Facilitative Effects of Group Feeding on Performance of the Saddleback Caterpillar (Lepidoptera: Limacodidae)

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ABSTRACT Gregarious feeding by insect herbivores is a widely observed, yet poorly understood, behavioral adaptation. Previous research has tested the importance of group feeding for predator deterrence, noting the ubiquity of aposematism among group-feeding insects, but few studies have examined the role of feeding facilitation for aggregates of insect herbivores. We tested the hypothesis that group feeding has facilitative effects on performance of the saddleback caterpillar, *Acharia stimulea* Clemens, a generalist herbivore of deciduous trees. In an understory forest setting, we reared caterpillars alone or in groups on two different host plants, white oak (*Quercus alba* L.) and American beech (*Fagus grandifolia* Ehrlich), and recorded multiple measures of insect performance during regular field censuses. As predicted, *A. stimulea* caterpillars feeding in groups on white oak had increased relative growth rates compared with caterpillars feeding alone, and the magnitude of this facilitative effect varied among censuses, conferring benefits both early and late in development. By contrast, no facilitative effects of group feeding were detected on beech, suggesting that the benefits of facilitative feeding may be host specific. On both hosts, caterpillar development time was slightly faster for group-feeding cohorts compared with their solitary counterparts. Because early instar caterpillars are particularly vulnerable to predation and parasitism, even modest increases in growth rates and reductions in development time may decrease exposure time to enemies during these vulnerable stages. On both hosts, group feeding also reduced the trade-off between individual development time and cocoon mass, suggesting that feeding efficiency is improved in group feeders relative to solitary caterpillars.

KEY WORDS facilitation, gregarious, group feeding, Limacodidae, plant–insect interaction

Gregariousness is a widespread phenomenon among insect herbivores, and is commonly observed in treehoppers, aphids, sawflies, and caterpillars (Costa and Pierce 1997). Benefits of gregariousness typically manifest as increases in insect survival, growth rates, and body size (Stamp 1980, Hunter 2000). Within insects, gregarious feeding behavior is believed to have evolved many times as an adaptation to a wide variety of selective pressures (Bowers 1992, Costa and Pierce 1997), including repellant defense against predators (Fitzgerald 1993, Costa 1997, Hunter 2000, Allen 2010), dilution of predation risk (Hunter 2000), increased feeding efficiency via managing or overcoming host plant defenses (Young and Moffett 1979, Tsubaki and Shiotsu 1982, Clark and Faeth 1997, Fordyce and Agrawal 2001), microclimate control (Porter 1982, Bowers 1992, Klok and Chown 1999), and enhancement of aposematic signaling (Sillen-Tullberg

and Bryant 1983). For example, in the saturniid caterpillar, *Hemileuca oliviae* Cockerell, aggregative feeding is thought to discourage predator attacks by exaggerating the appearance of urticating spines (Capinera 1980). When basking in the sun, caterpillars in groups are better able to retain heat due to their proximity to one another, as well as the convective recycling of heat emanating from one individual to its neighbors (Porter 1982, Benrey and Denno 1997). A group's control over the extent of its aggregation and the individual proximity of its members facilitates thermoregulation, which can reduce water loss and thus increase growth rate (Bowers 1992, Klok and Chown 1999). A variety of other largely anecdotal benefits to aggregation exist, such as vibrational communication to track conspecifics (Cocroft 2001) or to warn each other of nearby predators (Yack et al. 2001). In addition to gregariousness as a behavioral adaptation, it may also arise as a secondary outcome of egg-clustering, which is thought to increase fecundity in insects facing a high likelihood of mortality from predation and adverse environments (Stamp 1980, Courtney 1984, Faraji et al. 2002).

The prevalence of group feeding generally decreases as insects mature, and in the case of caterpil-

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lars, later instars often mark distinct shifts in sociality (Inouye and Johnson 2005, Grant 2007). For example, both the eastern and western tent caterpillars (*Malacosoma americanum* F. and *Malacosoma disstria* Hübner, respectively) are highly social until they reach the ultimate instar, when caterpillars suddenly abandon their tents and leave the group (and often the host plant) to complete development and locate pupation sites (Fitzgerald 1995). In the gregarious caterpillar *Doratifera casta* Scott (Limacodidae), caterpillars feed in groups of several 100 individuals for the first several instars, after which group size decreases gradually until individuals reach the sixth and seventh instars, during which they mainly feed alone (Reader and Hochuli 2003). These ontogenetic shifts from gregarious to solitary behavior may be influenced by a variety of factors, including a shift in the balance of costs and benefits of gregariousness (Reader and Hochuli 2003), an avoidance response to pathogens (Hochberg 1991), avoidance of food limitation, or the restricted proximity of adjacent caterpillars due to defensive armature, such as urticating spines (Capinera 1980).

Although the anti-predator and thermoregulatory benefits of group feeding have been well established, the direct, facilitative effects of group feeding on consumption and growth rates have received considerably less attention. Group feeding ideally enables herbivores to limit consumption of induced allelochemicals by quickly consuming an area of foliage before allelochemicals can be induced in damaged leaves (Krischik et al. 1991). Alternatively, group feeding may permit insects to overcome physical plant defenses such as trichomes and leaf toughness, which are effective deterrents for solitary insects (Young and Moffett 1979). Finally, group feeding may simply permit gregarious insects to increase consumption rates (Tsubaki and Shiotsu 1982, Rhoades 1985, Benrey and Denno 1997, Fordyce 2003).

In this study, we designed an experiment to explicitly test for facilitative effects of group feeding in the saddleback caterpillar, *Acharia stimulea* Clemens (Lepidoptera: Limacodidae). *A. stimulea* caterpillars are well-known throughout the eastern United States for their vivid coloring (Fig. 1A) and intensely urticating spines, which are an effective defense against an array of predators (Murphy et al. 2010). Early instars typically forage in sibling groups (Fig. 1B), but whether group feeding benefits them through facilitative bottom-up effects is unknown. We recorded multiple measures of performance for *A. stimulea* caterpillars foraging alone or in groups inside of predator exclosures on two different host plants, which allowed us to assess the direct benefits of group feeding in the absence of enemies.

Materials and Methods

Study System. *A. stimulea*, commonly known as the saddleback caterpillar, is a temperate species of slug caterpillar (Lepidoptera: Limacodidae) that has an aposematic, fluorescent green, saddle-shaped pattern
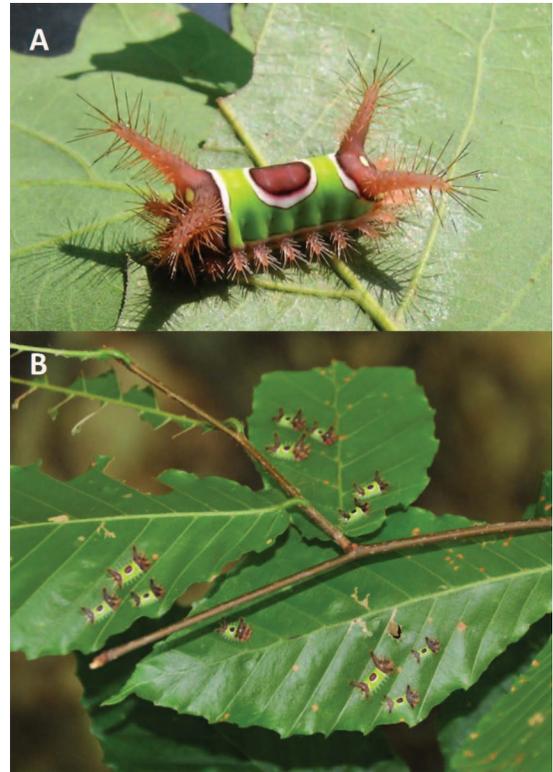
Fig. 1. The saddleback caterpillar, *Acharia stimulea* (Limacodidae). (A) A late-instar caterpillar with typical color patterning and stinging spines. (B) Early instar *A. stimulea* caterpillars feeding in a group, with their previous feeding damage visible in the upper left corner. Photo credits: John Lill and Doug McCaskill.

on its dorsum and protruding tubercles containing numerous urticating spines (Fig. 1; Dyar 1899, Epstein 1996, Murphy et al. 2010). These caterpillars can be found throughout eastern deciduous forests from Massachusetts to Florida and west to Missouri (Covell 1984). Adult moths fly in July and August, and caterpillars are generally found in the late summer (Wagner 2005, Murphy et al. 2011). Final-instar caterpillars form a cocoon of calcium oxalate coated with urticating deciduous spines (Epstein 1996, Murphy et al. 2010).

Like most species of Limacodidae, the caterpillars are polyphagous, and have been found feeding on a wide assortment of mostly woody host plants (Wagner 2005, Lill 2008, Murphy et al. 2011). In the vicinity of our study site, common hosts include oak (*Quercus* spp.), hickory (*Carya* spp.), American beech (*Fagus grandifolia* Ehrlich), pawpaw (*Asimina triloba* L.), spicebush (*Lindera benzoin* L.), black locust (*Robinia pseudoacacia* L.), and Eastern redbud (*Cercis canadensis* L.). *A. stimulea* caterpillars are classified as presocial, having an intermediate level of sociality between solitary insects, like the praying mantis, and eusocial insects, like ants and vespid wasps (Fitzgerald and Peterson 1988, Costa 1997).

Our experiment took place at the Little Bennett Regional Park in northern Montgomery County, MD. This 1,500-ha park is located in the Piedmont plateau east of the Blue Ridge Mountains and consists of a mix of upland hardwood forest and managed grasslands. The second growth forest contains a mixed canopy of oaks, hickories, maples (*Acer* spp.), walnut (*Juglans nigra* L.), and tulip poplar (*Liriodendron tulipifera* L.), and an understory of saplings of the canopy species as well as flowering dogwood (*Cornus florida* L.), ironwood (*Carpinus caroliniana* Walter), black gum (*Nyssa sylvatica* Marshall), sassafras (*Sassafras albidum* [Nutt.] Nees), viburnum (*Viburnum* spp.), and black cherry (*Prunus serotina* Ehrlich).

Experimental Design. Our objective was to determine whether in the absence of predators, group feeding facilitated growth and survival of saddleback caterpillars on each of two host plants: white oak (*Quercus alba*) and American beech (*Fagus grandifolia*). To assess caterpillar performance, the growth rate, survival, development time, and cocoon mass were recorded for caterpillars placed in mesh exclosure bags in each of three densities: 1, 7, and 14 caterpillars per bag (the first density was the "solitary" treatment and the latter two densities were our "group" treatments). We chose a group size of seven individuals as a "typical" group size, based on the mean number of eggs laid per cluster in *A. stimulea* (range, 1–85 eggs per cluster; Murphy et al. 2011). The larger group size of 14 was chosen based on our estimate of how many caterpillars could reasonably be contained in exclosures.

Experimental *A. stimulea* caterpillars originated from a laboratory colony that we established using a mix of locally caught caterpillars and adult moths, and experimental caterpillars were derived from 20 different female lineages that hatched between 25 and 28 June 2008. White oak and beech are known to differ in host plant quality for *A. stimulea* caterpillars (S. M. M. and J. T. L., unpublished data), so we initially reared all caterpillars on the same high-quality host plant, Eastern redbud (*Cercis canadensis:* Fabaceae), to minimize differences in caterpillar body size at the start of the experiment. One week before beginning the field experiment, 500 early instar *A. stimulea* caterpillars that had been reared since hatching on redbud were transferred to either white oak or beech leaves (*n* = 250 on each) to allow them time to habituate to their assigned host plants.

Eight large trees (four white oak and four beech) located across a single hillside at the field site were haphazardly chosen for use in the experiment. On 17 July 2008, caterpillars were placed onto foliage in green zippered 20- by 40-cm fine-mesh insect-rearing sleeves (BioQuip, Rancho Dominguez, CA; referred to as "exclosure bags" hereafter) so that larvae could be relocated, larval groups would remain associated, and predators would be excluded. Exclosure bags were tied onto one of the lower branches of each of the eight trees after removing resident arthropods. Each of the eight trees contained 11 exclosure bags; seven bags with one individual ("solitary"), two bags

with seven individuals ("small group"), and two bags with 14 individuals ("large group"). This resulted in 7 solitary and 42 group caterpillars on each of the eight trees, totaling to 392 caterpillars. Solitary caterpillars within the same tree, as well as group caterpillars within the same exclosure bag, shared the same hatch date. To homogenize potential genetic (i.e., family) effects, each of the eight trees included offspring from no fewer than five females, and a minimum of three different females contributed to each group of multiple caterpillars, as well as each tree's suite of solitary individuals.

The status (alive/dead/missing) and size of each caterpillar were recorded weekly. Missing caterpillars were assumed to be dead. Body length of each caterpillar (to the nearest 0.1 mm) was measured with dial calipers on the first day of field exposure and weekly thereafter for 5 wk, for six censuses in total over a span of 36 d (17 July–21 August). We used body length rather than head capsule width because it is not possible to measure head capsule widths in Limacodidae and standard curves relating body length to mass for *A. stimulea* have been generated previously (Murphy et al. 2011). Bags and caterpillars were transferred to fresh branches as needed (weekly and more often as caterpillars grew larger) to avoid food limitation in the largest group sizes; when bags had to be moved for one treatment, bags from all treatments were moved to equalize handling time of larvae. At each census, we also noted whether any of the caterpillars in the multiple-caterpillar exclosure bags were actively feeding together (i.e., clustered, feeding in proximity on the same leaf).

Five days following the final field census, when the most rapidly developing caterpillars were nearing pupation, all caterpillars were harvested and returned to the laboratory, keeping track of the tree, treatment, and bag they came from. Once in the laboratory, caterpillars were reared individually in 0.5-liter deli containers to complete their development. The containers were provisioned with a moistened filter paper disc and fresh excised leaves of their assigned host plant species collected from the field site. The date that each individual formed a cocoon was recorded and cocoons were weighed to the nearest 0.01 mg with a microbalance within 30 d of cocoon formation. Cocoons were overwintered in environmental chambers and their emergence success and sex were recorded the following spring.

Data Analysis. All statistical analyses were conducted using SAS 9.1 or JMP Pro 9 (SAS Institute Inc., Cary, NC). In preliminary analyses, there were no differences between the small- and large-group treatments ($N = 7$ or 14 per bag), so we combined these two treatments into a single category (group feeding) for final analyses. To test whether the initial size of caterpillars in the density treatments was similar, we conducted *t*-tests on initial lengths of caterpillars in the two treatments (solitary vs. group) on each host plant separately. To obtain measurements of relative growth rate (RGR, hereafter), we converted field measures of caterpillar body size (body length in mm)

to biomass (mg) using a standard curve developed for *A. stimulea* reared on each host plant, as described in Murphy et al. (2011): white oak: $\log_{10}(\text{mass}) = \log_{10}(\text{length}) \times 3.133 - 1.400$; beech: $\log_{10}(\text{mass}) = \log_{10}(\text{length}) \times 3.245 - 1.568$. The RGR of each solitary caterpillar was then estimated as: $\text{RGR} = (\ln[\text{mass}_{t+1}] - \ln[\text{mass}_t])/(t_2 - t_1)$. For caterpillar groups (density of 7 or 14), the RGRs of individuals could not be calculated due to our inability to track individuals across censuses; instead, we calculated the RGR for each group using the mean mass/bag/census, which also avoided problems with nonindependence of caterpillars within bags. In sum, all analyses were conducted using the "bag" as the unit of replication. Density effects on RGR were analyzed using PROC Mixed (Littell et al. 1996) with tree as a random block effect and density (solitary or group) and census as fixed effects; the two host plants were tested separately. The REML option was used to estimate random effects and compound symmetry was used in structuring the covariance matrix (Littell et al. 1996).

To test for relative differences in caterpillar performance between density treatments within each tree, we conducted paired *t*-tests comparing the mean values for the response variables cocoon mass and development time (days from egg hatch to cocoon formation), for each density treatment (averaged across bags) on each tree (N = eight pairs). Preliminary analyses showed that responses differed between host plants, but there was no evidence of host plant × density treatment interactions for either variable, allowing us to examine the *relative* differences in performance for the combined set of eight trees. In addition, we examined the relationship between individual development time and cocoon mass using linear regression and used *t*-tests to compare the regression coefficients between density treatments for each host plant (Zar 1999). Survival of caterpillars in each density treatment during the field portion of the experiment was compared using the Yates' corrected χ^2 test (Zar 1999).

To test for potential effects of unequal sex ratios among treatments, we conducted two-sample *t*-tests to compare the cocoon mass, and development times of solitary vs. group feeding caterpillars separately by sex for the subset of individuals in each treatment group that survived to cocoon formation and emerged as moths the following spring (white oak: solitary = 71% of original experimental caterpillars, group = 63%; beech: solitary = 68%, group = 57%).

Results

Overall, field survival of the bagged caterpillars (through Census 6) was high (96% vs. 89% for solitary and gregarious caterpillars, respectively) but did not differ among the two density treatments on either host (white oak: Yates' corrected $\chi^2 = 0.68$, $P = 0.41$; beech: Yates' corrected $\chi^2 = 0.70$, $P = 0.40$; Fig. 2). Caterpillars never entirely consumed the food in their bags, but there were two or three instances when caterpil-
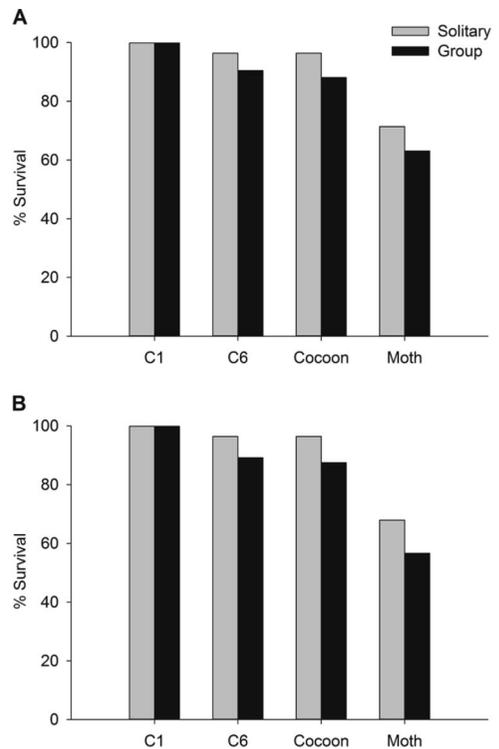
Fig. 2. Percent survival of *A. stimulea* experimental caterpillars in both density treatments, solitary (one individual per exclosure bag) and group (seven or 14 individuals per exclosure bag), on two host plants, (A) white oak and (B) American beech, at four time points: the first day of the field experiment (Census 1 [C1]), the last day of the field experiment (Census 6 [C6]), after cocoon formation in the laboratory (Cocoon), and after moth emergence the following spring (Moth).

lars feeding in the largest group size (14 caterpillars per exclosure bag) may have experienced short-term food limitation before moving them to a fresh branch. We note, however, that any incidental food limitation would tend to bias against detecting feeding facilitation, making our results conservative. We observed evidence of active group-feeding in the exclosure bags during 73% of the white oak censuses and 59% of the beech censuses.

Initial Lengths of Experimental Caterpillars. The initial lengths of caterpillars in the two density treatments (solitary and group) did not differ (white oak: $t_{188} = 0.77$, $P = 0.44$; beech: $t_{189} = 0.82$, $P = 0.41$). However, initial sizes of caterpillars did differ among host plants; on average, caterpillars reared on white oak for 1 wk before field placement measured 0.4 mm, or 10% greater body length than caterpillars reared on beech ($t_{379} = 4.76$, $P < 0.0001$).

Density Effects on RGRs. The RGR of *A. stimulea* caterpillars feeding on both host plants varied over the course of development (census effect on white oak: $F_{4, 202} = 63.53$, $P < 0.0001$; beech: $F_{4, 202} = 24.43$, $P < 0.0001$; Fig. 3). On white oak, the average RGR for cohorts of caterpillars feeding in groups was higher
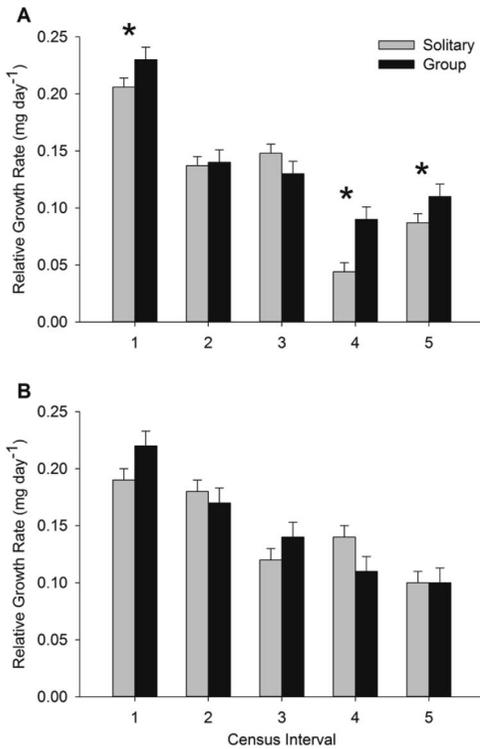
Fig. 3. Relative growth rate (LSM + 1 SE; mg × day^{-1}) of *A. stimulea* caterpillars in solitary (one caterpillar per exclosure bag) and group (7 or 14 caterpillars per exclosure bag) treatments on (**A**) white oak and (**B**) American beech over the course of five intercensus intervals in the field. Asterisks denote censuses where treatment differences were significant according to post hoc tests (Tukey's honestly significant difference tests).

than for caterpillars feeding alone ($F_{1, 202} = 14.81$, $P = 0.0002$), but the magnitude of this effect varied among censuses (census × density interaction: $F_{4, 202} = 2.85$, $P = 0.025$), appearing both early and late in development (Fig. 3A). In contrast to caterpillars feeding on white oak, group feeding did not influence RGR for caterpillars feeding on beech (density: $F_{1, 202} = 0.48$, $P = 0.49$; census × density: $F_{4, 202} = 1.65$, $P = 0.162$) (Fig. 3B).

Density Effects on Cocoon Mass. Within a tree, the cocoon mass obtained by caterpillars reared in groups vs. alone did not differ (paired *t*-test: $t_7 = 0.50$, $P = 0.63$). However, the mean cocoon mass obtained by caterpillars reared on white oak was 20% greater than those reared on beech (across density treatments; $t_{14} = 3.59$, $P = 0.003$). Female cocoons were significantly heavier than male cocoons on both host plants (48 and 38% heavier on white oak and beech, respectively). When examined separately by sex, cocoon mass comparisons between solitary and group treatments (averaged within trees) did not differ on white oak (female: paired $t_7 = 1.18$, $P = 0.33$; male: $t_7 = 0.87$, $P = 0.44$) or on beech (female: $t_7 = 0.33$, $P = 0.76$; male: $t_7 = 0.56$, $P = 0.61$).

Density Effects on Caterpillar Development Time. All caterpillars experienced 41 d of field exposure, which was, on average, 54% of their total development time (the remainder of their development occurred in the laboratory, both before and following the field experiment). Development time was reduced by ≈2 d for group-feeding compared with solitary caterpillars (one-tailed paired $t_7 = 2.25$, $P = 0.03$), which represents a modest (3%) reduction for these slow-developing caterpillars. The mean caterpillar development time of females was significantly longer than that of males on both white oak ($t_{112} = 4.50$, $P < 0.0001$) and beech ($t_{110} = 3.91$, $P \leq 0.0001$). Development time and cocoon mass were positively correlated for caterpillars on both host plants (white oak, solitary: $r^2 = 0.33$, df = 27, $P = 0.0017$; white oak, group: $r^2 = 0.18$, df = 138, $P < 0.0001$; beech, solitary: $r^2 = 0.27$, df = 26, $P = 0.0061$ [outlier excluded from regression]; beech, group: $r^2 = 0.16$, df = 147, $P < 0.0001$; Fig. 4A–D). In comparing the slopes of the relationship between development time and cocoon mass between density treatments, we found that for both white oak and beech, the slope of the relationship (β) was reduced for the group-feeding caterpillars compared with solitary caterpillars ($\beta \pm 1$ SE for white oak, group = 11.12 ± 2.06; white oak, solitary = 20.41 ± 5.80; beech, group = 6.46 ± 1.22; beech, solitary = 10.10 ± 3.36; Fig. 4A–D). While *t*-tests comparing the slopes between density treatments were not statistically different, there was a strong trend (white oak: $t_{161} = 1.35$, $P = 0.09$; beech: $t_{169} = 1.13$, $P = 0.13$).

Discussion

We found that *A. stimulea* caterpillars feeding in groups had increased RGRs compared with those feeding alone on white oak, which supports the hypothesis that in at least certain ecological contexts, group feeding can facilitate individual growth. However, the benefits of group feeding varied over the course of development, as indicated by the significant treatment × census interaction on white oak, with benefits accruing both early and, somewhat surprisingly, later in development.

Many species of gregarious caterpillars feed in groups earlier in their development and their behavior often becomes more solitary as they near pupation (Hochberg 1991, Reader and Hochuli 2003, Inouye and Johnson 2005, Grant 2007). When adjusted for body size, RGRs and foliar consumption are typically highest in early instars and decline as insects grow, as was seen here on both host plants. Very early in development, *A. stimulea* caterpillars (and Limacodidae more generally) feed by skeletonizing foliage, scraping small epidermal patches with their mandibles (Epstein 1996). It is generally thought that such feeding behaviors in neonate caterpillars result from an inability to generate sufficient mandibular force to chew through leaf veins and/or cuticles and may promote higher rates of assimilation due to the greater selectivity of tissues (i.e., consuming less fiber; Godfrey et al. 1989, Hochuli 2001). However, around the third
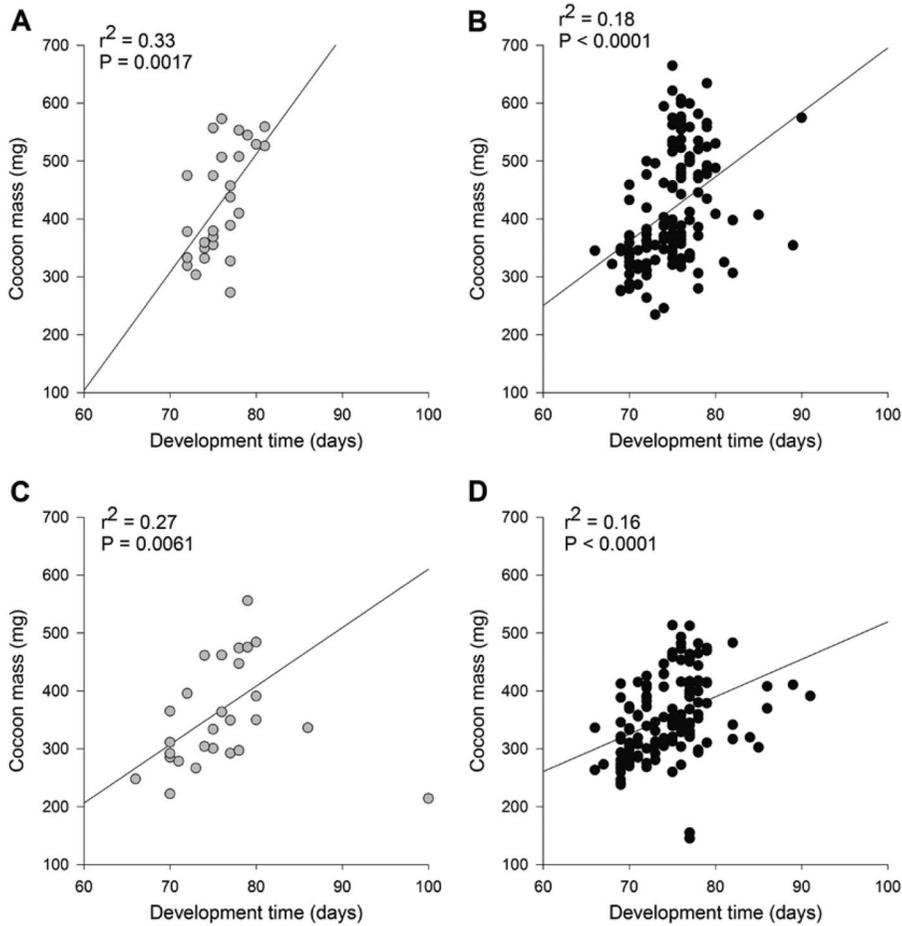
Fig. 4. Regression of caterpillar development time vs. cocoon mass (mg) of individual *A. stimulea* caterpillars in the (A) white oak solitary treatment, (B) white oak group treatment, (C) American beech solitary treatment, and (D) American beech group treatment. The outlier in "C" was excluded from the regression (development time 100 d). Note the reduced slopes of the regression in the group treatments relative to the solitary treatments.

instar, *A. stimulea* caterpillars begin group "edge-feeding," and have been observed to spin silken pads on the leaf surfaces, which likely aid in adhesion. The caterpillars used in this experiment were all in the edge-feeding stage by the time they were placed in the field, and it may have been easier for those in groups to overcome the physical barriers of these relatively tough, late-season oak and beech leaves. Our finding of significant facilitative effects of group feeding on white oak but not beech may in part reflect differences in physical characteristics of the foliage; on average, beech foliage is tougher, has more fiber, and has less water content than white oak (Ricklefs and Matthew 1982), making it a low-quality host, which is reflected in reduced performance measures of *A. stimulea.* Group feeding may also be inhibited in some way on beech, perhaps due to the smaller leaf size and biomass compared with white oak, and was reflected in the lower incidence of observed group feeding on beech vs. white oak (59 vs. 73% of censuses).

Density treatment effects on RGR later in the development of *A. stimulea* are somewhat more difficult to explain. If anything, larger instars of *A. stimulea* might be expected to have decreased RGR in groups due to possible food limitation inside the exclosure bags. However, we have observed wild late-instar caterpillars feeding gregariously, which suggests that aggregation late in development is likely to be beneficial for *A. stimulea* in nature. One possible explanation is that group feeding may generate a nutritional sink, resulting in increased plant quality (Karban and Agrawal 2002). This may be especially important for late instars that feed late in the season, when plant quality is declining. In addition to bottom-up facilitative effects, group feeding may serve to deter predation by amplifying the aposematic signal of these bright, spiny caterpillars.

Gregarious feeding may also facilitate faster consumption, often of more nutritious tissue. For instance, aggregation might enable caterpillars to feed on highly nutritious and thus highly protected apical portions of leaf tissue (Fordyce and Agrawal 2001, Fordyce 2003). The removal or consumption of trichomes, or other defensive structures, can increase

the speed of locomotion (Young and Moffett 1979, Fordyce and Agrawal 2001). An increase in the speed of locomotion may increase total consumption, thereby increasing growth rate and reducing development time, with possible indirect effects on survival when exposed to natural enemies.

After just 1 wk of feeding on the two host plants before field exposure, caterpillars fed on white oak were significantly larger than those fed on beech, most likely due to the nutritional advantage of white oak leaves. However, because there were no differences in mean initial size for caterpillars in the two density treatments within a host plant, differences in RGR detected in the field represented real treatment effects. White oak has higher foliar nitrogen content than beech (2.32 vs. 2.16%) and slightly higher water content (59 vs. 57%; J. T. L. and S. M. M., unpublished data). This superior nutrition resulted in larger cocoon masses for caterpillars developing on white oak compared with beech, but was not evident in either growth rates or total development time.

In addition to overcoming physical defenses, group feeding of caterpillars can also enhance its members' nutritional intake by preventing or limiting the ingestion of harmful host plant allelochemicals. Because the sheer number of caterpillars in a group causes the group to progress rapidly across leaf tissue while feeding as compared with the speed of a solitary caterpillar's feeding, groups can consume tissue before induced defensive allelochemicals reach the area (Rhoades 1985, Tallamy and Raupp 1991, Fordyce 2003). Under this scenario, group feeding enables caterpillars to escape consumption of allelochemicals induced by their herbivory, thus reducing their negative effects, while still exploiting the maximum amount of host plant tissue (Tsubaki and Shiotsu 1982). Benrey and Denno's (1997) study supports the idea of allelochemical avoidance because they found a lack of nutritional benefit for laboratory-reared groups of caterpillars fed on leaves detached from trees before feeding. However, this type of rapid allelochemical induction has not been described for plants in the family Fagaceae, for example, white oak and beech, both of which mainly contain high-molecular-weight phenolics characterized by slow turnover (Coley et al. 1985), so are not likely to explain the facilitation observed in this study.

The facilitative effects of gregarious feeding were also seen in the shorter caterpillar development time for group vs. solitary caterpillars. This shorter time spent in the caterpillar stage can increase an individual's fitness by decreasing the amount of time it is exposed to predation and/or parasitism (Zalucki et al. 2002). Yet, there is an ecological trade-off between short development time (days spent as a caterpillar) and cocoon mass. Although short development times may be advantageous in the field for avoiding natural enemies, heavier cocoons are known to be advantageous for *A. stimulea* overwintering survival (Murphy and Lill 2010) and result in higher lifetime fecundity for *A. stimulea* females (Murphy et al. 2011). To grow larger and achieve these longer-term benefits, cater-

pillars need more time to consume the necessary nutrition, which may place them at greater risk in the short-term. We found that cocoon mass and development time are positively correlated, yet *A. stimulea* caterpillars feeding in groups enjoy a slightly shorter development time, and thus a likely reduction in predation risk, while suffering less of a reduction in cocoon mass, as evidenced by the trend of reduced slopes of development time vs. cocoon mass for caterpillars in the group vs. solitary treatments. Facilitative effects of this type may be subtle and likely require large field experiments to uncover.

Our study on the gregarious feeding behavior of *A. stimulea* demonstrates that there is moderate evidence to support the hypothesis that feeding in groups enhances caterpillar fitness by increasing growth rates and reducing development time, which may indirectly affect fitness by reducing exposure to natural enemies. Because placing caterpillars together in exclosure bags does not ensure that all individuals feed gregariously (although many certainly did in this experiment), the facilitative benefits of group feeding observed here are likely to be underestimates because not all caterpillars in the group-feeding treatment fed gregariously for the entire experiment. Future experiments that examine the benefits of group feeding in *A. stimulea* in both the presence and absence of enemies are needed for a more complete understanding of this behavioral phenomenon.

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