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**Ilkka Hanski: The legacy of a multifaceted ecologist**

# Group size, and egg and larval survival in the social butterfly *Melitaea cinxia*

Mikko Kuussaari[1,*] & Michael C. Singer[2]

[1] *Finnish Environment Institute (SYKE), Natural Environment Centre, P.O. Box 140, FI-00251 Helsinki, Finland (*corresponding author's email: mikko.kuussaari@ymparisto.fi)*
[2] *Biological Sciences, Plymouth University, Drake Circus, Plymouth PL4 8AA, U.K.*

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Gregarious, social caterpillars have stimulated research because group size may affect survival, growth rate, thermoregulation, and interactions with other species, yet group size is often variable both within and among populations. We used a combination of observations and experiments to study the importance of group size for egg and larval survival in the Glanville fritillary butterfly, *Melitaea cinxia*, which lives in groups from egg hatching until the last larval instar. Both experimental manipulation of egg clutches placed in the field and observations of naturally occurring groups showed that survival increased with increasing group size. This pattern was present independently during all four developmental stages studied: eggs, prediapause larvae, diapausing larvae and post-diapause larvae. However, it was significant only during two stages: pre-diapause (in one year only) and diapausing larvae (in all years). Large group size increased survival of entire larval groups as well as that of individual larvae within surviving groups. These results may explain why cluster size is large and why adults oviposit infrequently. Large cluster size, coupled with correlated survival of group members, in turn helps to explain the unstable local dynamics and short average persistence time of local *M. cinxia* populations.

## Introduction

Aggregation of potentially independent individuals into social groups occurs in almost all groups of animals (Hamilton 1971). Its adaptive functions are diverse: for example, collective decision-making in slime moulds (Reid & Latty 2016), efficiency of prey capture in lions (Caraco & Wolf 1983), enhanced vigilance of vervet monkeys (Josephs *et al*. 2016), aposematic display in *Tropidothorax* bugs (Gamberale & Sillen-Tullberg 1998) reduced risk of predator ambush in seals (DeVos & O'Riain 2010), and predator satiation in turtles (Santos *et al*. 2016). Lepidopterans are no exception: even though some 90%–95% of species lay their eggs singly (Stamp 1980), egg clustering behaviour, followed by gregarious behaviour of young larvae, occurs in a taxonomically diverse array of species, serves a diversity of functions and has evolved independently on at least 15 occasions in butterflies (Sillén-Tullberg 1988, Costa & Pierce 1997). In most species, larval aggregation is restricted to the first few larval instars (Zalucki *et al*. 2002) but in some species the larvae remain in groups almost until pupation (Fitzgerald 1993).

Oviposition in clusters has been suggested as an adaptation of adult female butterflies to conditions in which their reproduction would be time-limited rather than egg-limited if they laid eggs singly (Courtney 1984, Parker & Courtney 1984). However, most of the adaptive explanations put forward to account for the evolution of egg clustering address the consequences of gregariousness for success of the larvae rather than consequences of clutch size for their mothers' realized fecundities. Several field and laboratory experiments have demonstrated increased larval growth rate and survival with increasing group size (Lawrence 1990, Clark & Faeth 1997, Denno & Benrey 1997, Costa & Ross 2003, Reader & Hochuli 2003, Fordyce 2006). These effects reflect benefits accruing to larvae from group living that have been shown to include:

1. feeding facilitation during the first larval instar (Fitzgerald 1993, Clark & Faeth 1997, Zalucki *et al*. 2002, Reader & Hochuli 2003),
2. improved thermoregulation through group basking (Porter 1982, Stamp & Bowers 1990, Bryant *et al*. 2000) and larval webs (Casey 1993),
3. amplified strength of warning signals (Bowers 1981, 1993, Stamp 1980, Fitzgerald 1993, Riipi *et al*. 2001, Reader & Hochuli 2003), and
4. active defences like head-jerking behaviour (Stamp 1984), regurgitation (Stamp 1984, Peterson *et al*. 1987) and construction of protective webs (Fitzgerald 1993) and leaf shelters (Damman 1987).

The Glanville fritillary *Melitaea cinxia* (Nymphalidae), is a butterfly whose larvae remain in groups until close to the time of pupation (Thomas & Simcox 1982, Kuussaari 1998). This species has been the subject of detailed long-term studies of metapopulation dynamics in the Åland Islands (Hanski 2011, Ojanen *et al*. 2013). Investigations have shown that individual populations are typically unstable with frequent local extinctions and colonizations observed annually (Hanski 1999, Ehrlich & Hanski 2004, Hanski & Meyke 2005, Tack *et al*. 2015, Hanski *et al*. 2017). Mortality of larval groups is often high, but it varies much among years and in different stages of the larval development: prediapause, winter-diapause and postdiapause larvae (van Nouhuys *et al*. 2003, Tack *et al*. 2015). Typical to the study system is that in any one year a considerable proportion of local populations consists of only one group of diapausing larvae (usually the offspring of one female butterfly) and also inbreeding is common (Saccheri *et al*. 1998).

The aim of this study was to investigate the importance of group size for egg and larval survival in field populations of *M. cinxia* and to assess its role in population dynamics. We conducted a field experiment in which group size was experimentally manipulated — with group size varying from very small (10 eggs) to very large (500 eggs) — in order to be able to detect potential negative effects of unusually small and unusually large group sizes. Additional data on group size and larval survival was gathered by monitoring a large number of naturally occurring larval groups. In all cases we followed larval survival by counting larvae and measuring their locations in successive stages of their development in order to see how the effects of group size vary during larval growth.

## Material and methods

### Study organism

*Melitaea cinxia* is a widely distributed butterfly species in the temperate regions of Europe and Asia (Tolman 1997). In Finland, the distribution of *M. cinxia* is restricted to the Åland Islands in SW Finland, where the butterfly occurs in small local populations on several hundred dry meadows containing the larval host plants *Plantago lanceolata* (Plantaginaceae) and *Veronica spicata* (Plantaginaceae) (Hanski 1999, Nieminen *et al*. 2004, Ojanen *et al*. 2013, Hanski *et al*. 2017). In Finland, the butterfly has one generation per year.

Adult butterflies fly in June and lay eggs in batches underneath the leaves of host plants. The larvae are gregarious and spin a communal "feeding" web on the host plant immediately after hatching in July. On entering diapause, usually in August, the larvae change their colour from light-brown to jet black and form a compact group inside a "winter nest" made of dense silk very different in appearance and texture from the feeding web. Larvae become active again early in the spring, in late March or early April. They are still black and spend much time basking in the sun in conspicuous aggregations. They remain in groups typically until the beginning of the last larval instar and pupate within the vegetation close to the ground in early May.

## Egg batch size

We gathered data on egg batch sizes by catching 151 butterflies in the field and allowing them to oviposit on potted host plants in outdoor cages with one female per cage. Half (48%) of these females laid at least three egg clusters in captivity. The sizes of the egg batches obtained from the caged females were counted under a microscope. In addition, the sizes of 68 naturally occurring egg batches were estimated in the field without breaking the clusters of eggs.

## Monitoring of naturally-occurring eggs and larval groups

We collected information on a total of 1049 naturally occurring larval groups by surveying dry meadows occupied by *M. cinxia* in two larval generations in 1993–1994 and 1994–1995. A total of 588 and 461 prediapause larval groups were examined during the autumns of 1993 and 1994. During the springs in 1994 and 1995, 178 and 368 groups were re-examined after their winter diapause. In the summer of 1995, we searched for naturally occurring egg batches in four *M. cinxia* populations and checked the survival of the hatched larval groups ($n = 68$) later in August. During these surveys we always recorded information on every larval group and egg batch that we encountered.

During the autumn surveys we recorded the following variables for each larval group: local population, day of observation, estimated egg batch size (only in summer 1995), larval group size, larval web type (feeding web or winter nest) and larval winter nest size (area covered by the winter nest in $cm^2$; only in autumn 1994).

Group size of larvae in feeding webs was estimated directly by counting the larvae. This was not done when counts were made at the winter nest stage, because opening up the nest would have been destructive. Winter nest size (area covered by the winter nest in $cm^2$) correlated well with group size counted earlier in the autumn (Pearson's correlation for the log-transformed variables: $r = 0.91$, $n = 24$, $p < 0.001$). The strength of this correlation justified the use of the winter nest size as an estimator of group size. By this means, group size in winter nests was estimated on a scale from 1 to 4 based on the size of the nest. We marked the locations of egg batches and larval groups in the field with sticks and drew a map of the locations of the groups in each population in order to be able to monitor their development.

During spring we recorded the number of larvae in each larval group. No information was collected from groups that had potentially become mixed with their neighbours.

## Field experiment

To study the effects of a full range of potential group sizes on egg and larval survival in a natural environment, we conducted an egg-transplant experiment in which group size was experimentally manipulated. We used six egg-batch sizes: 10, 50, 100, 200, 300 and 500 eggs. Each size class was replicated 10 times, except size class 500, which was replicated 11 times. The total of 61 egg batches was divided among five meadow patches occupied by *M. cinxia* so that each meadow received one or two full sets of experimental egg batch sizes.

In order to obtain eggs for the experiment we caught female butterflies in the field, allowed them to lay eggs in cages and transplanted the eggs into the same habitat patch from which each butterfly was originally collected. After counting the eggs in the laboratory into equally sized clusters, we placed them in tiny nylon mesh baskets and transferred them to the meadows used for the experiments. Some of the experimental egg batches, especially those in the largest size class, included eggs from different females.

In the field, we selected plants for the experiment similar in shape, size and microhabitat to

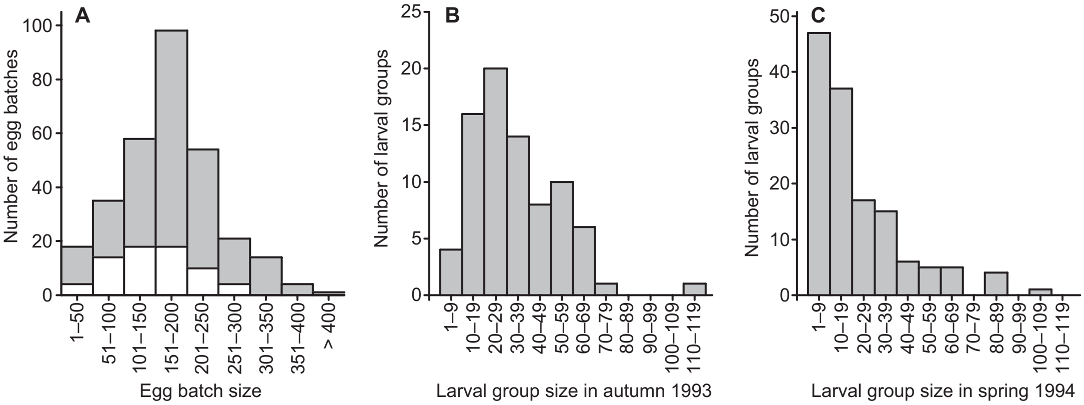

**Fig. 1.** Group size distribution in (**A**) eggs, (**B**) prediapause larvae during autumn ($n$ = 80), and (**C**) postdiapause, penultimate instar larvae during spring ($n$ = 137). In **A** the grey bars show the distribution of egg batch sizes ($n$ = 304, counted in the laboratory) of wild-caught butterflies allowed to oviposit in outdoor cages, whereas the white bars show the distribution of estimated cluster sizes for naturally occurring egg clusters ($n$ = 68).

the plants that *M. cinxia* females use for oviposition, but excluded especially small as well as isolated plant individuals in order to avoid starvation of larvae due to food limitation during the prediapause development. We hung the mesh baskets gently from a host leaf located close to the ground in similar places to those that the females prefer for oviposition. The leaf covered the basket completely and the group of eggs was located at the bottom of the basket within 5 mm below the host leaf. This method was expected to minimize egg predation, while the larvae hatched in a natural position, immediately below a host leaf. An advantage of this method was that the unhatched eggs remained in the basket and could be subsequently counted in the laboratory. In the beginning of the experiment, all egg clusters were located on plants with several other *Plantago* individuals within the normal movement distance of prediapause larval groups of *M. cinxia*.

We assessed egg survival by collecting the egg baskets after larvae had hatched and counting the remaining unhatched eggs. Larval survival was estimated by counting the surviving larvae in the field twice in the late summer and autumn and three times in the following spring. In contrast to the naturally occurring larval groups, in the transplant experiments it was possible to measure larval survival accurately also at the prediapause stage in the autumn.

### Statistical analyses

We analysed the effect of group size on egg and larval survival separately for four phases of development: egg stage, prediapause stage in autumn, diapause stage in winter, and postdiapause stage in spring. Survival of larval groups (0 or 1) and larval survival within the surviving groups (0–1) were analysed separately using logistic and linear regressions, respectively. Linear regression could be used because larval survival was normally distributed (Shapiro-Wilk's test). The effects of laying order on egg cluster size was tested using one-way ANOVA as egg cluster size was approximately normally distributed (estimated visually, *see* Fig. 1A).

## Results

### Group size

Wild-caught females allowed to oviposit in outdoor cages in 1996 laid 304 egg batches. The mean egg-batch size was 174 eggs (commonly varied from 50 to > 250 eggs; Fig. 1 and Table 1). The maximum egg batch size recorded in the laboratory was 453 eggs while the size of the smallest egg batch was 10 eggs only. The size distribution of egg batches that were observed in the field in 1995 matched the distribution observed in laboratory-counted egg batches (Fig. 1).

Following egg hatching in July, larval group size declined gradually until the time of pupation in the following spring when the larvae dispersed individually (Fig. 1). There was some variation in average larval group size between years. For example, in spring 1994 the average postdiapause group size was two times greater than in the previous spring (Table 1, Figs. 1B and C). The long tail in the group size distribution in the spring (*see* Fig. 1C) indicates high variation in within-group survival during larval development.

### Group size and survival

In the egg transplant field experiment, in the 61 groups the number of surviving individuals declined gradually at various stages of prepupal development (Fig. 2A). In this experiment, survival of entire groups was significantly positively affected by group size in two out of four developmental stages (Table 2 and Fig. 2C–D): in prediapause larval groups during autumn and in diapausing groups during winter. A similar pattern at the egg stage failed to reach significance (Fig. 2B), and group-level survival of post-diapause larvae was 100% (Table 2). Again in the experiment, within-group survival of individual larvae tended to increase with increasing group size in all life stages studied, but this pattern reached significance only for diapausing insects (Table 2 and Fig. 2E).

Natural survival of larvae varied greatly among groups and years (Table 1). The results from monitoring of survival of naturally occurring groups were in broad agreement with the experimental results in that all observed patterns comprised positive effects of group size on survival of both groups and individuals within groups (Table 2). The effect on overwintering survival of groups (Table 2 and Fig. 3A) was particularly clear with very high significance in both years of study, aided by large sample sizes. This result was almost identical in the field observations and in the experiment (Fig. 2D).

In contrast, other positive effects of group size in naturally occurring groups were less clear, being significant only in single study years for the following: within-group survival of prediapause and diapausing larvae, and group-level survival after diapause (Table 2). No negative effects of even the largest group sizes on survival were detected, either in the experiment or in the observations on naturally occurring groups.

## Discussion

The results showed that there is much variation in egg and larval group size in natural populations of *M. cinxia*, that survival increases with group size throughout larval development and that larval survival is highly variable both within and among years. Below we discuss each of these three issues separately.

**Table 1.** Variation in mean group size and survival of eggs and larvae of *Melitaea cinxia* in natural populations during 1993–1995. Number of egg batches and larval groups studied indicated by *n*.

| Developmental stage | Years | Group size | | | Surviving groups | | Within-group survival | | |
|---|---|---|---|---|---|---|---|---|---|
| | | mean | SD | *n* | fraction | *n* | mean | SD | *n* |
| Eggs | 1995[a] | 159 | 67.5 | 68 | – | – | – | – | – |
| | 1996[b] | 174 | 75.6 | 304 | – | – | – | – | – |
| Prediapause larvae | 1993 | 35.5 | 25.5 | 121 | – | – | – | – | – |
| | 1994 | – | – | – | 0.84 | 50 | 0.30 | 0.13 | 42 |
| | 1995 | 35.6 | 54.3 | 26 | 0.62 | 50 | 0.18 | 0.23 | 25 |
| Diapause | 1993–1994 | – | – | – | 0.77 | 170 | 0.52 | 0.33 | 61 |
| | 1994–1995 | – | – | – | 0.97 | 368 | 0.62 | 0.22 | 44 |
| Postdiapause larvae | 1994 | 22.3 | 21.6 | 105 | 0.94 | 64 | 0.70 | 0.30 | 60 |
| | 1995 | 42.4 | 33.1 | 232 | 1 | 37 | 0.89 | 0.17 | 37 |

[a] Field estimated sizes of naturally-occurring egg batches.

[b] Laboratory counted egg batch sizes from field caught females allowed to lay eggs on potted plants in cages.

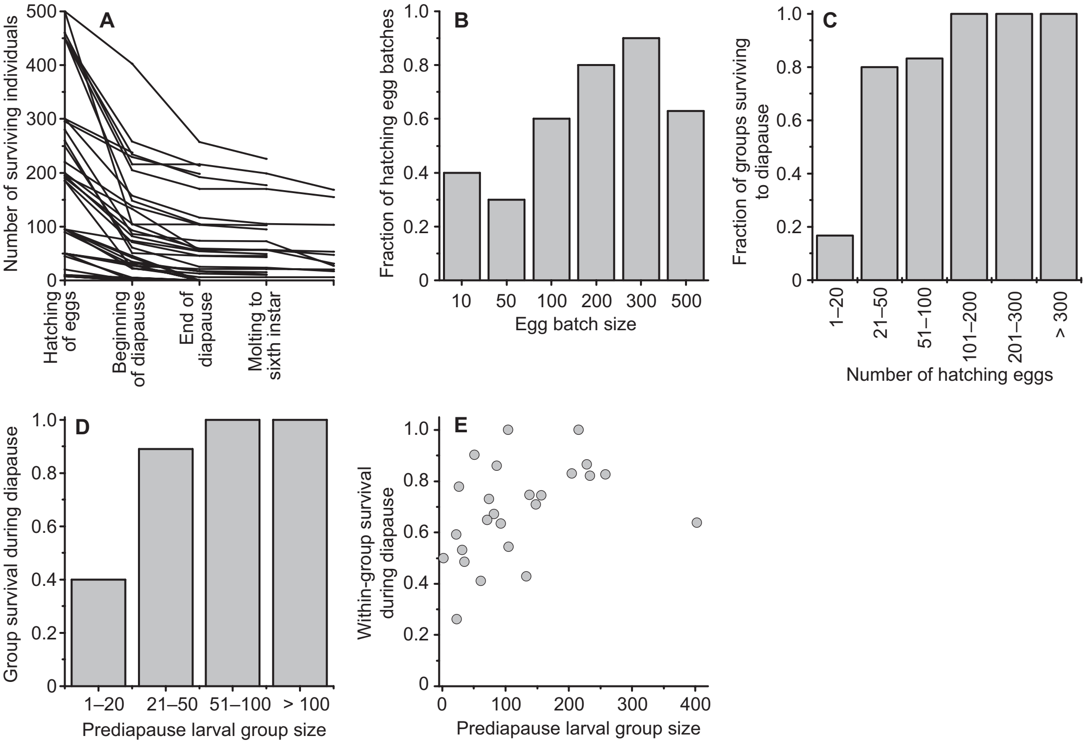

**Fig. 2.** Egg and larval survival in the group size field experiment. (**A**) Numbers of surviving individuals in the experimental groups at the various stages of development. The relationship between group size and the fraction of surviving groups (**B**) at the egg stage, (**C**) in prediapause larval groups and (**D**) in diapausing larval groups. (**E**) Within-group survival during diapause in relation to group size in those groups that survived over the winter. In **C**–**E** the relationship between group size and survival was statistically significant: (**C**) logistic regression: coefficient = 0.041, $p = 0.030$, 92% of cases classified correctly, $n = 37$; (**D**) logistic regression: coefficient = 0.102, $p = 0.048$, 93% of cases classified correctly, $n = 29$; (**E**) linear regression: coefficient = 0.0008, $r^2 = 0.13$, $p = 0.045$, $n = 25$.

## Variation in group size

Average cluster size was 174 eggs, which generated a fairly high probability of producing last instar larvae. However, small clusters with low probability of survival also occurred both in the field and in captivity. Why did adults lay clusters smaller than those that would maximize survival of their offspring? There are several very different reasons why this may occur. First, there is likely to be parent–offspring conflict. A female can increase offspring survival by delaying oviposition until an extremely large clutch can be laid. But once enough eggs have been matured to generate a clutch with relatively high survival probability, further delay poses a risk of the mother dying before those eggs are laid. Therefore, such delay may reduce maternal fitness even if it increases offspring survival. The balance between these opposing selective forces on clutch size is likely to shift with female age if older females mature eggs more slowly (Boggs & Nieminen 2004), as is suggested by the observed decline in size of successive clutches in females that laid several times. Based on the observations of 65 females that laid at least three egg clusters, the effect of laying order on egg-cluster size was significant (one-way ANOVA: $F_{2,192} = 9.15$, $p = 0.0002$). The first clusters laid in captivity (mean size = 201 eggs) were larger than the second clusters (mean size = 175), and the second clusters were larger than the third ones (mean size = 155).

A second reason for the observed clutches to be so small as to jeopardize larval survival is that oviposition may be interrupted at any stage, for example by attack from other invertebrates (Wahlberg 1995), reduction in solar insolation due to cloud cover (authors' pers. obs.) and presumably also due to harassment by conspecific males and grazing livestock. Egg predation by insect predators, e.g. lady beetles and lacewing larvae (van Nouhuys & Hanski 2004), may also be a reason for unusually small egg batches being observed in the field in cases when the entire cluster is not eaten.

Especially large larval groups in the field result from the fusion of groups when more than one egg batch has been laid on the same host plant, a phenomenon that is not uncommon in *M. cinxia*. A survey of naturally-occurring egg batches on 4300 randomly selected *Plantago lanceolata* plants in five *M. cinxia* populations demonstrated that — even in relatively low density populations of *M. cinxia* — some host plants receive more than one egg cluster, and that multiple egg batches on one plant occur more often than predicted by chance (Kuussaari *et al.* 2004). Laboratory experiments produced evidence for two mechanisms explaining the pattern observed in the field. Firstly, some host plant individuals tend to be especially attractive to egg-laying females (Singer & Lee 2000), and secondly, ovipositing butterflies are attracted to plants bearing conspecific eggs (Singer *et al.* 2017). The lack of observed negative effects on larval survival of even the largest group sizes in the present study suggests that laying eggs on a host plant already containing conspecific eggs may be adaptive for *M. cinxia* females, if density of host plants is high.

## Significance of group size for survival

Large group size increased both the probability of survival of groups as well as of the larvae within surviving groups. Group size has been shown to increase growth rate and survival in several other lepidopteran species (e.g. Lawrence 1990, Clark & Faeth 1997, Denno & Benrey 1997, Bryant *et al.* 2000, Reader & Hochuli 2003, Fordyce 2006, McBride & Singer 2010), whereas in some other studies positive effects only on growth rate and not on survival were found (Costa & Ross 2003). A number of hypotheses associated with both feeding efficiency and defence against natural enemies have been proposed to explain

**Table 2.** Effect of group size on survival at the egg stage and in three consequent stages of the larval development in the field experiment and in naturally occurring larval groups in 1993–1995. Survival of the entire groups was analysed using logistic regression, and survival within the surviving groups using linear regression. For further details (coefficients, percentage of correctly classified cases and $r^2$) of the main statistical results *see* captions to Figs. 2 and 3.

| Developmental stage | Survival | Field experiment | | | Naturally occurring groups | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | 1993–1994 | | | 1994–1995 | | | 1995 | | |
| | | *n* | effect direction[1] | *p* | *n* | effect direction | *p* | *n* | effect direction | *p* | *n* | effect direction | *p* |
| Eggs | entire group | 61 | (+) | 0.062 | | | | | | | | | |
| | within group | 37 | (+) | 0.748 | | | | | | | | | |
| Prediapause larvae | entire group | 37 | + | 0.030 | 13 | (+) | 0.147 | 26 | all survived | | 33 | (+) | 0.080 |
| | within group | 32 | (+) | 0.468 | 8 | (+) | 0.878 | 13 | + | 0.003 | 19 | (+) | 0.343 |
| Diapause | entire group | 29 | + | 0.048 | 169 | + | < 0.0001 | 392 | + | 0.0001 | | | |
| | within group | 25 | + | 0.045 | 61 | + | 0.009 | 19 | (+) | 0.428 | | | |
| Postdiapause larvae | entire group | 20 | all survived | | 64 | + | 0.035 | 17 | all survived | | | | |
| | within group | 20 | (+) | 0.747 | 60 | (+) | 0.778 | 17 | (+) | 0.107 | | | |

[1] Effect directions in parentheses are non-significant.

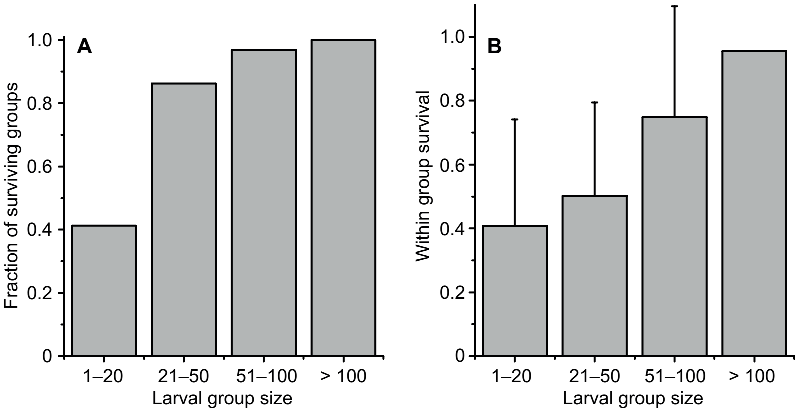

**Fig. 3.** Overwintering survival of naturally-occurring larval groups in relation to group size in 1993–1994. (**A**) Survival of entire groups (logistic regression: coefficient = 2.09, $p < 0.0001$, 81% of cases classified correctly, $n = 169$), (**B**) within-group survival (+ SD) in those groups that survived over the winter (linear regression: coefficient = 0.007, $p = 0.009$, $r^2 = 0.15$, $n = 61$).

the benefits of increasing group size (Clark & Faeth 1997, Costa 2006). In some species the advantages of large group size were restricted to the first one or two instars of larval development, but in *M. cinxia* the benefits of large group size last at least through diapause (normally in fifth instar) and possibly to almost full-grown larvae (Table 2). In melitaeine butterflies, the group to which *M. cinxia* belongs, there is much variation in mean egg cluster size and degree of gregariousness among species (Wahlberg *et al.* 2004). There is also heritable intraspecific variation: populations of Edith's checkerspot (*Euphydryas editha*) adapted to feed on *Collinsia* laid around 5 eggs in one clutch ten times per day while those adapted to *Pedicularis* laid about 50 eggs once per day (Singer & McBride 2010). Hybrids between the two laid around 25 eggs twice per day (McBride & Singer 2010).

In addition to group size, larval survival of *M. cinxia* is affected by several environmental variables. Both starvation due to food limitation (sometimes caused by unfavourable weather conditions) and parasitism by specialist parasitoids are common causes of larval mortality (Kuussaari *et al.* 2004, van Nouhuys & Hanski 2004, van Nouhuys & Punju 2010). Food shortage can occur where host plant density is low or when larval density is high, especially after winter diapause when the larvae are large and may completely defoliate host plants in large areas (first author's pers. obs.). Starvation may also happen when host plants wither before caterpillars have completed development. In the Åland Islands, large-scale starvation of prediapause larvae has occurred several times since the beginning of *M. cinxia* monitoring in 1993 because of occasional late-summer droughts which typically affect large areas simultaneously (Kuussaari 1998, Hanski 1999, Tack *et al.* 2015).

Two specialist parasitoids, *Cotesia melitaearum* and *Hyposoter horticola*, can both cause significant larval mortality in *M. cinxia* populations (Lei *et al.* 1997, van Nouhuys & Hanski 2004), but their effects differ in relation to *M. cinxia* population density (van Nouhuys 2005). In principle, *C. melitaearum* has the potential for reversing the positive effect of large group size during the postdiapause larval stage because the risk of parasitism of *M. cinxia* larval groups has been observed to increase with larval group size in areas of high parasitoid abundance (Lei & Camara 1999). However, because *C. melitaearum* rarely persists in low-density *M. cinxia* populations it rarely significantly affects its host's population dynamics (van Nouhuys & Hanski 2002, van Nouhuys & Punju 2010). In contrast to *C. melitaearum*, parasitism by *Hyposoter horticola* does not vary with *M. cinxia* density (van Nouhuys 2005). It typically causes ca. 30% mortality of the postdiapause larvae with very little spatial or temporal variation (van Nouhuys & Ehrnsten 2004, Couchoux *et al.* 2016). Therefore, it has only limited effect on *M. cinxia* population dynamics (van Nouhuys & Ehrnsten 2004, van Nouhuys & Punju 2010).

In addition to food limitation, unfavourable weather conditions and parasitism, substantial larval mortality is caused by cattle and sheep grazing (van Noordvijk *et al.* 2012) which is reflected by the significantly lower probability of occurrence of *M. cinxia* in grazed than in ungrazed dry meadows (Hanski *et al.* 1995, 2017).

In the group size experiment of the present study the above-mentioned four common causes of larval mortality played only a limited role (partly because they were avoided in the experimental design): host plant availability was not a limiting factor before winter diapause, there were no drought events in the study area during the experiment, the abundance of the specialist parasitoid, *C. melitaearum*, in the study populations was low and none of the experimental study sites was managed by grazing.

### Consequences of variation in group survival for population dynamics

A striking feature of the prepupal development of *M. cinxia* is the large variation in survival of all developmental stages. The results of the present study, together with those from monitoring survival of entire diapausing larval groups and post-diapause larval group sizes of all *M. cinxia* populations in the Åland Islands in 1993–2013 (Hanski 1999, van Nouhuys *et al.* 2003, Ojanen *et al.* 2013, Tack *et al.* 2015) show that variation in larval survival is high among years, among geographical regions, among local populations within the same region and among individual larval groups within the same population. It is clear that such high variation in survival of the developmental stages is also reflected in the population sizes of *M. cinxia*. Indeed, the local populations of *M. cinxia* have been observed to be exceptionally unstable, some 40%–50% of the small local populations going extinct every year in the Åland metapopulation (Hanski 1999, Nieminen *et al.* 2004, Ojanen *et al.* 2013, Hanski *et al.* 2017). High population fluctuations have also been typical for the monitored British populations of *M. cinxia* (Curtis *et al.* 2015).

Highly variable egg and larval survival are likely to be among the main causes of unstable local dynamics and short average persistence time of local *M. cinxia* populations. Factors contributing to high variation in egg and larval survival include varying weather conditions, e.g. the occurrence of late summer droughts (Hanski 1999, Nieminen *et al.* 2004, Tack *et al.* 2015), regionally varying parasitoid abundance (van Nouhuys & Hanski 2004) and genetic inbreeding depression (Saccheri *et al.* 1998, Nieminen *et al.* 2001, Haikola *et al.* 2001). The relative importance of these factors varies from year-to-year, but the recent results of Tack *et al.* (2015) suggest that the importance of spatially correlated weather effects has recently been increasing. This implies increased spatial synchrony in *M. cinxia* population dynamics which in turn has the general effect of reducing long-term metapopulation viability (Tack *et al.* 2015). The results presented here show that, in a very general sense and at several life-history stages, large groups out-perform small ones and individual larvae survive better in large groups. This will affect both local population dynamics and genetics, and contribute to the observed population instability.

Small populations frequently contain only a single surviving larval group and when this is so the effect of group size, with the initial size of the group positively related to the proportion of larvae surviving, will generate Allee effects (Kuussaari *et al.* 1998). The disproportionate contribution of large clusters to each cohort increases inbreeding and decreases effective population size relative to actual population size. These effects are clearly important in this system where inbreeding depression is widespread and population extinction rates are correlated with heterozygosity (Saccheri *et al.* 1998).

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