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RESEARCH ARTICLE

Group size effects on survivorship and adult development in the gregarious larvae of *Euselasia chrysippe* (Lepidoptera, Riodinidae)

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Abstract Caterpillars living in aggregations may derive several benefits that outweigh the costs, including better survivorship and improved growth rates. I tested whether larval group size had an effect on these two vital rates in *Euselasia chrysippe*. These caterpillars feed gregariously during all instars and move in processionary form over the host plant and even pupate together. There was a positive relationship between group size and larval survivorship in the field, although genetic variability was not taken into account in this experiment. Under laboratory conditions, there was also a positive relationship between group size, and larval growth rate and adult weight. This supports the hypothesis that aggregations facilitate feeding and larval growth. Single sixth instar larvae in the laboratory also had a lower survivorship than larvae in groups. These results provide further evidence of the benefits of group living for gregarious caterpillars.

Keywords Adult mass · Clutch size · *Euselasia chrysippe* · Gregariousness · Larval survivorship

Introduction

Some degree of gregarious behavior is shown by caterpillars in more than 20 lepidopteran families, and it has been supposed that this behavior most likely evolved in response to similar selective pressures (Costa and Pierce, 1997). Gregariousness has probably evolved independently more than 23 times just within the superfamily Papilionoidea (not including Lycaenidae and Riodinidae), and laying eggs singly is considered plesiomorphic for this group (Sillén-Tullberg, 1988). Lepidopteran societies are simple in structure when compared with other social insects. Sociality in Lepidoptera is characterized by laying eggs in clusters (Stamp, 1980; Courtney, 1984; Hunter, 2000) and larval aggregations (Sillén-Tullberg and Leimar, 1988; Fitzgerald, 1995; Tullberg and Hunter, 1996; Costa and Pierce, 1997; Reader and Hochuli, 2003; Costa and Ross, 2003). The number of individuals per aggregation is low and each group usually consists of only one generation; moreover, groups are not long lived. In many cases, however, lepidopterans share communication features with more complex social insects (Costa and Pierce, 1997). For instance, some lepidopteran societies use pheromone-based recruitment trails while foraging (Fitzgerald and Pescador-Rubio, 2002; Fitzgerald, 2003).

Several potential benefits of larval aggregations have been identified in some lepidopteran families. For example, for gregarious species, the higher probability of being detected by predators may be more than compensated by the increased effectiveness of anti-predator defenses such as glands with repellent chemicals, long hairs or spines, silk tents, leaf shelters, violent coordinated head nods (Costa, 1997), and regurgitation of toxins derived from the host plant (Peterson et al., 1987). Similarly, resource localization and assimilation can be improved through a combination of behavioral thermoregulation (Bryant et al., 2000) and cooperative (Fordyce, 2003) or synchronized foraging. In some species of caterpillars, the weak mandibles of the early stages cannot break through the cuticle

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of their host plant, but once larger larvae make a hole, the others concentrate in that area, and thus individual survival is promoted through group behavior (Costa, 1997). Larger group size is also more effective in overcoming the barrier imposed by plant trichomes. *Battus philenor* (Papilionidae), for instance, achieves greater larval growth but not higher survival in larger groups (Fordyce and Agrawal, 2001; Fordyce, 2006). Rapid growth could be an important indirect benefit of living in large groups, especially if predation rates are high (Fordyce and Agrawal, 2001), and it can also reduce exposure to probable adverse abiotic conditions (Stamp and Bowers, 1990a). For *Malacosoma americanum* (Lasiocampidae) survival does not seem to be affected by group size, but larval growth does, probably due to better thermoregulation (Costa and Ross, 2003). Improved thermoregulation has been found in the early stages of *Imbrasia belina* (Saturniidae); groups allow individuals to reach higher and more stable temperatures, and their rate of water loss is decreased, leading to higher survival (Klok and Chown, 1999). Similar studies from additional families could help in delineating the general factors that favor larval gregariousness in lepidopterans.

Here, I present the first study on the benefits of larval aggregations in a member of the family Riodinidae. *Euselasia chrysippe* ranges from Guatemala to Colombia, and occurs from sea level to 1,500 m. In Costa Rica, it is found on both the Atlantic and Pacific slopes, and in primary and secondary rain forest, where it feeds (although not exclusively) on *Miconia calvescens* (Melastomataceae) (DeVries, 1997). This tree, which is native to America from southern Mexico to northern Argentina (Medeiros and Loope, 1997), is an invasive species in some tropical oceanic islands of the South Pacific, Hawaii and Australia. The larvae of *E. chrysippe* synchronize their movements, feeding, resting and molting. This synchronization is known to occur in seven of the 27 *Euselasia* species in Costa Rica (DeVries, 1997; Nishida, 2007). Information on the gregarious behavior of all larval stages in this genus is still scarce and fragmented (Zanuncio et al., 1990; Zanuncio et al., 1995; Brévignon, 1997; Zanuncio et al., 2009). I studied the gregarious behavior of *E. chrysippe* throughout all larval stages and evaluated whether gregarious behavior favors larval survival and adult development in this species.

Methods

Egg clutches were collected from four sites in Costa Rica during the rainy season of 2003: Lago Arenal (10°28′17″N, 84°46′11″W; 525-m altitude), El Ángel-Cariblanco (10°15′44.2″N, 84°10′19″W; 750 m), Jicotea (9°48′29″N, 83°31′23″W; 900 m) and Hitoy Cerere Biological Reserve (9°40′19″N, 83°01′28″W; 100 m). Each site was visited at least once and the eggs were taken from *M. calvescens* trees. Not all clutches were collected; some were just photographed for additional data on clutch size in the field. The egg clutches (attached to a piece of their leaf) were placed in petri dishes and transported to the laboratory at the University of Costa Rica (UCR) in San José. In the laboratory, after hatching, the larvae were placed on potted *M. calvescens* plants, one clutch per plant, and the pots were placed in large plastic containers surrounded with water to prevent the caterpillars from escaping. Larval behavior and mortality was monitored daily. After the larvae pupated on the pots, these were placed in a controlled environmental chamber (Model 518, Electro-Tech Systems: 23°C, 14 h D/L).

When the adults emerged, they were released in the Leonel Oviedo Biological Reserve close to *M. calvescens* trees that had been planted there. Only healthy looking, full-sized butterflies were released. The Leonel Oviedo Biological Reserve is a 0.75-ha fragment of secondary forest in the middle of the UCR campus in San José (9°56′15″N; 84°03′00″W; 1,200 m), which is characterized by a dry season with little or no rain between December and April. Twenty *M. calvescens* trees were planted in the reserve between July 2002 and March 2003. As soon as the adults were released, I began surveying the *M. calvescens* trees daily to determine when and where the egg clutches were laid. Digital photographs (Nikkon Coolpix 4500) were taken of the egg clutches to quantify the number of eggs per clutch. After hatching, each caterpillar group was followed and photographed to quantify the number of larvae and to follow larval growth. These data were used to calculate the larval mortality of each cohort (each individual egg clutch) throughout all larval stages in the reserve. Sixth instar larvae abandon the plant the night that they pupate, so it was not possible to determine pupal mortality.

The effect of group size on survivorship was determined by comparing the proportion of live individuals at the end of each larval stage among three categories of cohort size in the reserve. These categories were defined according to the initial number of eggs per cohort: (1) fewer than 50 eggs (small); (2) between 50 and 80 eggs (medium); and (3) more than 80 eggs (large). All survivorship data were converted to stage-specific survivorship (proportion of each cohort that enters the population as an egg and survives to each larval instar). Mean survivorship per stage was compared between categories using analysis of variance (ANOVA); data were normalized using the arcsine transformation.

To quantify the effect of larval group size on adult weight, larvae were reared in four treatments: 1, 5, 10 and 20 larvae per plant in captivity during November and

December 2006. Individuals of two cohorts, but the same age, were collected in the field on the same day (11/4/2006) on different trees (Jicotea site); one had 48 individuals and the other 52. Both cohorts were separated into the treatments 2 days before molting to the sixth larval stage. One larva was placed on each of 20 potted *M. calvescens* plants (8 and 12 from each cohort), 5 larvae per plant on 4 plants (2 groups per cohort), 10 larvae per plant on two plants (1 group per cohort) and 20 larvae per plant on two plants (1 group per cohort). Pots were placed in large plastic containers surrounded by water. After pupation, the pots were covered with a mesh cage. After emergence adults were allowed to fully extend their wings and were then frozen (15 min), and placed in a drying oven (40°C) for 24 h. Finally, the dry body mass was measured for each individual. To examine the effect of group size on adult dry mass, simple linear regressions were employed using a log transformation. Results were separated by sex, and the slope and elevation of the regression lines were compared to determine differences between sexes, using a *t* test (Zar, 1999: 360–364).

Results

First and second larval instars fed on the undersides of leaves, scraping the surface. Starting in the third instar, larvae fed side by side on the whole leaf. They moved from leaf to leaf in procession, the trailing caterpillars following silk trails left by the ones in front; they also rested and molted synchronously ($n = 23$ cohorts, field). Under laboratory conditions, the larvae pupated together synchronously, and adults emerged synchronously by sex; males emerged approximately 24 h after females in all cases ($n = 30$ cohorts).

The mean number of eggs per clutch was 62.7 ($SD = 22.3$, $n = 84$, range = 13–134) in the field and 67.3 ($SD = 22.9$, $n = 26$, range = 15–113) in the reserve; there was no significant difference in clutch size between the two ($t = 0.91$, $df = 108$, $p = 0.36$). There was no difference in hatching rates between small (<50 eggs), medium (51–80 eggs) and large (>81 eggs) clutches in the reserve ($F_{2,20} = 0.10$, $p = 0.90$; Fig. 1). Survivorship ranged from 67.0% in the smallest groups to 73.5% in the largest ones. No cohorts in any group died off during the first instar (Table 1) and survivorship remained similar between clutch sizes ($F_{2,20} = 0.11$, $p = 0.89$; Fig. 1) ranging from 55.8 (large) to 60.4% (medium). By the end of the third instar, survivorship dropped to 6.2% in small groups, to 20.0% in medium groups, and to 30.4% in large groups, but still with no significant difference between treatments (second instar $F_{2,20} = 1.26$, $p = 0.31$; third instar $F_{2,20} = 2.57$, $p = 0.1$; Fig. 1). This trend continued throughout the fourth ($F_{2,20} = 2.60$, $p = 0.1$) and fifth instars ($F_{2,20} = 2.51$, $p = 0.11$), where larger groups tended to have a higher survival rates (Fig. 1). By the end of the sixth instar, the proportion of individuals that survived was lowest in the small group treatment ($F_{2,20} = 3.68$, $p = 0.04$; Fig. 1) and the number of cohorts that survived to the last instar was also lower in this treatment ($G = 19.9$, $df = 2$, $p < 0.001$; Table 1).

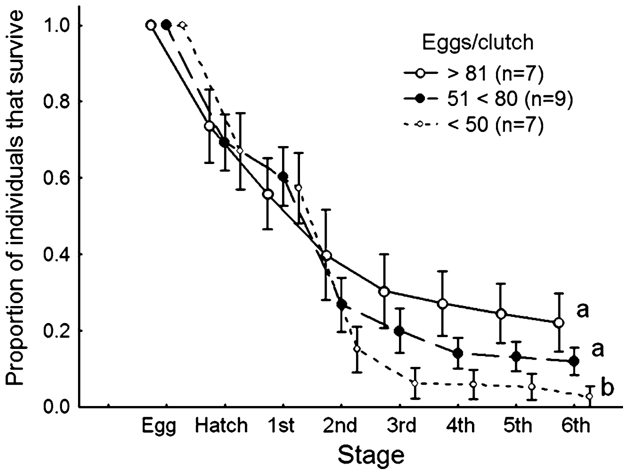

Fig. 1 Survivorship (mean ± SE) of *Euselasia chrysippe* on *Miconia calvescens* by life stage, separated by initial cohort size (clutch size); in the Leonel Oviedo Biological Reserve (Costa Rica) during the 2003 rain season. *Letters* represent significant differences between categories ($p < 0.05$, ANOVA) in the proportion of individuals that survive to the last instar

Table 1 Summarized life table for the immature stages of *Euselasia chrysippe* on *Miconia calvescens*, in the Leonel Oviedo Biological Reserve (Costa Rica)

	Small	Medium	Large
Clutches (cohorts)	7	9	7
Eggs/clutch[a]	37.7 (13.4)	67.9 (8.4)	93.7 (11.2)
First instar (cohorts)	7	9	7
Second instar	4	7	5
Third instar	2	6	5
Fourth instar	2	6	5
Fifth instar	2	6	5
Sixth instar	1	6	5
Larvae/cohort sixth instar[a]	1.0 (2.4)	7.8 (6.8)	21.6 (19.3)

Numbers represent quantity of cohorts that have living individuals at the end of each stage. Three categories were defined according to initial number of eggs per clutch

[a] Mean (SD)

As shown in Fig. 2, there was a significant positive effect of group size during the larval period on the weight of the adults for both sexes (males $F_{1,9} = 42.9$, $p < 0.001$; females $F_{1,11} = 68.9$, $p < 0.001$). The regression lines

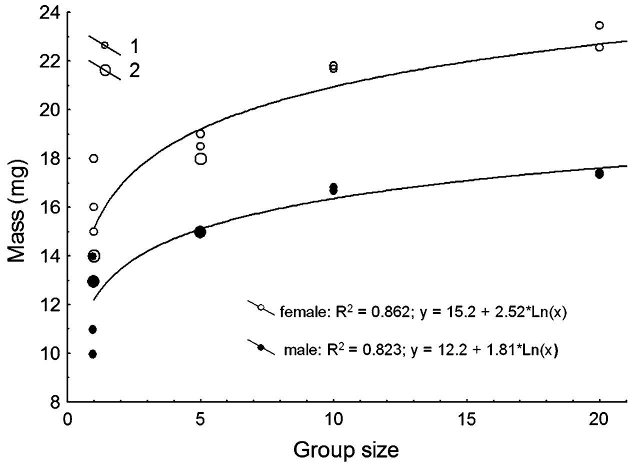

Fig. 2 Regression of dry mass of adult *Euselasia chrysippe* and group size in which they were reared as larvae, on *Miconia calvescens* during their sixth instar, under laboratory conditions (2006). The *size of the circles* represents the number of points that share the same value (top left corner)

have similar slopes ($t = 0.36$, $df = 20$, $p = 0.73$), but the female line is more elevated ($t = 5.8$, $df = 21$, $p < 0.0001$); for all group sizes, females were heavier (30% on average, Fig. 2). In both the laboratory ($n = 35$) and in the reserve ($n = 12$), the sixth instar lasted for 6–7 days for all treatments. Survival was also lower among the single sixth instar larvae in the laboratory experiment when compared with larvae reared in groups: only 63% of single larvae survived while 94% in the 5 larvae per plant treatment survived, 92% in the 20 larvae per plant treatment, and 100% in the 10 larvae per plant treatment.

Discussion

Euselasia chrysippe larvae are gregarious during all instars and the results of this study provide evidence of benefits to living in groups. In Lepidoptera, there are few studies of gregariousness throughout the entire larval period (for examples see Floater and Zalucki, 1999, 2000) since most studies on gregarious Lepidoptera have been done on species in which the first three or four stages are gregarious with the last ones being solitary (Tsubaki and Shiotsu, 1982; Damman, 1987; Fitzgerald, 1995; Clark and Faeth, 1997, 1998; Reader and Hochuli, 2003; Costa and Ross, 2003; Despland and Hamzeh, 2004). This phenomenon and its benefits have also been studied in other insect orders (Ghent, 1960; Boevé, 1991; Costa and Louque, 2001; Nahrung et al., 2001; Costa et al., 2004; for a detailed review see Costa, 2006). The results from this study support the hypothesis that group size has a positive effect on adult mass by facilitating larval feeding and therefore increasing growth rates (Denno and Benrey, 1997). This is particularly beneficial for lepidopteran females, for which fecundity increases with body size (Wiklund et al., 1987; Saastamoinen, 2007). Large *E. chrysippe* females probably carry more eggs or more resources for their production. Average sized females (>20 mg) have more than 50 fully formed eggs after 48 h of emergence ($n = 3$), whereas a small female (<16 mg) had no mature eggs after 96 h of emergence (Allen, unpubl.). Sibling larvae may stimulate each other to eat, a response that could explain why growth rates are sometimes enhanced by group feeding (Stamp and Bowers, 1990b). The fact that average adult mass is lower in smaller groups relative to adults in larger groups suggests that group size also has an effect on group feeding benefits. Although the physiological mechanism enhancing growth rate is still unknown, it is clear that larval aggregations promote greater growth in this species.

In *E. chrysippe* cohorts of larvae in different stages (non-sibling) sometimes joined to form larger groups, both in the field and in the laboratory (Nishida, 2007; Allen, unpubl.); in the laboratory they can also form a larger group consisting of two different species ($n = 1$, *E. chrysippe* and *E. bettina*). In both cases, larvae behave in the same manner as they did before joining together, feeding, moving, molting and pupating in synchrony. Similar cases have been reported for other lepidopterans, *M. americanum* (Costa and Ross, 2003) and *B. philenor* (Fordyce, 2006); in these cases no costs and only benefits have been found for larger groups. This suggests that the benefits of living in large groups, in this species, outweigh the costs of intra- or inter-specific competition.

Larval group (cohort) size had a positive effect on survivorship at the sixth instar. In other studies with lepidopteran species that lay eggs in clutches, such as *Halisidota caryae* (Arctiidae; Lawrence, 1990), *Malacosoma* sp. (Lasiocampidae; Fitzgerald, 1995) and *Chlosyne lacinia* (Nymphalidae; Clark and Faeth, 1997), larvae living in larger groups also have higher survivorship. The causes of death of *E. chrysipp*e in the field are in most cases unknown, but temperature changes have been found to affect their survivorship, especially in early stages (Allen, 2007). Based on the results from this study, it would be expected that females of *E. chrysippe* lay large egg clutches. Small egg clutches (<50 eggs) found in the field and the reserve could have been laid by small females (in the field), or they might be secondary clutches (Lawrence, 1990), or they could be the result of interrupted oviposition (Lawrence, 1990; Clark and Faeth, 1998). This study was conducted under practically natural conditions, which did not allow controlling for environmental conditions or genetic variability; clutch size has also been found to be influenced by these two and many other factors in some lepidopterans (Saastamoinen, 2007).

Gregariousness may have evolved in some caterpillars to reduce the impact of anti-herbivore defenses (Fordyce and Agrawal, 2001). In the case of *E. chrysippe*, there is little to suggest this. Host leaves lack trichomes and other obvious morphological defenses. Leaf toughness does not appear to dissuade caterpillars, either, including small groups of first and second instars that scrape the undersides of leaves. Secondary compounds, like cyanogenic glycosides, appear absent (Michelangeli and Rodriguez, 2005), as indicated by the large array of phytophagous insects that feed on *M. calvescens*. For example, 38 insect species were found to feed on *M. calvescens* in Brazil (Picanço et al., 2005) and over 50 in Costa Rica (Hanson et al., 2009).

Group living in *E. chrysippe* confers at least two different advantages for larvae during their development: early on gregariousness facilitates feeding by cryptic instars, which continue to benefit as they grow, and it also increases survivorship later on. Future studies should attempt to determine if mechanical and/or chemical defenses, thermoregulation or a combination, improve the survival rate as group size increases in this species. This may provide a better understanding of the evolution of gregariousness in the Lepidoptera.

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