss. In total, the design was replicated five times.

The effect of second groups on initial groups was analysed using a factorial ANOVA with initial and second group size as factors and average weight of initial groups as the response variable. The design of the experiment prohibits including initial group size and second group size for all time periods in a single model due to lack of appropriate control groups (for example, there were no groups that fed for the total of 7 days with no second group added). The number of plants, larvae, and time required for such controls was logistically prohibitive. To assess the effect of second groups on the growth of initial groups, separate ANOVAs were used for each time interval.

The effect of initial groups on the growth of second groups was assessed using the average weight of second groups after

![Fig. 1. Schematic of multiple clutch interaction experiment.](image-url)
2 days of feeding. A factorial ANCOVA using initial group size (zero, two, or 12 larvae), second groups size (two or 12 larvae), and number of days since establishment of the initial group as a covariate was used to determine if group size and days since initial establishment had an effect on the growth of a second group. Statistical analyses were conducted using JMP Version 5 (SAS Institute Inc., Cary, North Carolina).

Results

Clutch size adjustment in response to previously laid clutches

In the years 1999–2001, 526 clutches were observed on A. californica. Average clutch size was 13.06 ± 0.33 (mean ± SE). Thirty-eight of the plants contained multiple clutches (25 had two clutches, 11 had three clutches, two had greater than three). In total, 8.7% of the plants observed with B. philenor eggs present had greater than one clutch. The distribution of the null and observed data was log normal. No indication that females adjust clutch size when conspecific eggs are present was detected based upon the average difference in number of eggs observed compared with the null expectation (P = 0.71). The average difference in clutch size observed when multiple clutches were laid on the same host plant was 8.15 ± 1.36 (mean ± SE), the average difference of the null sample sets was 8.45 ± 0.12 (mean ± SE). The total number of eggs on plant stems that received multiple clutches (mean ± SE: 32.52 ± 2.39) was also not different from the random expectation (P = 0.14), similarly indicating that females do not adjust clutch size when conspecific clutches are present.

Group feeding behaviour and clutch relatedness

There was no indication that groups that consisted of mixed families behaved or foraged differently than groups that consisted of siblings. Sibling groups were equally as likely to separate into smaller groups as mixed family groups (χ² = 0, P = 1.0) (Conover, 1999). Of the 12 replicates, six of the control and six of the mixed-family groups remained feeding as a group after 48 h. All of the initial feeding groups that split into smaller groups remained on the initial leaf. Of the six mixed-family feeding groups that split into smaller groups, two replicates had groups that were equally represented by both families, one replicate had a single larva leave the original group, and the remaining three replicates had groups composed of at least 25% of the minority family. These observations indicate that the gregarious behaviour of larvae is not affected by the relatedness among individuals in the group.

Leaf age on larval growth

Leaf age affected larval growth over a 48-h period. Data from 2001 and 2002 were pooled after an ANCOVA detected no effect of year (F1,71 = 1.22, P = 0.27) or interaction between year and leaf age (F1,71 = 0.002, P = 0.82). Larval growth rate decreased as leaf age increased (Fig. 2a; F1,73 = 11.68, P = 0.001, r² = 0.14). The model including leaf age and leaf area consumed for the 2002 data indicated a significant effect of these factors on larval growth (F2,74 = 56.01, P < 0.001, r² = 0.75). Multiple regression using forward stepwise addition indicated that leaf area consumed explained most of the variation (Fig. 2b; F1,34 = 89.49, P < 0.001) compared with leaf age (F1,34 = 1.89, P = 0.18). This suggests that factors other than leaf nutritional value alone, perhaps leaf toughness, affected larvae confined to older leaves. Leaf area consumed was negatively correlated with leaf age (Pearson product-moment correlation: r = −0.33, P < 0.05).

Previously established feeding sites

Five of the paired replicates had at least one individual die over the course of the experiment. These pairs were...
excluded from analysis, leaving eight and seven pairs of larvae feeding on leaves previously damaged by groups of two or 12 larvae respectively. Larvae feeding on portions of the leaf with previous damage were 15% larger after 48 h of feeding compared with larvae feeding on portions of the same leaf that had not received previous damage \((F_{1,12} = 6.30, \ P = 0.03)\). No effect of the initial group size inflicting the damage was detected \((F_{1,12} = 0.20, \ P = 0.66)\). These results suggest that previously established feeding sites may be beneficial to later arriving larvae.

**Multiple clutch interactions**

The second groups that were introduced to plants with established feeding groups readily joined the feeding aggregation of the initial clutch. The effect of second groups on the growth of initial groups varied, depending upon the time interval between initial group establishment and second group establishment. There was no significant effect of second groups on initial groups established 5 or 3 days prior to their interaction \((F_{3,14} = 0.31, \ P = 0.82\) and \(F_{3,14} = 0.006, \ P = 0.99\) respectively). However, for groups that were established 1 day prior to the addition of the second group, there was an effect of the second group on the average weight of the initial group (Initial group size, \(F_{1,16} = 4.80, \ P = 0.04\); Second group size, \(F_{1,16} = 1.51, \ P = 0.24\); interaction, \(F_{1,16} = 5.31, \ P = 0.03\)). Specifically, initial groups of 12 were not affected by second clutches of either two or 12 larvae; however initial groups of two performed comparatively poorer when a second group of 12 larvae was introduced (Fig. 3).

The performance of the second group measured as average larval weight after 48 h of feeding was affected by group size. Although there was no effect of the initial group size alone on the performance of the second group, there was a significant interaction detected between initial group size and final group size on the performance of the second group (Table 1). Following detection of a significant interaction term, subsequent \(t\)-tests comparing the performance of second groups of two or 12 larvae was conducted for each of the initial group size treatments. These analyses showed that the significant interaction term was largely a consequence of groups of 12 gaining mass at an accelerated rate compared with groups of two larvae in the control groups that did not have previously established larvae. On plants where previous groups had been established, the accelerated rate of growth associated with larger group size was absent, indicating that this benefit of aggregative feeding is absent when previously established groups are present (Fig. 4). There was no effect detected for the number of days between initial groups and second groups. The possibility of an interaction between days since initial feeding group establishment and group size was explored in a separate ANCOVA where interaction terms with group size and days since feeding establishment were included in the model. Plants without initial groups were excluded from this model because of the inherent unbalanced design (i.e. there can be only zero days since initial damage for plants without initial groups). This analysis failed to detect any effect of time between introduction of larvae and group size on the performance of the second group (days and all interactions with days \(P > 0.5\)), supporting the conclusion that the presence of previously established groups negate the benefits of group feeding, regardless of size and time between group establishment.

**Discussion**

Previous studies on *B. philenor* indicate that females of some populations adjust their clutch size in response to the amount of available foliage for their larvae (Pilson & Rausher, 1988; Fordyce & Nice, 2004). Multiple clutches on the same plant stem were recorded on less than 10% of all stems observed in the field, consistent with observations of this and many other species of Lepidoptera that females avoid laying clutches on plants with previously laid eggs.

![Fig. 3.](image-url) The effect of a second group of neonate larvae introduced to feeding groups established 1 day earlier. Weights are of the initially established feeding group after feeding for 3 days total. Open bars indicate second group size of two larvae. Shaded bars indicate second group size of 12 larvae. Asterisk indicates significantly different weights at \(\alpha < 0.05\). Error bars are \(\pm 1\ SE\).

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groups. The number of larvae required for adequate control groups to assess the effect of second groups on the performance of initial groups was unobtainable. Thus, there are two possible interpretations of the effect of second groups on the growth of the first groups. Small, early hatching clutches showed reduced growth when a second larger clutch was introduced. This effect of a second, large clutch may be due to direct interference caused by a large number of larvae joining the feeding site. Alternatively, small initial groups may benefit by the addition of a second small group, but not by the addition of a second large group. Previous experiments have consistently shown that larger groups develop at an accelerated rate compared with small groups (Fordyce, 2003; Fordyce & Nice, 2004). In this study, small initial groups obtained a similar weight as large groups when a second small group was introduced. However, without adequate controls it is not known if the growth rate of the larger groups was compromised by the addition of a second group. Thus, only the relative effect of second group size can be considered; indicating that small groups are adversely affected by the introduction of a large group compared with the effects of a second, small group.

The effect of previously established feeding groups on later arriving groups is more straightforward. As has been established in previous studies, larger groups grew at an accelerated rate compared with small groups (Fordyce, 2003; Fordyce & Nice, 2004). This effect is mediated by group-feeding induced responses of the plant. This benefit of group size, however, was lost when feeding on plants with previously established groups. This is consistent with previous observations of induced resistance following the initial induced suitability caused by aggregative feeding of *B. philenor* (Fordyce, 2003). Thus, there is a plant-mediated negative indirect interaction between clutches where a second large clutch is unable to effectively manipulate host-plant quality by aggregative feeding. Without the benefit of accelerated growth, larger clutches would probably only experience the possible negative consequences of aggregative feeding, such as increased competition for higher quality foliage and increased conspicuousness to natural enemies. Although group defence may operate for aggregations of later instars (Stamp, 1980; Sillén-Tullberg, 1988; Hunter, 2000), various invertebrate predators readily consume first-instar larvae (Fordyce, 2001; Fordyce & Agrawal, 2001).

Although aggregative feeding may function as a defence for toxic Lepidoptera larvae such as *B. philenor*, previous work has indicated that they are not sufficiently defended, chemically or otherwise, until later instars when they begin to disperse into smaller groups (Fordyce, 2001). Thus, for *B. philenor*, fast growth and the consequent reduced period of time larvae spend in vulnerable stages is probably the most important realised benefit of aggregative feeding (Williams, 1999; Fordyce & Shapiro, 2003). The absence of this benefit when other groups are already present might explain why females generally avoid ovipositing on plants with other eggs present. By carefully selecting host plants, females can avoid direct negative interactions, such as

![Fig. 4. Weights of larvae after 2 days of feeding on plants with zero, two, or 12 previously established larvae. Open bars indicate second group size of two larvae. Shaded bars indicate second group size of 12 larvae. Asterisk indicates significantly different weights at $p < 0.05$. Error bars are ± 1 SE.](image-url)
competition, and exploit the plant-mediated benefits of aggregative feeding, namely accelerated growth.

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