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Egg parasitoids select for large clutch sizes and covering layers in pine processionary moths (*Thaumetopoea pityocampa*)

Tomás Pérez-Contreras* & Juan José Soler

*Estación Experimental de Zonas Áridas (CSIC), General Segura 1, 04001 Almería, Spain (*e-mail: tomaspc@eeza.csic.es)*

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Female insects have a limited energy budget to invest in reproduction. Clutch size and egg size are two traits typically involved in energy budget trade-offs, and an optimum clutch size is generally predicted. This trade-off, however, is influenced by many factors including the probability of egg parasitism. We studied this possibility in the pine processionary moth (*Thaumetopoea pityocampa*), which frequently suffers from parasitoids. We found support for a trade-off between clutch size and egg size in this species, but the intermediate clutch size did not correspond to higher hatching success. We suggest that the lack of an optimum clutch size in relation to hatching success was mediated by parasitoids: parasitoids preferentially selected small clutches containing larger eggs. In addition, we experimentally tested whether the scales that coat egg batches reduce the effect of parasitism. Egg batches with experimentally removed scales showed a significantly higher parasitism rate than control batches, which demonstrates that scales protect egg batches from parasitoids. We discuss three possible explanations for our results.

Introduction

Offspring of many species receive parental care, which increases the probability of survival to adult stage and, therefore, the probability of successful reproduction (Clutton-Brock 1991). For species without parental care, like most holometabolous insects, the adjustment of traits such as clutch size and egg size that influence optimal offspring development is of prime importance (Bernays & Chapman 1994). For example, many phytophagous insects without parental care adopt the strategy of laying eggs in aggregated groups. In this case, the average number of eggs laid per plant and per female can be considered the result of a balance between the costs and benefits of different clutch sizes (Damman 1991, Crowe 1995).

Large clutch sizes would be advantageous if, for instance, they increase the effectiveness of defensive traits (Hunter 2000) or competitive ability relative to other clutches on the same plant (*see* examples in Alexander 1974, Pulliam & Caraco 1984). Larvae from those taxa, however, usually have a limited dispersal ability and only feed from the plant selected by the mother (Parker & Begon 1986). Therefore, clutch size would influence survival probability of an individual larva because limited resources will be competed for by siblings and other conspecific larvae (Charnov *et al.* 1976, Buss 1981). Moreover, a high number of eggs per plant would directly increase egg detectability for visual predators or parasitoids (Kareiva & Odell 1987, Dobson 1988), or indirectly increase egg detectability because herbivorous larvae may induce plant volatile emissions that attract predators or parasitoids (e.g. Hoballah & Turlings 2001, Kessler & Baldwin 2001).

An additional cost of large clutch size is the production of small eggs due to the general trade-off between clutch and egg sizes. In insects without parental care where reproduction is linked to earlier accumulated resources (capital breeders, Tammaru & Haukioja 1996) all of the female's available energy should be invested in the clutch because the residual reproductive value of these females is zero (e.g. Boggs 1997). For such species, an increase in egg size requires a decrease in clutch size. A larger egg volume implies a larger amount of proteins and resources for developing embryos (i.e. Begon & Parker 1986, Ricklefs & Stark 1998; for insects and birds, respectively) resulting in an increase in offspring quality and a higher probability of survival to the adult stage (Wiklund & Karlsson 1984, Braby 1994; but *see* also Wiklund & Persson 1983, Karlsson & Wiklund 1985; for controversial results). There may also be a trade-off between clutch size and clutch dispersion. When a female produces a large clutch, the female may produce fewer clutches over her lifetime and her progeny may be more concentrated in the habitat. When stochastic mortality factors are important it may be advantageous to produce smaller but more scattered clutches (Bernays & Chapman 1994).

Hatching success is also affected by abiotic (temperature, humidity, etc.) and biotic (predators, parasitoids, egg viability, etc.) factors. For example, small variations in temperature and/or humidity inside the egg are the main cause of embryo death in insects (Browder *et al.* 1991, Wolpert 1991). However, there exist several adaptations minimizing the effects of changes in environmental conditions on the embryo. One strategy is the construction of microhabitats by females in which to lay their clutches. This may be the case of some moths that isolate their clutches from external environmental conditions by covering them with protective layers (Montoya & Robredo 1972, Floater 1998, Schmidt *et al.* 1999).

Parasitoids are perhaps the most important biotic factor affecting hatching success in insects (DeBach & Rosen 1991, Wajnberg & Hassan 1994, Hoballah & Turlings 2001). Parasitoids generally kill or prevent the host from reproduction and, therefore, natural selection favours host traits that reduce probability of parasitism. One possible adaptation to counteract parasitism could be related to clutch size (Richner & Heeb 1995). In insects, an increase in a clutch size may compensate for losses during both egg and larval stages when host selection by parasites is not related to the clutch size (Hamilton 1971, Parker & Courtney 1984). However, parasitoids not only have to locate a potential host's clutches but also have to access the eggs. Accordingly, selection will favor host adaptations preventing accessibility of the eggs (Hawkins 1994). In this context, adding material or protective layers to the clutch could be another host adaptation that reduces the probability of parasitoids finding the clutch and/or accessing the eggs. If parasitoids exert a selection pressure on clutch characteristics, natural selection should favour: (i) small clutch sizes when the clutch size is positively related to the probability of parasitoids detecting the clutch (one would predict the opposite when larger clutches dilute the per capita parasitoid risk) (Hamilton 1971); (ii) clutches cryptic to the parasitoid, either in appearance or in odour; (iii) clutches with protective layers that make it difficult for parasitoids to physically access the egg.

In this paper, we study some potential factors affecting hatching success of the pine processionary moth (*Thaumetopoea pityocampa*). This moth lays all its eggs in a single clutch and covers the entire clutch with scales produced in the distal part of the abdomen (Schmidt 1990). Females lay a single clutch a few hours after emerging as adults and die shortly afterwards. Thus, this is an ideal species to study life history traits because it is possible to accurately estimate total female reproductive investment (i.e. clutch size, egg size) and variables related to reproductive success (i.e. hatching success). Here we examine the influence of clutch and egg sizes on hatching success and attempt to demonstrate a trade-off between these variables. If a trade-off exists (Hypothesis 1), we predict a negative relationship between number and size of the eggs in a clutch (Prediction 1a). Moreover, the result of that trade-off should be an optimal clutch and egg size and, accordingly, we should find that a quadratic function explains the relationship between clutch size and number of eggs that hatch successfully better than does a linear function (Prediction 1b), because a large number of eggs implies a small amount of resources per egg. Furthermore, the percentage of eggs that successfully hatch should be negatively related to the clutch size (Prediction 1c).

We also studied the negative impact of parasitoids on clutches of different size because the clutch size may affect the number of parasitoids visiting the clutch, or because a large clutch size may dilute the effect of parasitism (*see* above). If larger egg-batches are more easily detected by parasitoids (Hypothesis 2), we should find that larger clutches are more frequently parasitized (Prediction 2a). Moreover, if we assume that the number of parasitized eggs in a clutch is related to the number of parasitoids that find and parasitize a clutch, then larger clutches should have more parasitized eggs (Prediction 2b), but a smaller percentage of parasitized eggs (Prediction 2c), because of the dilution effect of the large clutch size.

From the parasitoid’s perspective, the parasite should choose clutches containing bigger eggs because these parasites lay one egg per host egg (pers. obs. for the parasitoid species in our study population) and a larger egg will provide more resources for a developing young (Hypothesis 3). If this is true, the percentage of parasitized eggs in clutches of larger eggs should exceed the percentage in clutches of small eggs (Prediction 3). The selective pressure of the parasitoid should select for an increase in clutch size due to the generalized trade-off between the clutch and egg sizes in nature (Hypothesis 4). Accordingly, we predict that the number of non-parasitized eggs per clutch should be positively related to the clutch size (Prediction 4).

We also experimentally tested hypotheses regarding the functions of layers coating batches by removing these layers from some clutches and keeping others untouched as a control group. If the main function of the coating is thermal insulation (Hypothesis 5), we expect that the incubation period (Prediction 5a) and number of eggs that failed to hatch (excluding parasitized eggs; Prediction 5b) will be higher in experimental clutches. Covering the egg batches could also increase clutch mimicry, thereby minimising the probability of clutches being detected by parasitoids (Hypothesis 6). If so, we predict that experimental clutches with removed coating layers will be more frequently parasitized than control clutches (Prediction 6). Finally, the coating may function as physical or “visual” barriers to the parasitoid because they prevent locating individual eggs in the clutch or impede the accessibility to host eggs (Hypothesis 7). All of these hypothetical barrier functions predict that the percentage of parasitized eggs should be greater in clutches with experimentally removed coating than in the control clutches (Prediction 7). It should be noted that these functional hypotheses are not mutually exclusive, but testing the above predictions will greatly impact our understanding of the adaptive function of the egg covering behavior.

Material and methods

Study site

The field study was carried out in a pine plantation 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.

Study species

The pine processionary moth is a highly gregarious species distributed throughout southern Europe, and is the principal defoliator of pines in the Mediterranean region (Devkota & Schmidt 1990). The flying and egg-laying periods, although dependent on factors such as weather and altitude, is usually from May to October (Douma-Petridou 1989). Each female lays only a single cylindrical clutch that she covers with scale-like hairs. Oviposition takes place on one or two pine needles predominantly from the base of the needles towards the tip (Schmidt *et al*. 1999). The number of eggs per batch is variable (between 37 and 312; reviewed in Schmidt *et al*. 1999), and varied in our studied population from 77 to 263 (mean = 181.56 ± 4.55, N = 90). Eggs hatch after 5–6 weeks (Schmidt 1989) and l arval development involves five instars (Douma-Petridou 1989). Although larvae move around to feed, they build a silk nest where all individuals from the same clutch stay when not feeding (Pérez-Contreras pers. obs.). 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).

With respect to parasitoids, in a previous study in a pine forest close to our study site, Schmidt *et al*. (1999) found only three species of Chalcidoidea with *Ooencyrtus pityocampae* being the most abundant (i.e. responsible for 70.8% of parasitism). This species frequently parasitizes host eggs in the basal sector of the clutch (Tiberi 1990), although other studies have shown this parasitoid to attack all parts of the egg-batches (Tsankov 1990). Egg parasitoids of *Thaumetopoea pityocampa* play a leading role in bio-control of the host, by reducing the population and with it the damage to the host plant (Biliotti 1958, Masutti 1964, Tiberi 1978). All above species of parasitoid either emerge in the summer when the host eggs are laid or in the following spring as mature larvae after overwintering in the parasitized egg (Tiberi 1990). To our knowledge, mechanisms of host selection or hyperparasite aviodance are unknown for those species. Parasitoid females deposit one egg per host egg and one female can parasitize approximately 27 eggs (Halperin 1990). It has been suggested that scales covering an egg clutch constitute an obstacle for successful parasitism (Biliotti 1958).

Variables studied

To carry out this study, we randomly selected 30 clutches from a single parasitized pine (*Pinus halepensis*) in 1994, 1995 and 1996. We collected all the egg batches after the egg hatching and parasitoid emergence periods. In the laboratory, we manually removed the scales covering the clutch and classified eggs into the following four categories:

- Hatched eggs: those with a big hole resembling the successful hatching of a host larva,
- Unhatched eggs: those with no hole,
- Partially-hatched eggs: those presenting a hole, but with a host larva dead inside, and
- Parasitized eggs: those with a small hole through which a parasitoid had emerged.

We dissected each of the unhatched eggs to determine whether the embryo was inside or if the egg was empty (Tsankov *et al*. 1996, 1998). The sum of these four egg categories is the clutch size. Hatching success is defined as percentage of eggs that successfully hatched. Since the widths of eggs that are generally laid around a couple of pine needles are relatively constant

Table 1. Inter-annual variation in clutch size, egg size, hatching success, and parasitism of egg batches of pine processionary moths. Sample size was 30 clutches in each year. For mean comparisons between year an ANOVA test was used. Values are means ± SE.

	1994	1995	1996	$F_{2,87}$	Probability
Length	2.79 ± 0.10	2.79 ± 0.09	2.95 ± 0.11	0.74	0.475
Clutch size	184.26 ± 8.58	184.53 ± 7.34	175.90 ± 7.85	0.38	0.683
Number of successfully hatched eggs	128.03 ± 9.42	142.46 ± 8.83	125.33 ± 8.05	1.09	0.337
Hatching success (%)	68.92 ± 3.84	76.47 ± 3.02	70.07 ± 2.16	1.73	0.187
Number of parasitized eggs	9.93 ± 1.57	6.40 ± 0.74	26.30 ± 2.67	26.23	0.000
Percentage of parasitized eggs	5.62 ± 0.94	3.56 ± 0.42	15.08 ± 1.43	35.87	0.000

(mainly egg lengths vary), we estimated an average egg size as clutch length (using a digital calliper, Mitutoyo, accuracy = 0.01 mm) divided by the clutch size. We use this index because it is very difficult to isolate eggs from the clutch without breaking them.

Experimental procedure

To test the functional explanations for the scale-like hairs coating the clutch, in 1995, at the beginning of the laying period, we randomly selected 40 pines that received only one clutch of the pine processionary moth. During the laying period, pines were visited every two days to detect laying date. When a clutch was detected it was randomly assigned to the experimental or control group. All of the egg batches selected were uniformly covered with scales. In the clutches belonging to the experimental group the scale-like hairs were manually removed, whereas the clutches in the control group were handled but hairs were not removed. All the clutches were visited 30 days after manipulations and every two days afterwards, to determine hatching date and, thereby, estimate the incubation period. Once hatching was detected, we collected all egg batches and, in the laboratory, estimated the variables previously described.

Statistical analyses

To achieve approximately normal distributions, we transformed the number of parasitized eggs by the formula log (x + 1), and the percentage of parasitized egg in the clutch by arcsin $((x/100)^{-0.5})$. After these transformations, none of the variables' distributions differed significantly from normal distributions (Kolmogorov-Smirnov test for continuous variables, $P > 0.1$), and thus the use of parametric tests was justified (Sokal & Rohlf 1995). To account for inter-annual variability in the number and percentage of parasitized eggs in a clutch (Table 1) we used residuals from year mean-values. All statistical tests were two-tailed and values are means (± SE).

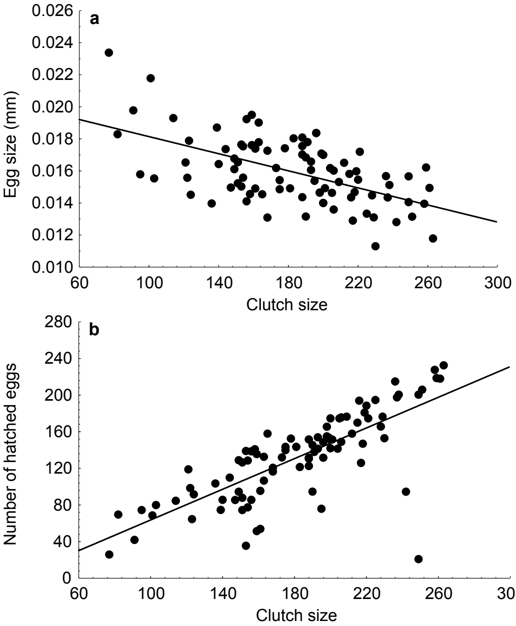

Fig. 1. (**a**) Relationship between clutch size and egg size in egg batches. Regression line is $y = 0.0001x + 0.020$; (**b**) Relationship between clutch size and number of hatched eggs in egg batches. Regression line is $y = 0.837x - 20.04$.

Results

Clutch size, egg size and hatching success

Our results show a highly significant negative relationship between the clutch size and the egg size ($r = -0.56$, $t = 6.33$, $N = 90$, $P < 0.00001$; Fig. 1a), as predicted if there exists a trade-off between these variables. The egg size, however, did not constrain hatching success: the number of eggs that successfully hatched in a clutch was positively related to the clutch size ($r = 0.760$, $N = 90$, $P < 0.00001$; Fig. 1b) and the square term was not significant (Partial regression coefficient of the square term (SE) = 0.0001 (0.001), $t = 0.34$, $P = 0.73$). Contrary to the egg size constraint hypothesis, we found that the hatching success was negatively related to the mean egg size ($r = -0.324$, $N = 90$, $P = 0.001$; Fig. 2). This result occurs because parasitism is an important determinant of hatching failure in pine processionary moths (average hatching failure due to parasitism = 31.5% ± 2.3%), and the number

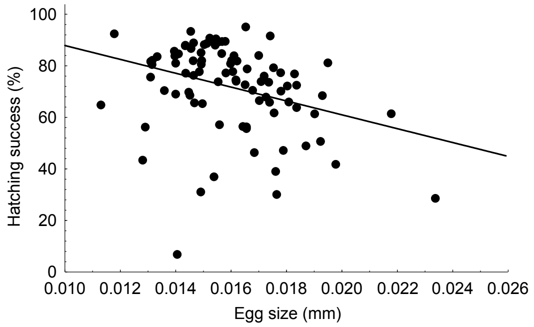

Fig. 2. Relationship between hatching success and average egg size of egg batches. Regression line is $y = -2687.8x - 114.7$.

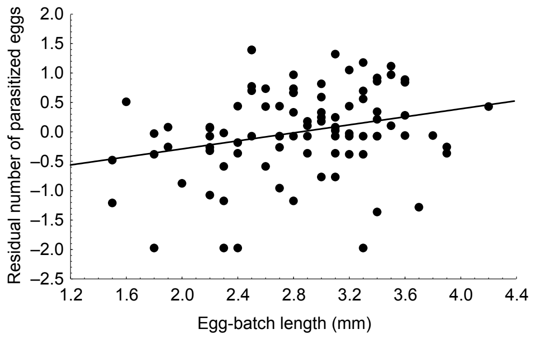

Fig. 3. Relationship between egg-batch length and number of parasitized eggs of egg batches. Residuals are log of number of parasitized eggs after controlling for year-to-year variation. Regression line is $y = 0.341x - 0.972$.

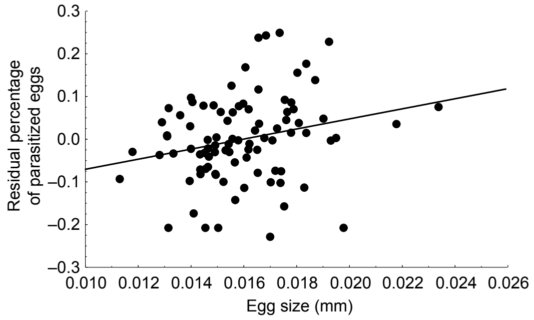

Fig. 4. Relationship between average egg size and percentage of parasitized eggs of egg batches. Residuals are arcsin of percentage of parasitized eggs after controlling for year variations. Regression line is $y = 11.80x - 0.188$.

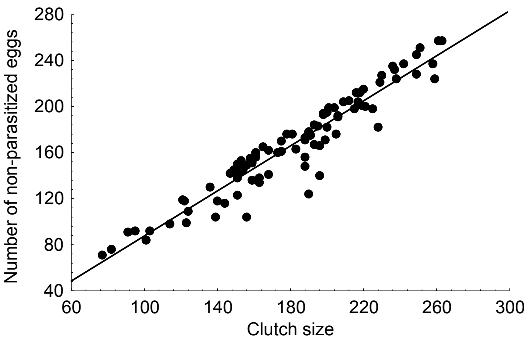

Fig. 5. Relationship between the number of non-parasitized eggs and clutch sizes of egg batches. Regression line is $y = 0.977x - 10.1$.

of unparasitized eggs is larger in clutches with small eggs (*see* below).

Clutch size, egg size, egg-batch size and parasitoids

We found one or more parasitized eggs in 95.5% of the analyzed egg batches ($N = 90$). Hence, contrary to Prediction 2a, egg-batch detection by parasitoids did not depend on the egg-batch length. However, in accordance with Prediction 2b, the number of parasitized eggs was positively and significantly related to egg-batch length ($r = 0.263$, $N = 90$, $P = 0.012$; Fig 3). Large egg batches were probably located by more individual parasitoids than were small egg batches. Accordingly, when analyzing the percentage of parasitized eggs in a clutch the positive relationship disappeared ($r = 0.03$, $N = 90$, $P = 0.78$).

From the parasitoid's point of view, selection of egg batches with larger eggs to parasitize would be beneficial due to greater resource availability for their offspring (Hypothesis 3). In agreement with this hypothesis, we found a positive relationship between average egg size and percentage of parasitized eggs in a clutch ($r = 0.24$, $N = 90$, $P = 0.023$; Fig. 4).

These results suggest that selection pressure from parasitism influences the trade-off between clutch and egg sizes. Females of the pine processionary moth maximize the clutch size. As such, laying eggs of small size should be advantageous because parasitism is the main cause of hatching failures, and the number of

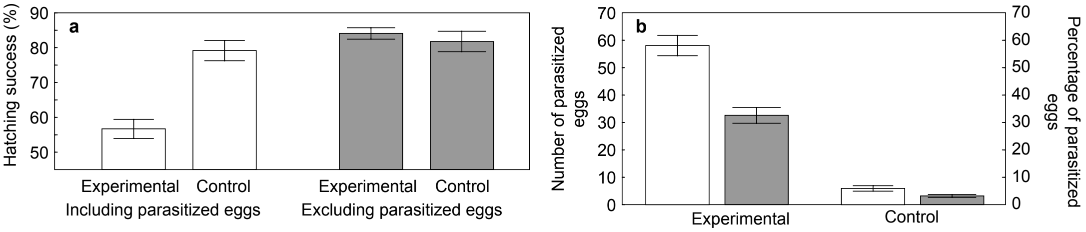

Fig. 6. (**a**) Hatching success of experimental and control egg batches including (empty bars) and excluding (filled-bars) parasitized eggs within a clutch. (**b**) Number of parasitized eggs (empty bars) and percentage of parasitized eggs (filled bars) of experimental and control egg batches are also shown. Whiskers represent standard errors.

unparasitized eggs increases with clutch size (Prediction 4) ($r = 0.95$, $N = 90$, $P = 0.00001$; Fig. 5).

Experimental tests of functional hypotheses of egg-batch coating

The incubation period of the control clutches was significantly shorter than that of the clutches with layer coats removed (Table 2), suggesting a thermoinsulative property of the scale-like hairs covering clutches (Hypothesis 4). In addition, hatching success was significantly lower in the experimental group ($t = 5.64$, df = 38, $P = 0.00001$; Fig. 6a). However, all clutches from experimental and control groups were parasitized. However the experimental group showed significantly more parasitized eggs per clutch ($t = 13.47$, df = 38, $P < 0.00001$; Fig. 6b) and, thereby, a higher parasitism rate ($t = 13.82$, df = 38, $P < 0.00001$; Fig. 6b). When we removed parasitized eggs from the analyses, differences in hatching success between experimental and control groups disappeared ($t = 0.68$, df = 38, $P = 0.49$; Fig 6a). These results strongly suggest that the scales protect the eggs against parasitism.

Discussion

Clutch size, egg size and parasitoid selection pressure

Clutch and egg sizes are traits typically involved in trade-off because females have a limited amount of energy to invest in reproduction and, as such, an increase in the clutch size is related to a decrease in the egg size (Stearns 1992). Given that the egg size is generally related to the probability of offspring hatching and reproducing (Begon & Parker 1986), a female should optimize clutch and egg sizes according to the environmental conditions (Stearns 1992). In insects, great intra- and inter-specific variations in clutch sizes exist. Most of this variation has been explained as the result of adjustments to adult phenotypic quality (Parker & Begon 1986), availability of resources (Osier *et al.* 2000), sibling competition (Mock & Parker 1997) or predation and parasitism (Moreau *et al.* 2000). Thus, variations in such selection pressures could influence the result of the trade-off between clutch and egg sizes. In accordance with a trade-off, we found a negative relationship between clutch size and egg size. However, an intermediate clutch size did not result in a

Table 2. Comparisons between egg batches with experimentally removed and non-removed (control) scales with respect to incubation time (in days), clutch size and length (mm) of the egg batches. Mean values (SE) are shown, and sample size is 20 for both experimental and the control groups.

	Experimental group	Control group	Statistical test
Incubation time	38.15 (0.42)	35.60 (0.36)	$t = 4.58$, $P < 0.001$
Egg-batch length	2.97 (0.13)	2.78 (0.11)	$t = 1.07$, $P = 0.287$
Clutch size	190.00 (11.12)	188.40 (8.66)	$t = 0.11$, $P = 0.910$

higher hatching success, as would be expected if optimum values of clutch size and egg size existed (Fig. 1b).

We explored the possibility that parasitism pressure could influence the trade-off between clutch size and egg size. Parasitoids are very common and may drastically reduce host reproductive success (i.e. Weseloh 1993). Natural selection should favour traits that counteract the effects of parasitoids, such as reduced reproductive effort when the risk of parasitism is high, thereby increasing the probability of survival for future reproduction (Keymer & Read 1993, Forbes 1993, Poulin *et al.* 1994, Richner & Heeb 1995). However, insects that reproduce only once do not have this possibility and should, therefore, invest as much as possible in their unique reproductive attempt.

Clutch size of insects with phytophagous larvae is typically constrained by the quality and quantity of resources available in the plant selected, because a large clutch size would decrease resource availability per individual larva (Parker & Begon 1986). However, in capital breeders (laying one single egg batch), the size of egg batches would not be constrained by any characters of the plant selected for oviposition, but would only depend on the resources a female has accumulated as a larva (Tammaru & Haukioja 1996). This should be the case for pine processionary moths because females lay all their eggs on the same individual host plant (*see* above). Occasionally, the infestation of host plants becomes very high, resulting in overcrowed trees and starvation of most of the caterpillars (Schmidt *et al.* 1999). In this case, parasitism of some of the eggs in the clutch, although decreasing reproductive success of adult moths, increases resource availability per individual larva. Accordingly, an increase in the clutch size could be adaptive because it counteracts the effect of parasitism.

This possible adaptation to counteract parasitism would have the cost of reducing an average egg size and thereby decreasing the hatching success (*see* above). However, parasitoids may select clutches with large eggs, which would provide a larger amount of resources for the parasitoids' offspring development (Rivero 2000). If so, in a population with high parasitism prevalence, larger eggs would not increase the probability of successful hatching. In accordance with this scenario, we found that the percentage of eggs that successfully hatched was higher in clutches of small sized eggs (Fig. 2), and that this was due to the preferential parasitism of clutches of large sized eggs (Fig. 4). Therefore, these results suggest that parasitoid pressure favours large clutches of small eggs in the pine processionary moth. In general, female insects maximize the clutch size independently of the hypothesized negative effects of the related decrease in egg size (Parker & Courtney 1984, Parker & Begon 1986, García-Barros 2000). The evolutionary explanation for the lack of optimal clutch and egg sizes may be related to the differential negative effects that parasitoids exert over clutches of large eggs.

Functional explanations of egg-batches' layer coats

Although there are several hypotheses explaining the function of the scales covering egg batches of some moth species (e.g. Montoya & Robredo 1972, Halperin 1990, Kitt & Schmidt 1993), none have been experimentally tested. Our results indicate a clear effect of scales on hatching success. Clutches with experimentally removed coatings experienced lower hatching success than control clutches. However, this result was mainly mediated by the differential negative effects of parasitoids over the experimental egg batches (Fig. 6). It should be noted that a thermoinsulating function, cannot be disregarded because incubation time was shorter for eggs in the control group (*see* Results). These results are in agreement with another study that has shown that the scales in the processionary pine moth increase egg-batch temperature (Milani 1990). Thus, the scales allow the eggs to develop more quickly.

There are several possible explanations for the result that the experimental clutches suffered more from parasitism than did the control ones. One explanation could be related to the hypothetical barrier effects that scales may have for parasitoids trying to gain access to the eggs. However, this hypothesis is unlikely because at least one egg was parasitized in all the experimental and control clutches.

A second explanation could be related to the possibility that the scales covering the egg batches camouflage the clutch and thereby minimize the probability of detection. Insects have a very limited visual discrimination (Heinrich 1984) and many species depend on their sense of smell to detect their prey (Vinson 1985, Wardle & Borden 1989). Thus, chemical rather than visual crypsis would be more likely in insects. In accordance with this functional hypothesis, we found that the experimental clutches were more frequently parasitized (more parasitized eggs per clutch) than controls (*see* Results). Alternatively, we also found that both experimental and control clutches were detected by parasitoids. Indeed, the larger egg batches did not show more parasitized eggs than smaller ones (*see* Results), as would be expected if chemical stimuli increased with the egg batch length.

Finally, a third possible explanation for the reduction of parasitism mediated by the scales covering egg batches would be that parasitoids are not able to locate individual eggs within a clutch because of the scales covering them. Parasitoids access the eggs by introducing the ovipositor perpendicularly (Hawkins 1994). The uncertain localization of individual host eggs could drastically decrease successful parasitism and increase the costs of detecting and parasitizing a host egg. Moreover, parasitoid moths in our study area lay a single egg per individual host egg (pers. obs.). Since host eggs are small and contiguous, parasitoids are not able to easily estimate their sizes in a clutch. Therefore, parasitoids should select eggs sufficiently distant to ensure that only one egg is laid per host egg. This may also explain why the clutches with small eggs suffered less from parasitism (*see* above). We believe that this also explains why the clutches without covering scales were more frequently parasitized than the ones with scales.

In summary, we find strong evidences supporting the hypothesis that parasitoids affect the resulting trade-off between the egg size and the clutch size in the pine processionary moth, and that scales covering the egg batches reduce the negative effects of parasitism. Most studies showing the influence of parasites in the evolution of host life history traits (*see* reviews in Clayton & Moore 1997) have been performed on birds. However, because many insects reproduce only once, and some of them lay all their eggs in the same batch, parasitoid–insect systems are ideal models for testing predictions related to the hypothesis that parasites affect their host's life history traits.

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