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Why do pine processionary caterpillars *Thaumetopoea pityocampa* (Lepidoptera, Thaumetopoeidae) live in large groups? An experimental study

Tomás Pérez-Contreras[1]*, Juan J. Soler[1] & Manuel Soler[2]

[1)] *Estación Experimental de Zonas Áridas (CSIC), General Segura 1, 04001-Almería, Spain (*e-mail: tomaspc@eeza.csic.es)*
[2)] *Departamento de Biología Animal y Ecología, Campus Universitario de Fuentenueva, Facultad de Ciencias, 18071-Granada, Spain*

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Optimal group size of gregarious larvae is the result of a trade-off between the costs and benefits undergone by individuals living in groups of different sizes. Thus, females should adjust their clutch size to an optimal-minimum group size. In this study, we experimentally manipulated the size of colonies of pine processionary caterpillars, a capital breeder species, to test the hypothesis that a large group size enhances larval growth and survival. We also explored whether this relationship fits a quadratic or an asymptotic curve and estimated an optimum or a minimal-optimum group size. The results showed significant differences in the final larval sizes in the various treatments, being greater in the larger groups. In addition, according to the existence of a minimal-optimum group size, we found that a Piecewise Linear Regression fits the above relationship better than does a linear regression. Groups larger than 32 individuals did not differ in growth or survival parameters. Although the number of dead larvae per group did not differ between experimental treatments, large experimental colonies suffered a lower percentage of mortality. Thus, the probability of reaching the pupal stage was greater for larvae from large colonies because of dilution effects. Our results demonstrated a minimum group size, above which group size did predict larval growth or mortality, thereby explaining why pine processionary caterpillars live in large groups.

Introduction

In nature, groups of animals can be considered as "true social" groups or as mere associations of individuals that prefer to forage, breed, or defend against predators in groups (i.e. flocks, colonies). Living in groups may confer benefits such as stronger defences against predators and greater capacity to locate food (Bowers 1993, Fitzgerald 1993). However, group living may also exact costs such as increased competition for resources (Day 2001) and conspicuousness that could attract predators (Elgar 1989). Therefore, an optimal group size is the result of a trade-off between costs and benefits associated with different group sizes, these depending on environmental condi-

tions and specific life-history traits (Stamp 1981, Rannala & Brown 1994, Uetz & Hieber 1997).

In the case of insects, larval aggregation is relatively frequent and occurs mainly in a taxonomically diverse array of Lepidoptera species (Fitzgerald 1993). Gregarious larvae have the advantage of a higher foraging efficiency (feeding facilitation), because aggregation may facilitate the establishment of a feeding site for first-instar siblings (Shiga 1976), or enhance the ability to overcome morphological (i.e. trichomes, Young & Moffett 1979) or chemical (Neuvonen & Haukioja 1991, Tallamy & Raupp 1991) defences of their host plant. As a result, larval growth rate is positively related to aggregation level in some species (Long 1953, Lawrence 1990). Group living may also enhance defence against natural enemies, given that larger larval aggregations reportedly have lower mortality rates from natural enemies than do smaller groups or solitary individuals (Lawrence 1990, Fitzgerald 1993; but *see* Stamp (1981) for an opposite pattern in Lepidoptera). Moreover, individuals living in groups may have a lower risk of being attacked by predators because of the stronger warning signals (Guilford 1990, Bowers 1993, Fitzgerald 1993, Alatalo & Mappes 1996), chemical, and behavioural (twitching) defences (Stamp 1982, 1984, Peterson *et al.* 1987, Vulinec 1990), or simply because of the dilution effect (Foster & Treherne 1981, Wcislo 1984), which is purely a question of probability without requiring any complex or cooperative behaviour. To some extent the dilution effect may be offset by the increased number of attacks on larger and more conspicuous groups, but usually the net effect probably favours living in a group (Krebs & Davies 1993). Larger groups of caterpillars are also able to construct leaf or web shelters that provide effective protection from invertebrate predators (Damman 1987). Another advantage to larval aggregation is the facilitation of thermoregulation by group basking (Casey 1993, Fitzgerald 1993), because high body temperatures in aggregated larvae result in a high foraging rate, fast digestion, or in an effective escape from natural enemies (Casey *et al.* 1988, Stamp & Bowers 1990a, 1990b, 1990c, Fitzgerald 1993).

Documented disadvantages of group living include higher risk of infectious disease (Hochberg 1991) and parasitism (Dobson 1988), increased competition for food between grouping larvae (Damman 1991, Le Masurier 1994) and greater visibility to predators (Stamp 1981, Le Masurier 1994). The presence of conspicuous non-warning coloration in gregarious species may prove costly because these individuals are more easily discovered by potential predators. This may also be the case for warning-coloured individuals if their defences are not effective against some predators (Guilford 1990). Thus, above a certain group size, costs associated with competition or coexistence among group members may exceed advantages associated with cooperation (Zemel & Lubin 1995).

Therefore, optimal group size would be the result of the trade-off between the costs and benefits described above (e.g. Wilson 1975, Krebs & Davies 1993). However, optimal group size has two limitations. First, individuals in a group may attain different pay-offs and may have different optimal groups sizes, and second, optimal-sized groups may be unstable because they tend to be joined by individuals from smaller groups (Krebs & Davies 1993). Adult fitness and adult body size, which is related to fecundity (e.g. Spurgeon *et al.* 1995, Webber & Ferro 1996, García-Barros 2000), depend on larval growth and size, but ultimately on larval survival (Kamata & Igarashi 1995). Moreover, group size, which is determined mainly by clutch size (Sillen-Tullberg 1988, Gregiore 1988), is positively related to larval survivorship and growth, as suggested by field and laboratory experiments (e.g. Denno & Benrey 1997, Fordyce & Agrawal 2001, Nahrung *et al.* 2001). Since large groups may also suffer repercussions (*see* above), evidence of stabilizing selection acting on larval group size has been detected in several insect species (e.g. Matsumoto 1990, Crowe 1995).

The pine processionary (*Thaumetopoea pityocampa*) is a highly abundant moth species with larvae that constitute the main pest of pines in the Mediterranean region. Females lay only one clutch (capital breeder), and, after hatching, highly gregarious larvae normally build a single nest where all siblings stay while not feeding. The larvae, highly gregarious in all growth stages, stay on the same tree while food is not a limiting factor. When more than one clutch per

pine exists, larvae from different clutches may group and build a single nest to share (Douma-Petridou 1989). Thus, clutch size determines colony size when there is only one clutch per tree because the number of eggs hatched is strongly and positively related to clutch size (T. Pérez-Contreras & J. J. Soler unpubl. data); however if more than one clutch exists in the same tree, clutch size determines the minimum group size only. Due to the hypothetical costs associated with small groups, females should adjust their clutch size to that related to an optimal-minimum group size because of the possibility that more than one female may be laying in the same tree and offspring therefore may be suffering the costs associated with groups larger than the optimum.

In the present study, we experimentally manipulated the size of pine processionary colonies within their natural range, and tested the hypothesis that a large group size enhances larval growth and survival. We used clutches that were alone in a single pine, reduced the negative effects of competition for food between larvae from different clutches, and ensured that all individuals from the same colony were genetically related. Because of the hypothetical control of group size by adult females explained above, we predicted that group size of natural colonies should be close to that for which the relationship between group size, growth rate, and sizes of larvae reach the optimum. However, due to possible costs associated with an oversized group, we further explored the expected positive relationship between experimental group size and growth because it may be quadratic or asymptotic.

Materials and methods

Study site

The field study was conducted in an area of pine forestation located in the high-altitude plateau Hoya de Guadix (37°18´N, 3°11´W), Spain, approximately 1000 m above sea level with a semi-arid climate. Two pine species were present and susceptible to attack by the pine processionary moth, the Aleppo pine (*Pinus halepensis*) and the maritime pine (*Pinus pinaster*). The former is the most abundant, representing some 90% of the trees. The research site is a young forestation area with an average pine height of four meters. Distance between pines is quite uniform, about 4–5 meters.

Study species

The pine processionary caterpillar is highly gregarious and is distributed throughout southern Europe being the principal defoliator of pines in the Mediterranean region (Devkota & Schmidt 1990). The flight and egg-laying period, though depending on factors such as weather and altitude, usually spans from May to October (Douma-Petridou 1989). Females lay a single cylindrical clutch that is covered with scale-like hairs. Oviposition covers one or two pine needles, predominantly from the base of the needles towards the tip. The eggs hatch after 5–6 weeks (Schmidt 1989). Larval development involves five instars (Douma-Petridou 1989) and, although larvae move around the pine feeding on needles, they build a silk nest where all the larvae from the same clutch stay while not feeding. When more than one clutch is laid in a pine, larvae from different clutches sometimes build a single nest to share. In colonies formed from a single clutch, the number of individuals per colony at the first instar ranges from 47 to 149 in our study area (data from the present study; mean = 94.2, SE = 2.27, N = 90). After larval development, the larvae leave the nest in a procession and search for a suitable underground pupation site. The pupal diapause varies from a few months to 1–2 years (Schmidt 1989).

General procedures

In 1995, during egg laying, we randomly selected 90 Aleppo pines that had a single pine processionary clutch. All selected pines were of similar size (2.5–3 m), making food availability similar for all selected clutches. We randomly assigned 60 of those 90 clutches to one of the four experimental treatments. Treatments consisted of removing recently hatched larva to leave 25 (Group I), 50 (Group II), 75 (Group III) and

100 (Group IV) larvae per clutch. The removed larvae were introduced into other colonies of the study area. In addition, we kept 30 colonies as a control to estimate the mortality rate and final larval length of natural colonies. Body length and group size of recently hatched larvae did not differ significantly between colonies of the four different experimental treatments (Table 1), or between experimental and control groups before manipulation (body length: $F_{1,88} = 0.17$, $p = 0.68$; group size: $F_{1,88} = 0.02$, $p = 0.90$), indicating that our experimental groups were not biased.

We monitored each of the experimental colonies monthly for up to five visits before larvae left the pine to pupate. Since we selected pines with a single colony, with non-limited resources for larval development, and we did not detect larval movements between different trees, differences in larval numbers between different visits were assumed to be due to larval mortality. If we found no individuals in an experimental colony in a target visit, we assumed that all larvae had died and consequently reduced sample size for larval length and growth, but not for group size. In subsequent visits we did not take these defunct colonies into account in our estimates of group size.

On each visit we counted the number of larvae per colony and estimated mean larval length. Larval lengths were measured with a digital calliper (Mitutoyo, 0.01 mm accuracy). We measured ten randomly collected individuals per colony when possible. When less than ten individuals were found, we measured all individuals in the colony. Larval growth was calculated as the difference in average larval sizes between two consecutive visits.

Statistical analyses

To achieve an approximately normal distribution of variables, we logarithmically transformed the number and percentage of larvae found dead in each visit. After these transformations, none of these variables differed significantly from normal distributions (Kolmogorov-Smirnov test for continuous variables, $p > 0.2$). Although larval size on the four first visits did not differ significantly from a normal distribution (Kolmogorov-Smirnov test for continuous variables, $p > 0.2$), larval size differed significantly from a normal distribution on the five last visits. Therefore, parametric tests were applied following Sokal and Rohlf (1995) except for the analyses where final larval length was included, in which we used non-parametric tests.

To explore whether the relationship between group size and mean body size of larvae in experimental groups fit better to a straight line, or rather the fitted function changed for different group sizes, we used a Piecewise linear regression with a breakpoint as implemented by Statistica 6.0 (StatSoft 1998) and compared correlation coefficients. Moreover, breakpoints of that regression would inform us concerning the values of group size where the type of relationship between larval size and group size changes.

Results

Effect of aggregation size on larval growth

Group size prior to the manipulation did not predict larval-body length either before ($r = –0.17$, $N = 60$, $p = 0.17$), or after the experiment, at the fifth instar close to the pupation time ($r_s = 0.16$, $N = 50$, $p = 0.26$). In natural colonies, initial group size did not predict the initial larval body length ($r = –0.12$, $N = 30$, $p = 0.51$), but did predict the final larval body length ($r_s = 0.76$, $N = 28$, $p < 0.001$, Fig.1).

The experimental group size affected the larval body length during the four months of growth, and larval growth showed significant differences between groups for each visit except for the third (Table 1). After four months of growing, larvae from the largest experimental group size were largest in terms of body length (Table 1), and paired comparisons between experimental groups revealed significant differences (Mann-Whitney U-test: $Z_{(adjusted)} > 1.99$, $p < 0.05$), except for groups initially containing 75 and 100 individuals (Table 1; Mann-Whitney U-test: $Z_{(adjusted)} = 0.54$, $p = 0.59$).

In addition, larval growth between consecutive visits was explained by the colony size of the previous visit, except between the second

Table 1. Body size, group size, and growth of larvae from experimental and control groups. Mean values, standard errors (SE) and samples size (*N*) are shown for each group. Comparisons between experimental groups are also shown. Visits were monthly and first and fifth visits corresponded to the first and fifth instars, respectively.

	Groups I (25) Mean ± SE (*N*)	Groups II (50) Mean ± SE (*N*)	Groups III (75) Mean±SE (*N*)	Groups IV (100) Mean ± SE (*N*)	Natural Mean ± SE (*N*)	ANOVAs between experimental groups		
						F	df	*p*
First visit								
Body size	5.57 ± 0.10 (15)	5.59 ± 0.05 (15)	5.43 ± 0.05 (15)	5.42 ± 0.06 (15)	5.47 ± 0.07 (30)	1.48	3, 56	0.23
Group size	92.40 ± 5.69 (15)	91.86 ± 6.29 (15)	98.46 ± 6.31 (15)	93.20 ± 6.08 (15)	94.00 ± 3.39 (30)	0.24	3, 56	0.86
Second visit								
Body size	9.06 ± 0.16 (14)	9.25 ± 0.10 (15)	9.91 ± 0.05 (15)	10.14 ± 0.14 (15)		19.03	3, 55	< 0.0001
Group size	17.73 ± 1.70 (15)	42.47 ± 1.19 (15)	68.07 ± 1.39 (15)	90.73 ± 1.19 (15)		521.7	3, 56	< 0.0001
Growth 1	3.54 ± 0.21 (14)	3.66 ± 0.11 (15)	4.48 ± 0.06 (15)	4.71 ± 0.13 (15)		19.06	3, 55	< 0.0001
Third visit								
Body size	14.30 ± 0.21 (14)	14.93 ± 0.08 (15)	15.40 ± 0.15 (15)	15.90 ± 0.07 (15)		24.8	3, 55	< 0.0001
Group size	12.79 ± 1.05 (14)	35.40 ± 2.07 (15)	62.00 ± 2.18 (15)	83.73 ± 1.59 (15)		209.8	3, 55	< 0.0001
Growth 2	5.24 ± 0.21 (14)	5.68 ± 0.12 (15)	5.49 ± 0.15 (15)	5.76 ± 0.17 (15)		1.962	3, 55	0.13
Fourth visit								
Body size	23.82 ± 0.21 (12)	24.74 ± 0.18 (14)	25.73 ± 0.13 (15)	26.51 ± 0.17 (14)		46.70	3, 51	< 0.0001
Group size	5.50 ± 1.01 (14)	26.73 ± 2.81 (15)	54.87 ± 2.34 (15)	71.47 ± 5.41 (15)		75.22	3, 55	< 0.0001
Growth 3	9.66 ± 0.25 (12)	9.84 ± 0.16 (14)	10.33 ± 0.23 (15)	10.59 ± 0.15 (14)		4.52	3, 51	< 0.0001
Fifth visit								
Body size*	29.48 ± 0.54 (10)	30.80 ± 0.31 (13)	33.59 ± 0.12 (14)	33.72 ± 0.17 (13)	32.57 ± 0.29 (30)	χ^2 = 39.5	3	< 0.0001
Group size	3.58 ± 0.81 (12)	17.43 ± 2.39 (14)	44.53 ± 4.51 (15)	66.43 ± 5.59 (14)	62.53 ± 4.45 (30)	48.10	3, 51	< 0.0001
Growth 4	5.60 ± 0.52 (10)	6.09 ± 0.34 (13)	7.82 ± 0.18 (14)	7.25 ± 0.26 (13)		9.91	3, 46	< 0.0001

* since mean body length of larvae in the fifth instar did not follow a normal distribution, we used Kruskal-Wallis ANOVA

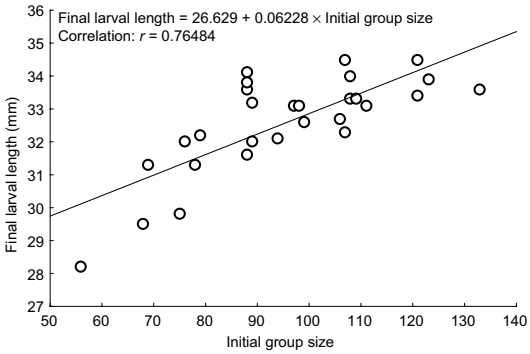

Fig. 1. Relationship between the initial group size and the final larval size in natural colonies. Test used was Spearman rank correlation. $N = 28$.

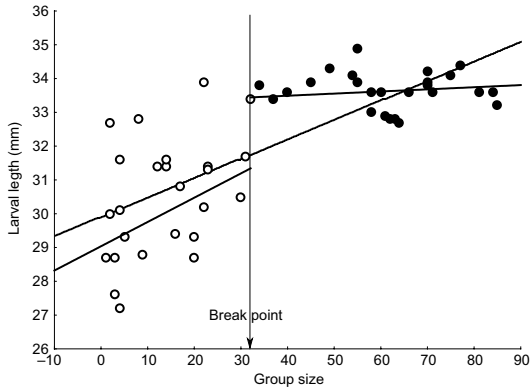

Fig. 2. Relationship between group size and larval length close to pupation time of experimental colonies. Solid line represent the Piecewise Linear Regression ($R = 0.91$, $N = 50$, $p < 0.001$) and discontinuous lines represent linear regression ($R = 0.76$, $N = 50$, $p < 0.001$). Differences between correlation coefficients: $p < 0.05$.

and the third visits (Table 2), and final larval length was explained by final group size both in experimental ($r_s = 0.75$, $N = 50$, $p < 0.001$; Fig. 2) and in control groups ($r_s = 0.58$, $N = 28$, $p = 0.0011$). Thus, since we experimentally manipulated group size, it can be concluded that this factor was causally responsible for variation in body size and growth of larvae from different colonies.

Regarding an optimal group size, we found that a Piecewise Linear Regression fit the relationship between final larval length and group size ($R = 0.91$, $N = 50$, $p < 0.001$) of experimental colonies better than did a linear regression ($R = 0.76$, $N = 50$, $p < 0.001$) (Fig. 2), differences between correlation coefficients being statistically significant ($p = 0.012$). When the colonies of final larval smaller and larger than 32 individuals were separated, the frequency distributions of subsamples became approximately normally distributed (Kolmogorov-Smirnov tests for continuous variables: $p > 0.2$). The break point from the Piecewise Linear Regression analysis was 32.08 and regression coefficient of first line (0.072) was more than 10-fold that of the second line (0.006). Moreover, the intercept of the second line proved larger (33.24) than that of the first line (29.04), and the second line did not show negative patterns, with intercept very close to the maximum larval length. Non-experimental colonies demonstrated a similar pattern (linear regression: $R = 0.55$, $N = 28$, $p = 0.002$; Piecewise Linear Regression: $R = 0.83$, $N = 28$, $p < 0.001$; Break point = 32.58; first line equation: $y = 0.040x + 29.27$; second line equation: $y = 0.002x + 33.41$; comparisons between correlation coefficients, $p = 0.049$). Thus, a positive relationship between group size and larval length was due mainly to colonies smaller than 32 individuals in our population.

Table 2. Correlation analyses between larval growth during consecutive visits and number of larvae per experimental colony in the previous visit.

	r	*t*	*p*	*N*
Growth 1 *vs.* group size 0	0.68	7.06	0.001	59
Growth 2 *vs.* group size 1	0.20	1.55	0.124	59
Growth 3 *vs.* group size 2	0.41	3.34	0.001	55
Growth 4 *vs.* group size 3	0.48	3.82	0.001	50

Relationship between aggregation size and larval survival

All individuals died in 17% of the experimental colonies ($N = 60$), while only 7% of the non-experimental colonies ($N = 30$) disappeared. That difference was primarily due to the higher mortality rate of the smallest experimental colonies with 25 individuals (5 out of the 15 colonies disappeared before pupation).

The number of dead larvae per group did

not differ between experimental treatments (ANOVA: $F_{3,56} = 2.39$, $p = 0.07$) and, thus, experimental colonies with large numbers of individuals suffered a lower percentage of mortality (ANOVA: $F_{3,56} = 19.63$, $p < 0.001$, Fig. 3) regardless of the larval age (ANOVA: $F_{3,48} > 6.4$, $p < 0.001$). In the natural colonies, initial group size did not predict the final number of dead larvae ($R = –0.14$, $N = 30$, $p = 0.44$) and, as in experimental colonies, those with a large number of individuals suffered a lower percentage of mortality ($R = –0.43$, $N = 30$, $p = 0.016$). Therefore, although we did not find that experimentally manipulated small colonies suffered more from mortality (i.e. predation or parasitism) than large colonies, the probability of reaching the pupal stage was higher for larvae from colonies with a large number of individuals.

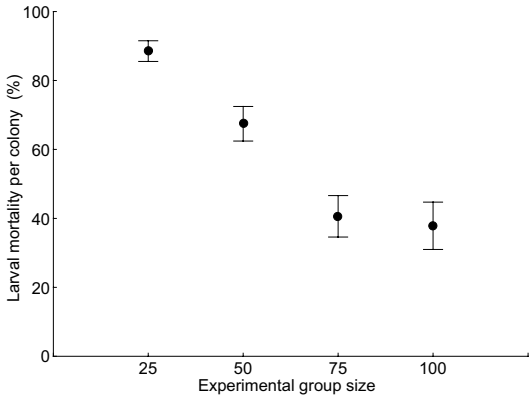

Fig. 3. The average percentage of larval mortality in the four group size treatments. Differences in the means were significant (ANOVA: $F_{3,56} = 19.63$, $p < 0.001$).

Discussion

Our results with *T. pityocampa* strongly support the hypothesis that aggregation enhances larval growth, in agreement on previous results on gregarious caterpillars (Long 1953, 1955, Lawrence 1990, Stamp & Bowers 1990c). The length of larvae from the experimental groups with the largest number of larvae was significantly greater than that of larvae from groups with a reduced number of individuals. However, no significant differences in growth rate or length appeared between the two largest groups, and the positive relationship between the final group size and larval length disappeared when taking into account only groups with more than 32 larvae. A large larval body size in *Thaumetopoea pityocampa* confers several advantages that result in a high probability of larvae reaching the pupal (Coyle *et al*. 1999) and adult stage (Kamata & Igarashi 1995). Moreover, body size before pupation is positively related to adult body size (Spurgeon *et al*. 1995), which in turn is related to female fecundity and adult dispersal capacity (Webber & Ferro 1996).

Large groups of larvae are known to have feeding advantages that would result in large body mass and growth. For instance, plant allelochemicals affect larval performance (Tallamy & Raupp 1991, Denno & Benrey 1997) and large groups would consume plant structures more quickly than would small groups, thus avoiding the brunt of induced plant defences, given the time required to produce chemicals and deploy them to the feeding site. Large groups may also benefit from their better thermoregulatory capacity (Porter 1982, Joos *et al*. 1988, Stamp & Bowers 1990c), which enhances larval growth (*see* Introduction). Although we have no data on feeding time or nest temperature, larvae from experimental groups I and II may have remained at the feeding site for a longer time and therefore have reached lower body temperature than those from groups III and IV. Thus, larvae from small groups may be subject to more severe negative effects of an induced chemical response by the pine (as shown for other species, Denno & Benrey 1997), in addition to less foraging time, and lower temperature, which could explain their lower growth rate.

On the other hand, larvae in large groups may suffer from a high intraspecific competition when suitable resources are limited (*see* Introduction). However, our experimental design considerably reduced intraspecific competition, given that in all pines more than 50% of pine needles remained uneaten after the larvae left the pine for pupation.

In any case, regardless of the causes for the high growth rates and large body sizes of the larvae from our largest experimental groups, our manipulation clearly affected these larval traits. In our experimental population, the average number

of larvae per group at the first instar was about 95. Following our results on larval mortality of natural groups (mean 40.2%, $N = 30$, SE = 4.1), 57 caterpillars from those groups of 95 individuals should survive to the last larval instar. Thus, this group size exceeds the minimum necessary to reach the maximum larval length (*see* break point in Fig. 2), and intermediate between final group size of our experimental groups III and IV (*see* Table 1). Interestingly, as is predicted from the optimisation theory, the average group size in our unmanipulated population coincides with that of maximizing larval size.

The causes of caterpillar death were related to malnutrition, group size (as explained above), parasitism, and predation (*see* Introduction), the latter being mainly related to group size (e.g. Damman 1987, Stamp & Bowers 1988, Hochberg 1991, *see* also Introduction). Thus, some life-history traits of caterpillars should have evolved to reduce these costs (Costa 1993). Defensive evolutionary responses may include specialized structures (setae, spines, tubercles, etc.), allelochemicals (secretion or regurgitation of toxic substances), and/or somatic modifications (crypsis and mimicry) (*see* examples in Owen 1980) that sometimes increase their effects as the caterpillar group size enlarges (*see* Introduction). Despite having no data on parasite- or predator-induced mortality for the experimental groups, our results clearly show a significant relationship between the size of the larval aggregation and the survival probability of individual larvae, and, therefore, it can be concluded that group size affects individual probability of survival until pupation.

Our experimental approach greatly reduced competition for resources among developing larvae (*see* above), and in all experimental groups some larvae survived until their last instar regardless of group size (*see* Table 1). These facts imply that, although we cannot rule out direct or indirect influences of plant chemical defences differentially affecting mortality in the various experimental group sizes (*see* above), most of the detected mortality should be due to parasitism and/or predation. Large groups of larvae may have suffered a low mortality rate by responding simultaneously to predator attacks using more effective defensive movements, releasing greater amounts of defensive chemicals, or building more elaborate and effective shelters (e.g. Morris 1972, Damman 1987). Conversely, smaller groups of pine processionary caterpillars may be less defended against predation simply because urticant receptacles (one of the main defensive mechanism in this and other species of caterpillars; Fitzgerald & Costa 1999), or other defensive mechanisms, may be more effective in large groups. However, with this explanation, independently of group size, we should find a larger number of dead larvae in the small than in the large experimental groups, but this was not the case (*see* Results). Therefore, although we cannot completely dismiss the possibility that caterpillar defences and group size were related in our results, it is unlikely mainly because group size also predicts other important variables affecting caterpillar survival (*see* above).

Another possible explanation for our results on caterpillar mortality is that the main predators and parasitoids of pine processionary larvae search for prey randomly, as occurs for some other species (Stamp 1980, Chew & Robbins 1984). Our results showing no differences in number of dead caterpillars between experimental groups (*see* Results) concurs with this explanation because if costs of individual detectability associated to group size were very important in our species or population, we should have found higher predation rates in larger groups. Thus, our results suggest that the main predators and parasites of pine processionary caterpillars are random searchers. In addition, the negative relationship between experimental group size and percentage of mortality also implies that predators and parasites do not detect larger colonies more easily than smaller ones. Hence, it can be predicted that caterpillars in large groups have a larger probability of survival than in smaller groups simply because of the dilution effect. Therefore, the negative relationship between group size and mortality found in this study, as well as the absence of differential mortality between group size treatments can be explained simply by the dilution effect of mortality risk in large groups.

Contrary to the last explanation, we found no differences in mortality rate between experimental groups of 75 and 100 larvae (*see* Results

and Fig. 3). Moreover, we found no differences in larval growth or body size in these two groups. This suggests that growth and body size could directly or indirectly (through associated variables such as foraging ability) affect larval mortality. These two experimental groups on average exceeded the 32 individuals per colony necessary to reach maximum larval size before pupation (*see* above) and approached the maximum survival rate (*see* Fig. 3). A larger number of individuals per group could be very costly for adult females mainly because the strong selection pressure exerted by parasitoids on eggs (more than 30% of the eggs per clutch resulted parasitized in our study population, T. Pérez-Contreras & J. J. Soler unpubl. data) and the cost associated to large clutch sizes. Hence, although it is clear from our results that groups with larger numbers of caterpillars than the average number in our population will boost adult fitness because more offspring will reach the pupal stage, groups with a reduced number of caterpillars (fewer than 32 during the last instar) would greatly reduce fitness because of the impact on offspring body size together with the lower probability of survival of individuals in small groups.

Although reasons for the association between group size and variables related to fitness in processionary caterpillar need further investigation, our results strongly suggest that larvae in large groups develop and survive better than those in small groups, thereby explaining why larvae of *T. pityocampa* live in large groups.

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