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LARVAL AGGREGATION AFFECTS FEEDING RATE IN CHLOSYNE POECILE (LEPIDOPTERA: NYMPHALIDAE)

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ABSTRACT

Larvae of *Chlosyne poecile* (Felder) (Lepidoptera: Nymphalidae: Melitaeini) on *Razisea* sp. (Acanthaceae) feed in large aggregations as early instars but disperse and feed in small groups or as solitary caterpillars in later instars. The effect of group size on per capita feeding rate was tested by manipulating the number of larvae on a leaf and measuring the leaf area eaten in short-term feeding trials. Feeding rate increased significantly with group size for first instars but decreased with group size for all larger instars. Although feeding rate decreased significantly with group size for second instars, second instars in the field were usually found in large groups and did not begin to disperse until the third instar. Variance-to-mean ratios indicate that larval aggregation was lower in later instars, slowly approaching a random distribution. The distributions of larger instars may therefore be the result of random dispersal to food and not the active avoidance of other larvae. If the observed lag between the predicted optimal time to disperse and the observed pattern is adaptive, then it may be due to unmeasured benefits of aggregation, such as lower predation rates and unmeasured costs of dispersal. Egg clustering and aggregation of larvae may be more common for butterflies in the Neotropics than in other areas.

Key Words: caterpillars, feeding facilitation, group defense, Costa Rica, Neotropical Lepidoptera

RESUMEN

Las larvas de *Chlosyne poecile* (Lepidoptera: Nymphalidae) comen hojas se *Razisea* sp. (Acanthaceae). Durante sus primeros estadios se formen agregados grandes, pero se dispersan y alimentan en grupos pequeños o solitariamente en los ultimos estadios. El efecto del tamaño de las agregaciones en las tasas de alimentación per capita fue puesto a prueba manipulando el número de larvas por hoja y metiendo el área de la hoja que a sido comida. La tasa de alimentación aumentó significativamente junto con el numero de individuos presentes en la hoja para el primer estadio, pero disminuyó en relación al tamaño del grupo para todo los demás estadios. Aunque la tasa de alimentación disminuyó significativamente con tamaño del grupo para las larvas del segundo estadio, estas larvas usualmente se encuentaron en grandes grupos en el campo, y su dispersión ocurrió solo en el tercer estadio. Las tazas promedio de varaza indicante que la agregación larval fue menor en los últimos estadios, aproximándose lentamente a una distribución tipo Poisson. Esto sugiere que las distribuciones de los estadios más grandes son el resultado de la dispersión al azar hacia el alimento y no un meanismo activo para evitar a otras larvas. Se propone que el retraso en la predicción del tiempo óptimo para la dispersión y el patron observado es debido de beneficio obtenidos al agregarse que no he sido cuantificado, como una reducción en las tasas de depredación y costos de dispersión. Las agregaciones de larvas y huevos de mariposas pueden ser mas frecuentes en el Neotropico que en otras áreas.

Translation provided by Authors.

Although most Lepidoptera lay single eggs and develop as solitary larvae, 5% to 15% of butterfly species are reported to lay eggs in large clusters and have larvae that feed gregariously during early instars (Stamp 1980). This life history has arisen independently in many different lineages but, it is especially common among the Nymphalidae and is common for species in the genus *Chlosyne* (e.g., Scott 1986; DeVries 1987; Clark & Faeth 1997; Denno & Benrey 1997). Proposed selective advantages of larval aggregation include increased feeding efficiency (Clark & Faeth 1997; Denno & Benrey 1997), enhanced group defense against predators (Stamp 1980; Chew & Robbins 1984; Vulinec 1990), and improved thermoregulation (Tsubaki 1981; Stamp & Bowers 1990; Casey 1993; Bryant et al. 2000). Selective pressures may lead females to oviposit in large clutches (Stamp 1980; Courtney 1984; Heard & Remer 1997), causing at least the first instars to be aggregated by default until they disperse to feed individually.

Aggregation may increase feeding efficiency by allowing early instars to overcome leaf toughness by a "group attack" in one spot (Ghent 1960), by

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overwhelming plant defenses (Storer et al. 1997), or by laying down an architecture of silk that aids the larvae in feeding (Rathcke & Poole 1975; Fitzgerald 1995). Higher larval feeding rate can reduce development time, potentially both raising intrinsic rate of increase and decreasing the duration of larval exposure to parasitoids and abiotic mortality sources (Clancy & Price 1987; Benrey & Denno 1997). Higher larval feeding rates also can result in larger adults, a characteristic that is positively correlated with fecundity in many insects (e.g., Juliano 1998).

Aggregating caterpillars often exhibit aposematic coloration and distastefulness (Sillén-Tullberg & Leimar 1988; Vulinec, 1990). Aggregation may therefore enhance the effects of caterpillar defenses because predators learn to avoid larvae after eating a few distasteful individuals (Sillén-Tullberg & Leimar 1988). Alternatively, the advantage of aggregation may be not to the larvae but to the ovipositing female or the eggs. Fresh females in the genus *Chlosyne* are often so heavy with eggs that they can barely fly (DeVries 1987), so the female may need to unload the eggs quickly because of energetic costs of carrying so much weight in flight or higher predation risk due to reduced evasion ability. Moreover, "dumping" eggs quickly may be advantageous to the female, especially when adult mortality risk is high, even if it lowers the average fecundity of the offspring (Courtney 1984). Egg clusters may also suffer a lower intensity of parasitoid attack than solitary eggs (Morrison & Strong 1981).

Many species with gregarious larvae, and most if not all in the genus *Chlosyne*, only feed in large groups as early instars, becoming increasingly solitary through later instars (Clark & Faeth 1997; Benrey & Denno 1997). Several hypotheses, which are not mutually exclusive, can explain this across-instar decrease in aggregation. If larvae are initially aggregated for increased feeding efficiency, these benefits may disappear in later instars as the larvae increase in size and are able to penetrate the leaf cuticle and/or overwhelm plant defenses without assistance. Moreover, effects of competition for leaf area may be greater in larger larvae and thus depress the feeding efficiency of groups. Group advantages for defense against predators may diminish in later instars if larger larvae are exposed to fewer potential predators or if later instars have more effective defense mechanisms (Stamp 1986). For example, later instars may have sequestered defensive compounds that were unavailable earlier, the aposematic coloration of individuals may be more visible, or larger larvae may deliver a more potent dosage of defensive compounds. If larvae were initially aggregated only because of advantages to the ovipositing female or the eggs, then larvae could be less aggregated as later instars merely because of random dispersal patterns.

Our objective was to characterize the effect of group size on the short-term larval feeding rate for different instars of *Chlosyne poecile* (Felder). This species is locally abundant in northwestern Costa Rica, where it feeds on shrubs in the family Acanthaceae in second-growth habitats and in light gaps. We hypothesize that any benefit to feeding in larger groups will be largest for the first instar and decrease for later instars, perhaps even becoming a cost of group feeding in the later instars. Finally, a review of the natural history of Costa Rican Lepidoptera suggests that aggregative behaviors (egg clustering and gregarious feeding) are more common in the Neotropics than in other regions of the world. Whether the difference is caused by differences in selective pressures among the regions deserves further research.

METHODS

Study System

Chlosyne poecile is found from Costa Rica to Venezuela (DeVries 1987). In Costa Rica it is locally abundant from sea level to 900 m on the Pacific slope in dry forest and semideciduous forest. Casual observations by the authors in multiple years suggest that *C. poecile* is abundant during the rainy season and rare or absent in the dry season, a pattern typical for this genus in the Neotropics (DeVries 1987). DeVries (1987) reports the eggs, larval stages, and host plants for *C. poecile* as unknown. We observed females ovipositing on, and larvae of all instars feeding on, a woody shrub in the family Acanthaceae, which we identified to the genus *Razisea* on the basis of vegetative characters. All egg clusters we found were on the undersides of leaves near the top of the plant. Newly laid eggs were yellow and turned tan and then brown shortly before hatching on their fifth day.

The study was conducted in the forest immediately adjacent to the Estación Biológica San Miguel (EBSM) within Cabo Blanco National Park, Puntarenas Province, Costa Rica. The maritime forest around EBSM is mostly 35-year-old second growth (C. Castrillo, pers. comm.). *Razisea* sp. grows commonly in the understory near EBSM, especially along trails and at the edges of gaps. Caterpillars of *C. poecile* were extremely abundant on the *Razisea* sp. shrubs growing near the station. *Razisea* sp. and *C. poecile* caterpillars also were found less abundantly at the edges of light gaps along streams near EBSM at 50–100 m elevation. All of the plants and larvae in the censuses and experiments were located along the "beach trail" at the EBSM. The experiments described below were initiated during the Organization for Tropical Studies course 2000-3 and were conducted from 16 to 22 July 2000.

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Larval Group Size and Aggregation

We used two types of censuses to quantify larval aggregation. In the first census we searched for *C. poecil*e larvae and recorded the instar and number of larvae in a group. These data were used to estimate the average group-size for each instar and revealed the instar at which larvae switched to feeding individually. In the second census we searched every leaf of 14 *Razisea* sp. plants and recorded the number of empty leaves as well as the group size and instar for all larvae we encountered. We used these data to estimate the degree of aggregation of larvae for each instar by calculating the variance-to-mean ratio of the number of larvae per leaf, including unoccupied leaves on the same plant. The degree of aggregation of the larvae was compared with the expected variance-to-mean ratio (equal to one) for a random (Poisson) distribution with a chi-square test (Krebs 1999).

Effects of Group Size and Instar on Feeding Rate

We estimated larval feeding rates for different instars by placing an individual or a group of sibling larvae on the underside of a single, large, undamaged leaf and measuring the leaf area eaten within a given amount of time. Leaves are lanceolate and approximately 15-25 cm long and 7 – 10 cm wide, and larvae were corralled on a leaf by a band of Tanglefoot Tangle-Trap® smeared around the petiole. No larvae were observed trying to cross the band of Tanglefoot®. Larvae were left to feed for 4 to 25 h, and all replicates of the same instar started and stopped at approximately the same time. Smaller instars were left to feed longer than larger instars. The leaf area eaten was estimated with gridded transparencies. Results are expressed as the leaf area eaten (in square millimeters) per hour per larva or per larval volume, based on the average volume measured for 10 individuals of each instar. Average volumes were estimated to be 0.72 mm^3 for first, 4.56 mm^3 for second, and 36.82 mm^3 for third instars and 149.92 mm^3 for the fourth and fifth instars, which differed more in head capsule size and coloration than in estimated volume. The results were analyzed by single classification ANOVA and regressions. By using as wide a range of group sizes as possible, instead of replicating only a few group sizes, we were better able to characterize the effects of group size and look for nonlinear effects of group size, including an intermediate optimum. All analyses were done with S-Plus 6.1 (Insightful Corporation 2001).

The *C. poecile* larvae fed both day and night, and on 12 leaves the groups of larvae ate too much of the leaf to permit accurate estimation of the leaf area removed. These leaves were excluded from further analyses, leaving 19 groups of first instars, 19 groups of second instars, 9 groups of third instars, and 16 groups of fourth/fifth instars. Group sizes in the final data ranged from 1 to 100 larvae, but instars differed in the maximum number of larvae in a group, because fewer late instars would fit on a leaf. Fourth and fifth instars were lumped together to increase the sample size of these late instars. The largest group of fourth and fifth instars that we used was 10 caterpillars, which consumed most of a large leaf in a few hours.

Results

Larval Aggregation

The mean group size for egg masses and each instar counted in the first census are shown in Fig. 1. The variance-to-mean ratio calculated from the second census was high in the second instars, intermediate for first and third instars, and near one for fourth and fifth instars. First instars were consistently highly aggregated in large groups. The larvae began to disperse in the second instar and continued in the third, so some of these larvae were found in large groups whereas others were found as solitary larvae, thus inflating the variance-to-mean ratio. Fourth and fifth instars were mostly found as solitary caterpillars and data suggest their distributions were not significantly different from a random distribution among all possible leaves, although sample sizes for these instars were too low to warrant a formal test.

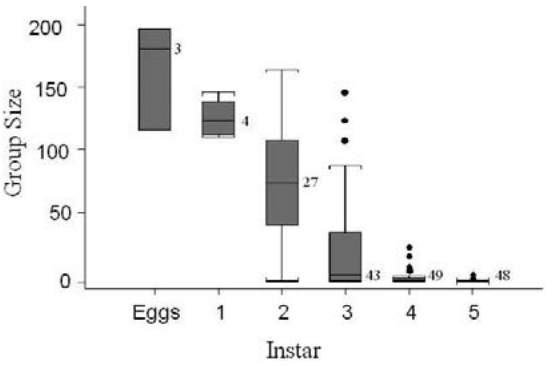


Fig. 1. Group sizes observed for eggs and for instars 1-5. The box contains 50% of the data, and the median is indicated by a line. The whiskers contain approximately 95% of the data, and outliers beyond the whiskers are shown as points. Observed group size decreased with increasing instar. The sample size for each instar is shown beside its box.

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Effects of Group Size and Instar on Feeding Rate

Instars differed tremendously in feeding rate. Larger larvae ate more leaf area per hour than small larvae ($F_{1,59} = 58.227, P < 0.0001$), but when feeding rate was expressed as leaf area consumed per hour per unit larval volume, the effect of instar on feeding rate was no longer significant ($F_{1,59} = 2.087, P = 0.154$). Feeding rate increased significantly with group size for the first instars (Table 1, Fig. 2). Nine of the 12 groups of first instars with fewer than 25 individuals never began feeding, whereas all 7 larger groups of first instars fed. Solitary first instars either never attempted to feed or were unable to break the leaf cuticle. The feeding rates decreased with group size for the second, third, and fourth/fifth instars, but this decrease was statistically significant only for the second instars (Table 1, Fig. 2). The effect of group size was therefore smaller in later instars. For all instars the effects of group size were linear; no higher-order terms were significant. Because the much smaller range of group sizes tested for the fourth and fifth instars would obscure interactions involving group size, we used data only for first, second, and third instars in a single-classification ANOVA. The interaction between group size and instar was significant ($F_{1,43} = 4.526, P = 0.039$); that is, these smaller instars differ significantly in the slopes of the relationships between feeding rate and group size.

Discussion

Our results clearly support the hypothesis that larval group size positively affects *C. poecile* feeding rate for first instars. First instars construct a sparse network of silk that appears to help them feed, and they appear less likely to deposit silk and begin feeding successfully when in small groups. Surprisingly, larval aggregation becomes a disadvantage for the second instars of *C. poecile*. These results are contrary to those of Denno & Benrey (1997), who found a positive effect of group size on larval growth rate in second instars of a congener, *C. janais* (Drury). The maximum group size that these authors tested was less than half of the mean group size in the field, however, so they would not have detected effects that became apparent only with larger feeding groups. Clark & Faeth (1997) concluded that feeding facilitation at least partly explained shorter development time from hatching to third instar in larger groups of *C. lacinia* larvae, but they did not separate group-size effects among instars. Our study supports their finding of feeding facilitation, but also shows large across-instar differences in feeding rate, suggesting different benefits and costs for different instars.

Larval aggregation and average group size decreased with increasing instar number, approaching a random distribution among available leaves by fourth instars. This behavior is consistent with the lack of significant effect of group size on feeding rate in the third through fifth instars. If intraspecific competition reduced the feeding rate of larger instars in groups, then we would expect the larvae to become overdispersed by avoiding other larvae. Instead, later instars seem to take random walks to search for available leaves and thus only slowly approach a random distribution among available leaves. In contrast, when the first and second instars disperse, they follow silk trails from their old leaves to new leaves, as do those of *C. lacinia* Geyer (Bush 1969), retaining most of their original feeding groups. Dispersal from aggregations in the congener *C. janais* occurs when the caterpillars reach a certain body length, often in the middle of an instar rather than at an instar transition (Denno & Benrey 1997). A similar pattern in *C. poecile* could explain the high level of variation observed in second and third instar group sizes.

Our results clearly indicate that on the basis of feeding rate alone, larvae should disperse as soon as they molt into the second instar. Why do many groups remain aggregated through the second and into the third instar when earlier group dispersal might increase feeding rate? Group thermoregulation is probably not an important factor because larvae were observed feeding through the night in this warm tropical climate. Unmeasured predation, parasitism, or travel costs may drive the delay in larval dispersal. Because early instars move much more slowly than the later instars (personal observation), the costs of travel

Table 1. Summary of linear relationships between feeding rate [leaf area eaten (mm^2) per larva per day per average larva volume (mm^3)] and group size for different instars. The positive effect of group size on feeding rate decreased with increasing instar.

Instar	Slope	$F_{1,(n-1)}$	*P*-value	Sample size *n*
First	2.5224	28.328	<0.0001	19
Second	–1.9494	8.770	0.009	19
Third	–2.6172	3.889	0.089	9
Fourth/fifth	–0.0968	0.002	0.965	16

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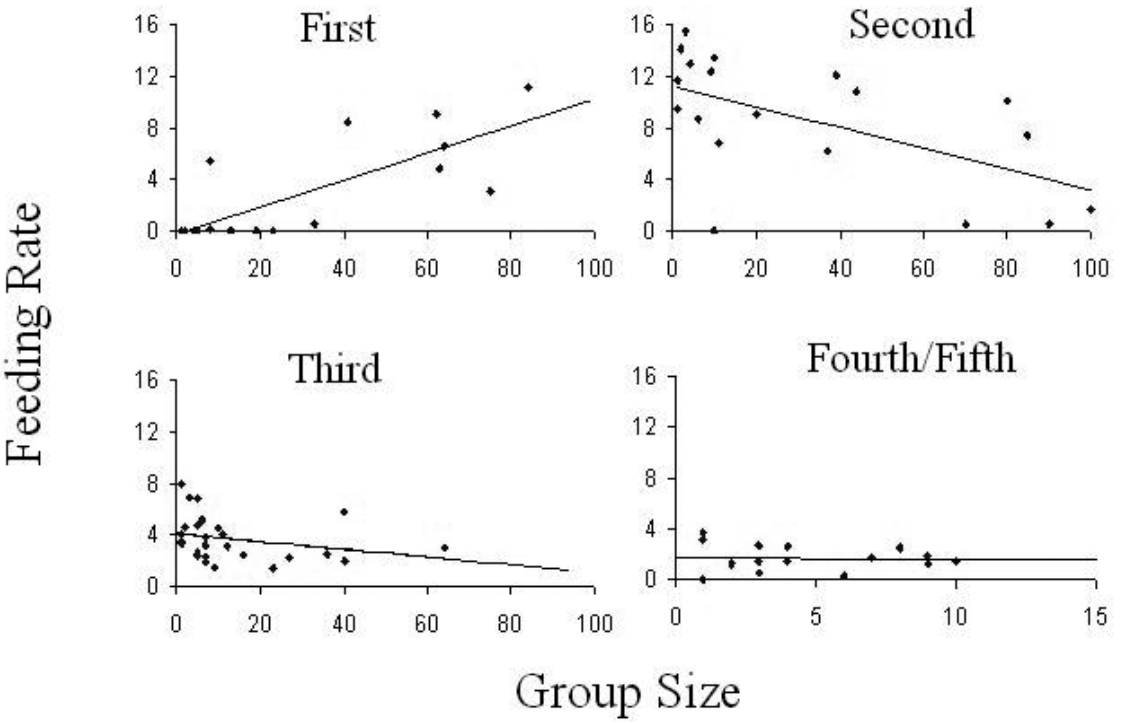


Fig. 2. The relationship between feeding rate [leaf area eaten (mm^2) per larva per hour per average larva volume (mm^3)] and group size (number of individuals) for different instars. The lines are linear regressions. Note that the range of group sizes for fourth/fifth instars is much smaller than that for the other instars. Feeding rate increased significantly with group size for the first instars then decreased significantly with group size for the second instars, and tended to decrease with group size with third and fourth/fifth instars.

time to a new leaf and risk of falling off the host plant may be substantial for even second instars. Moving to new feeding areas may also increase a caterpillar's risk of predation (Bernays 1997).

The changes in appearance of larvae in successive instars suggest that larger caterpillars are also better able to defend against natural enemies. The early instars have few spines and are tan to brown in color. Late instars have typical aposematic coloration; they are black with red heads and occasional orange markings on their backs. The spines on late instars are larger, more numerous, and mildly urticating, causing an itching rash on sensitive skin (personal observation). Although we do not have data on the palatability of the different instars, we noted that the most aposematic larvae fed individually, whereas the least aposematic larvae fed in large groups. Increased feeding efficiency could select for the aggregation of first instars, regardless of their distastefulness, and might be a more important factor than predation for this species. Changes in the risk of parasitism across instars also could contribute to their distributions.

Despite the short duration of the experiments, we were able to find significant effects of group size on the larval feeding efficiency of *C. poecile*. The large feeding groups of first instars and solitary feeding of late instars appear to maximize their feeding rates, but second instars present a conundrum because they were commonly observed in relatively large groups even though their feeding rate declines with group size. We did not examine the costs and benefits of group size for predator defense, which may help to explain the behavior of these caterpillars. We encourage further, more detailed studies of the costs and benefits of insect group-feeding behaviors for different instars, because these costs and benefits are likely to change with instar.

Here we present the first report of gregarious feeding in *C. poecile* larvae, although the behavior was previously known in congeners (DeVries 1987; Clark & Faeth 1997; Denno & Benrey 1997). Egg-laying behavior and gregarious feeding are nearly always coupled. For example, nearly all lepidopterans, including *Chlosyne*, that exhibit gregarious feeding also lay eggs in clusters (and vice versa) in species for which complete data are available—29 out of 30 in Costa Rica (DeVries 1987, 1997; present study) and 22 out of 23 in North America (Stamp 1980). To determine

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how common these aggregative behaviors are in Neotropical Lepidoptera, we reviewed the natural history of Costa Rican lepidopterans (DeVries 1987, 1997) and found that, of 234 species for which information is available, 26% lay eggs in clusters. This figure is much higher than estimates for other regions of the world: 5% in North American, 13% in Great Britain, 6% in Australia-New Guinea, and 3% in India (see Stamp 1980 for review). Moreover, although Stamp (1980) found that egg clustering is generally predominant in just one butterfly group per region, families in Costa Rica show consistently high levels of egg clustering: 26% in Papilionidae, 44% in Pieridae, 22% in Nymphalidae, and 32% in Riodinidae. These results raise the question of whether selective pressures acting on Lepidoptera in the Neotropics differ from those in other regions of the world. We suggest further research that compares top-down (predators and parasitoids) and bottom-up (leaf toughness and feeding-induced resistance) effects on gregarious feeding by larvae in the Neotropics with those in other regions of the world.

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REFERENCES CITED

BENREY, B., AND R. F. DENNO. 1997. The slow-growth-high-mortality hypothesis: a test using the cabbage butterfly. Ecology 78: 987–999.

BERNAYS, E. A. 1997. Feeding by lepidopteran larvae is dangerous. Ecol. Entomol. 22: 121–123.

BRYANT, S. R., C. D. THOMAS, AND J. S. BALE. 2000. Thermal ecology of gregarious and solitary settle-feeding nymphalid butterfly larvae. Oecologia 122: 1–10.

BUSH, G. L. 1969. Trail laying by larvae of *Chlosyne lacini*a. Ann. Entomol. Soc. America 62: 674–675.

CASEY, T. M. 1993. Effects of temperature on foraging of caterpillars, pp. 5-28 *In* N. E. Stamp and T. M. Casey [eds.], Caterpillars: Ecological and Evolutionary Constraints on Foraging. Chapman and Hall, New York. 587 pp.

CHEW, F. S., AND R. K. ROBBINS. 1984. Egg laying in butterflies, pp. 65-79 *In* R. I. Vane-Wright and P. R. Ackery [eds.], The Biology of Butterflies. Princeton University Press, Princeton, N.J. 429 pp.

CLANCY, K. M., AND P. W. PRICE. 1987. Rapid herbivore growth enhances enemy attack: sublethal plant defenses remain a paradox. Ecology 68: 736–738.

CLARK, B. R., AND S. H. FAETH. 1997. The consequences of larval aggregation in the butterfly *Chlosyne lacinia*. Ecol. Entomol. 22: 408–415.

COURTNEY, S. P. 1984. The evolution of egg clustering by butterflies and other insects. American Nat. 123: 276–281.

DENNO, R. F., AND B. BENREY. 1997. Aggregation facilitates larval growth in the Neotropical nymphalid butterfly *Chlosyne janais*. Ecol. Entomol. 22: 133–141.

DEVRIES, P. J. 1987. The Butterflies of Costa Rica and Their Natural History. Volume I: Papilionidae, Pieridae, Nymphalidae. Princeton University Press, Princeton, N.J.

DEVRIES, P. J. 1997. The Butterflies of Costa Rica and Their Natural History. Volume II: Riodinidae. Princeton University Press, Princeton, N.J.

FITZGERALD, T. D. 1995. The Tent Caterpillars. Cornell University Press, Ithaca, N.Y.

GHENT, A. W. 1960. A study of group-feeding behavior of larvae of the jack-pine sawfly *Neodiprion pratti banksianae* Roh. Behaviour 16: 110–148.

HEARD, S. B., AND L. C. REMER. 1997. Clutch-size behavior and coexistence in ephemeral-patch models. American Nat. 150: 744–770.

INSIGHTFUL CORPORATION. 2001. S-Plus 6.1. Insightful, Seattle, Wash.

JULIANO, S. A. 1998. Species introduction and replacement among mosquitoes: interspecific resource competition or apparent competition. Ecology 79: 255–268.

KREBS, C. J. 1999. Ecological Methodology. Second Edition. Addison-Wesley, Menlo Park, Calif.

MORRISON, G., AND D. R. STRONG. 1981. Spatial variation in egg density and the intensity of parasitism in a Neotropical chrysomelid (*Cephaloleia consanguinea*). Ecol. Entomol. 6: 55–61.

RATHCKE, B. J., AND R. W. POOLE. 1975. Coevolutionary race continues: butterfly larval adaptation to plant trichomes. Science 187: 175–176.

SCOTT, J. A. 1986. The Butterflies of North America. Stanford University Press, Stanford, Calif.

SILLÉN-TULLBERG, B., AND O. LEIMAR. 1988. The evolution of gregariousness in distasteful insects as a defense against predators. American Nat. 132: 723–734.

STAMP, N. E. 1980. Egg deposition in butterflies: why do some species cluster their eggs rather than deposit them singly? American Nat. 115: 367–380.

STAMP, N. E. 1986. Physical constraints of defense and response to invertebrate predators by pipevine caterpillars (*Battus philenor*: Papilionidae). J. Lepid. Soc. 40: 191–205.

STAMP, N. E., AND M. D. BOWERS. 1990. Variation in food quality and temperature constrain foraging of gregarious caterpillars. Ecology 71: 1031–1039.

STORER, A. J., D. WAINHOUSE, AND M. R. SPEIGHT. 1997. The effect of larval aggregation behavior on larval growth of the spruce bark beetle *Dendroctonus micans*. Ecol. Entomol. 22: 109–115.

TSUBAKI. Y. 1981. Some beneficial effects of aggregation in young larvae of *Pryeria sinica* Moore (Lepidoptera: Zygaenidae). Res. Popul. Ecol. 23: 156–167.

VULINEC, K. 1990. Collective security: aggregation by insects as a defense, pp. 251-288 *In* D. L. Evans and J. O. Schmidt [eds.], Insect Defenses: Adaptive Mechanisms and Strategies of Prey and Predators. State University of New York Press, Albany, N.Y. 482 pp.

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