

Delayed density-dependent parasitism of eggs and pupae as a contributor to the cyclic population dynamics of the autumnal moth

Tero Klemola · Tommi Andersson · Kai Ruohomäki

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Abstract Many populations of forest Lepidoptera exhibit 10-year cycles in densities, with impressive outbreaks across large regions. Delayed density-dependent interactions with natural enemies are recognized as key factors driving these cyclic population dynamics, but emphasis has typically been on the larval stages. Eggs, pupae and adults also suffer mortality from predators, parasitoids and pathogens, but little is known about possible density relationships between mortality factors and these non-feeding life stages. In a long-term field study, we experimentally deployed autumnal moth (*Epirrita autumnata*) eggs and pupae to their natural enemies yearly throughout the 10-year population cycle in northern Norway. The abundance of another geometrid, the winter moth (*Operophtera brumata*), increased in the study area, permitting comparisons between the two moth species in predation and parasitism. Survival of autumnal moth eggs and pupae was related to the moth abundance in an inverse and delayed manner. Egg and pupal parasitoids dominated as density-dependent mortality factors and predicted the subsequent growth rate of the host population size. In contrast, effects of egg and pupal predators were weakly density dependent,

and generally predation remained low. Parasitism rates did not differ between the autumnal and winter moth pupae, whereas predators preferred winter moth pupae over those of the autumnal moth. We conclude that parasitism of the autumnal moth by egg and pupal parasitoids can be related to the changes of the moth density in a delayed density-dependent manner. Furthermore, egg and pupal parasitoids cannot be overlooked as causal factors for the population cycles of forest Lepidoptera in general.

Keywords Forest Lepidoptera · Insect outbreaks · Parasitoids · Predators · Population cycles

Introduction

Causal explanations for regular multiannual cycles in abundances of herbivores and their predators have been at the core of population ecology for almost 100 years (Elton 1924). It has come to be recognized that trophic-level interactions are almost certainly density dependent and commonly occur with a delay (Berryman et al. 1987; Berryman 2002; Turchin 2003). Because such interactions are complex (e.g. Elder et al. 2013), it has proven to be difficult to reach consensus, even within a single species, about what causes herbivore populations to cycle. The significance of a particular interaction might also be strongly dependent on local conditions. Furthermore, cyclic dynamics with identical signatures may be generated by several different ecological mechanisms, and consequently, observational data must be interpreted with caution.

Forest insects, lepidopterans in particular, have been one of the most studied groups of cyclic herbivores (e.g. Baltenweiler et al. 1977; Royama 1984; Tenow et al. 2007). These pests reach outbreak densities with devastating

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T. Klemola (✉) · T. Andersson · K. Ruohomäki
Section of Ecology, Department of Biology, University of Turku,
20014 Turku, Finland
e-mail: tero.klemola@utu.fi

T. Andersson
Kevo Subarctic Research Institute, University of Turku,
20014 Turku, Finland

impacts on single trees, whole forests and consequently, on forestry (Aukema et al. 2011; Jepsen et al. 2013). The dominant periodicity in population cycles and outbreaks of forest Lepidoptera has been around 10 years with relatively minor variation among species; most cyclic peaks or regular outbreaks occur every 8–11 years (Myers 1988; Dwyer et al. 2004), although both shorter and longer periodicities can occur (Royama 1984; Elder et al. 2013). According to the concept of delayed density dependence, the time lag required between the change in moth density and crucial feedback from the driving factor is roughly the length of the cycle divided by four (May 1981). This implies a 2- to 3-year feedback delay for many of the cyclic species. Field studies across several years and cycle phases are therefore essential for shedding light on cycle determinants.

Despite countless numbers of studies, there is still a shortage of generally accepted driving agents also for population cycles of forest Lepidoptera (Myers 1988; Myers and Cory 2013). This uncertainty suggests that key mechanisms could lie among trophic interactions that are neither apparent nor easily explored. Good examples are sedentary egg and pupal stages of the moths, whose interactions with the upper trophic level, i.e. natural enemies, have not been adequately studied, apart from studies of generalist predators of the pupae of winter and gypsy moths in the UK and North America (e.g. Frank 1967a, b; East 1974; Roland 1994; Elkinton et al. 1996, 2004; Raymond et al. 2002; Dwyer et al. 2004). This deficiency is particularly manifested when the eggs are laid singly on several different host plants and pupation occurs underground. For instance, parasitism studies that include egg and/or pupal parasitoids seem less frequent in studies of cyclic moth species (e.g. Klomp 1966; Baltensweiler et al. 1977; Münster-Swendsen 2002; Régnière and Nealis 2007; Klemola et al. 2009) than those focusing primarily on larval parasitoids (e.g. Ruohomäki 1994; Berryman 1996; Hagen et al. 2010; Schott et al. 2010), as the latter are relatively easy to sample, except during the cycle trough.

We assessed the density-dependent mortality due to natural enemies in egg and pupal stages of the autumnal moth (*Epirrita autumnata* Borkhausen; Lepidoptera, Geometridae), starting from an increase phase and continuing throughout the whole 10-year population cycle. This nocturnal moth is one of the most studied species of forest Lepidoptera with cyclic population dynamics (Ruohomäki et al. 2000; Myers and Cory 2013). During our 11-year study in northern Fennoscandia, the mountain birch [*Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti] forest experienced a severe moth outbreak, density collapse and low phase.

Another geometrid, winter moth (*Operophtera brumata* L.), abruptly exhibited outbreak dynamics in the study area halfway through the long-term study (Jepsen et al. 2008,

2013; Klemola et al. 2008). This permitted comparisons between the two moth species in egg and pupal predation and parasitism. Furthermore, we examined variation in the mortality factors in relation to either the autumnal moth's own abundance or pooled moth abundances. To test the premise that the mortalities inflicted by density-dependent factors during the egg and pupal stages are able to account for the population dynamics of the autumnal moth, we regressed the rate of population change on estimates of survival and levels of parasitism of eggs and pupae (Hagen et al. 2010; Schott et al. 2010).

Materials and methods

Study species and site

The closely related autumnal and winter moths are forest-dwelling geometrids that have wide distributions, covering large areas of boreal and subarctic zones in Eurasia and North America (Macphee 1967; Tenow 1972). The generalist larvae feed upon many deciduous trees and dwarf shrubs. Both species are serious pests, particularly on the mountain birch in the Scandinavian mountain chain and elsewhere in northern Fennoscandia (Tenow 1972; Haukioja et al. 1988; Jepsen et al. 2013) (Online Resource 1). In addition to the death of individual birches, large-scale defoliation during moth outbreaks have caused dramatic, landscape-level vegetation changes with slow recovery (Tenow et al. 2001; Jepsen et al. 2013).

Autumnal and winter moths have cyclic population dynamics in large areas of Fennoscandia (Online Resource 1). Peaks of density occur either with or without true outbreak levels fairly regularly every 9–10 years (Tenow 1972; Haukioja et al. 1988; Neuvonen et al. 1999; Ruohomäki et al. 2000). The density peaks and outbreaks of the two species have been synchronous, or, as is typical in many locations, the winter moth has lagged 1–3 years behind the autumnal moth for reasons that have not been comprehensively determined (Tenow 1972; Hogstad 1997; Tenow et al. 2007; Klemola et al. 2008, 2009; Hagen et al. 2010; Ammunét et al. 2014).

Autumnal and winter moths are obligatorily univoltine. In northern Fennoscandia, eggs that are mostly laid singly hatch concurrently with the budding of the mountain birch in the spring. Larvae feed on foliage through five instars by mid-summer when they descend from the trees and burrow into the soil to pupate. Autumnal moths eclose from mid-August to late September and winter moths from mid-September to mid-October. Autumnal moths are roughly twice as large as winter moths in all life stages.

Egg and pupal survival surveys were conducted within about 2 ha in a mountain birch forest area in Hana

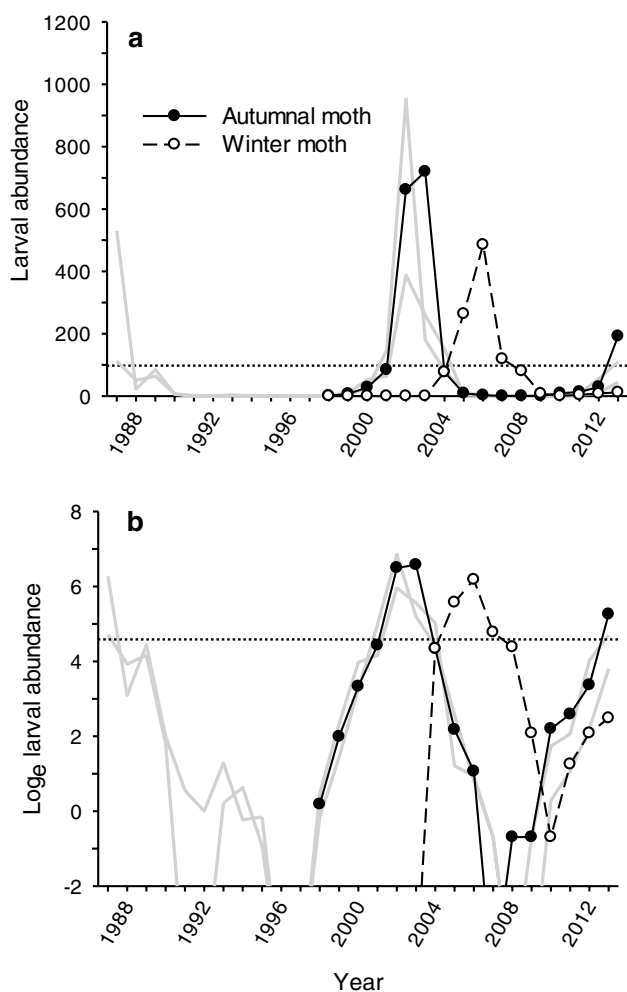


Fig. 1 Annual larval abundances (number of larvae around fourth instar in mountain birches per 10-min search) of autumnal and winter moths in the Hana study site, northern Norway, where egg and pupal survival surveys were conducted from 2001 to 2011. Larval abundances are given both in absolute scale (**a**) and after transformation by natural logarithms (**b**). Time-series data since 1987 (*grey lines*) of the autumnal moth are available for sites located 1.0 km (south-west) and 1.6 km (north-east) from the survey site. *Dotted horizontal line* gives the approximate larval abundance (100 larvae 10 min⁻¹) required for clearly visible defoliation of mountain birch forest, which can be considered as a lower limit for the outbreak density

(70°14'N, 28°27'E; 230 m a.s.l.), northern Norway (see map, Online Resource 1), where signs of the forthcoming density increase of the autumnal moth were observed in 1998 (Fig. 1). The Hana study site is at the transition zone between oceanic and continental areas, and winters are relatively mild compared to truly continental sites.

Estimation of larval abundance

Larval abundances of autumnal and winter moths were used as surrogate variables for annual egg and pupal

abundances, because there are no effective ways to estimate egg and pupal abundances, in order to avoid half of the years ending up with zero estimates. Larval abundance of the autumnal moth was estimated by one researcher (K. R.) observing mountain birch leaves at the same phenological stage each year, when the majority of larvae had moulted to the fourth instar (Ruohomäki 1994). With decreasing larval density, the search time was increased until approximately 15 larvae were found or a period of 1 h had expired. The number of autumnal moth larvae found per unit time was counted and an index of relative larval density per 10-min search was then calculated. This method has been superior to branch-specific larval counts during extremely low abundances at the trough of a cycle, because large amounts of leaves can be scanned in a relatively short time.

Winter moth abundance data are not available before 2004, due to the minor role it had at the Hana study site since monitoring began in 1987 (Fig. 1). For 2004–2006, winter moth larval abundance was estimated by counting the number of all geometrid larvae (in practice this means autumnal and winter moth only) on one random branch (50–100 cm long with about 100 short shoots) of ten random mountain birches. An index of larval numbers per 100 short shoots was then calculated separately for winter and autumnal moths (Tenow et al. 2007), and the obtained ratio between winter and autumnal moth numbers was used as a coefficient for converting the traditional larval density index of the autumnal moth (i.e. larvae per 10-min search) to that of the winter moth. From 2007 onwards, larval abundance of the winter moth was also estimated using the time-unit specific estimation method, similarly and at the same time as that for the autumnal moth. The pooled larval abundance index was summed for each study year from abundance estimates of the autumnal and winter moth. Finally, abundance indices for the autumnal moth alone and pooled with winter moth were natural log transformed and used as explanatory variables in statistical analyses. To obtain logarithm for statistical analyses, we substituted the smallest observed value (0.5 larvae 10 min⁻¹) for the zero value observed for the autumnal moth abundance in 2007 (see Fig. 1b). It was justified by time-series data from two nearby sites (Fig. 1), which both have the same larval abundance index (0.5 autumnal moth larvae 10 min⁻¹) for 2007.

Estimation of pupal predation and parasitism

The study of pupal predation and parasitism was conducted using established methods for the autumnal moth (Tanhuanpää et al. 1999). A total of 150 autumnal moth and 100 (only 50 in 2007) winter moth pupae were exposed yearly to pupal enemies for about 4–5 weeks (mean ± SE, 33 ± 0.7 days), which comprised approximately 70–80 % of the median natural pupal period in the study area.

Autumnal moth pupae were exposed in all study years, 2001–2011, whereas winter moths were added to the study in 2007. The pupal exposure trial was usually started in the first week of July (2–11 July, according to the phenology of the summer) and it was terminated in early August (2–15 August) before the beginning of the autumn flight season. To produce pupae for exposures, larvae from our breeding stocks were reared in the laboratory under parasitoid-free conditions and allowed to pupate in small plastic vials (48 ml) half-filled with pupation substrate of moist potting soil. The pupation substrate included glitter to enable easier retrieval of the cocoons after exposure (Tanhuanpää et al. 1999).

The study site had five different study plots situated some 50–100 m apart, with five parallel transects [three for autumnal moths and two (one in 2007) for winter moths] approximately 10 m apart in each plot. In each transect, ten conspecific pupae inside their cocoons were buried 2–4 cm into the soil or moss layer at 1-m intervals. Each buried pupa was marked with a wooden stick placed 10 cm from the pupa. During 2001–2007, three autumnal moth pupae (every third one) per transect (i.e. a total of 45 pupae per year) were buried in small cages of green plastic mesh (6 × 6 × 4 cm, 0.5-cm mesh, closed with a lid made of the same material). The cages were filled with moss and other natural soil material of the study site, resembling natural pupation substrates of the autumnal moth. With these protective cages, we clarified characteristics of pupal predators assuming that caged pupae could only be attacked by invertebrates small enough to get through the mesh, i.e. all parasitoids and small-sized invertebrate predators could enter the cages but vertebrate predators could not. In contrast, winter moth pupae were never protected by cages.

After field exposure, pupae were transferred to the laboratory where their fates (moth eclosion, parasitised, preyed upon or dead for unknown reason) were determined. Some pupae were found to have survived exposure, but the moth never eclosed (from a pupa). Because pupal parasitoids overwinter inside the pupal cocoon of the moth, all suspicious cases were retained intact in a refrigerator until the following spring. Invertebrate predation was identified by specific feeding marks on the pupa (Frank 1967a, b; East 1974). Predation by vertebrates, or potentially also by large-size invertebrates, was assumed to have occurred when the pupa had entirely disappeared (Tanhuanpää et al. 1999; Klemola et al. 2009). The status of parasitism was unknown for the pupae that were attacked by predators and these were considered as missing values in statistical analyses on parasitism. Similarly, the status of invertebrate predation was unknown for disappeared pupae, which were assumed to have been attacked by vertebrate or larger invertebrate predators (henceforth ‘vertebrate predation’). In contrast, both the successfully parasitised pupae as well

as those preyed upon by invertebrates were assumed to have survived vertebrate predation.

Estimation of egg predation and parasitism

Autumnal moths from our breeding stock were randomly mated, and females were allowed to lay their eggs (≤ 1 mm in length) on 4- to 6-cm-long, thin (diameter 4–5 mm) and dry (i.e. dead) sticks of pine (*Pinus sylvestris* L.) in plastic vials. The bark-covered, coarse-surfaced sticks were accepted by females, and the eggs adhered firmly enough that they could not be dislodged by shaking or during transfer to the field site. After oviposition, the sticks were checked under a stereo microscope. Surplus eggs were removed so that sticks had only two fertile autumnal moth eggs near (1–3 mm) each other. Fertilized red eggs were easily distinguished from unfertilized green eggs. Egg sticks of the winter moth were similarly produced, but because surplus eggs were not removed, varying numbers of eggs remained on the sticks. Within 1–3 weeks from oviposition, the egg sticks were attached by a thread to study trees at 0.5- to 1.5-m height in late August–early September (autumnal moth) or late September (winter moth) still at the time of natural oviposition. The exposure of autumnal moth eggs was conducted annually on 60–62 mountain birches (one stick with two eggs on each). The same study trees were used each year, and they were centrally located in the plots used in the pupal survival study.

The autumnal moth eggs were checked once a week during the flight season, but the checking was stopped over winter. Before egg hatching in spring, the eggs were again checked once a week. When live larvae had hatched from the eggs, the sticks with remaining eggs were taken to the laboratory to detect the emergence of parasitoids. In contrast, winter moth eggs were exposed on 17–20 mountain birches (one stick with a variable egg number on each) during the last four winters only, and were not checked until collection in spring.

Fates of the autumnal moth eggs were determined as survived, dead, parasitised or disappeared from the stick. Hatched eggs left a recognizable white egg shell, whereas dead eggs were wrinkled. Parasitoids emerged at room temperature not earlier than late July. In the three first exposures we unfortunately did not wait long enough to be able to record egg parasitism. Thus, some parasitised eggs were probably judged as dead. Before this study, egg parasitism had been poorly documented for the autumnal moth. At the beginning, we were aware of only one egg-larval parasitoid, *Copidosoma chalconotum* (Dalman) (family: Encyrtidae), which was, until recently, rarely found and only in non-outbreaking populations of the autumnal moth (Teder et al. 2000; Kenis et al. 2005). However, by collecting larvae for other purposes, we found for the first time in

summer 2012 that this parasitoid species parasitises autumnal moth in northernmost Fennoscandia, near the Hana study area. The current egg survival study revealed that both moth species are attacked also by an egg parasitoid whose adults emerge from eggs (see “Results”). In contrast to the autumnal moth, winter moth eggs were checked only for parasitoid numbers, not for successful hatching or death for unknown reasons.

Patterns of egg disappearances from the pine sticks offered an indirect way to assess whether autumnal moth eggs fell prey to predators or were just dislodged. A certain probability, p_d , could be assumed for the dislodgment of each egg in one checking interval. Consequently, two eggs of the same stick should have had a lower per capita probability (p_d^2) of disappearing than either one singly (p_d). However, our finding was clearly opposite to the assumption (see “Results”). Therefore, when both eggs of an egg stick were found to have disappeared at the same check, we assumed these to be taken by an ‘informed predator’. This kind of predator was assumed to restrict its foraging attention to the vicinity of the recent capture, i.e. an ‘area-restricted search’ (Kareiva and Odell 1987), and thereby prey on both adjacent eggs. These depredated eggs were also recorded as non-hatched, while their parasitism status remained unknown. In contrast, if only one egg disappeared, it was judged to have been dislodged, with the consequence that the status remained unknown for hatching, parasitism and predation (i.e. coded as missing data). The results from this procedure are naturally tentative, because there is no way to determine the reasons for egg disappearances during long winters.

Statistical analyses

Eight different \log_e -transformed abundance indices were analysed to disentangle patterns of density dependence in pupal and egg stages of the autumnal moth. The indices included either the abundance of the autumnal moth alone (Autumnal moth) as well as the summed (Pooled) abundance of the autumnal and winter moths. Both were further separated to be able to examine both direct (year t) and delayed (past 3 years, $t-1$, $t-2$, and $t-3$) density dependences.

Because response variables were dichotomous (e.g. a host was parasitised or not), generalised linear mixed models (GLMMs) with binary error distribution and logit link were used. Spatial and temporal arrangements of study designs were controlled for as random effects. Thus, the models for pupal survival (i.e. moth eclosion), parasitism and invertebrate or vertebrate predation included Year, Study plot nested within year and Transect nested within study plot and year as hierarchical random intercept effects. Due to convergence failures, the latter effect (transect) was

ignored in the models for the vertebrate predation of pupae. The main effect of the caging treatment (pupa buried inside a protective cage or uncaged) and its interaction with an abundance index were included as fixed effects, apart from in the models for vertebrate predation, in which the cage totally prevented predation (i.e. disappearance of the pupal cocoon). GLMMs for egg hatching, egg parasitism and predation or disappearance included only one of the abundance indices at a time as a fixed effect and Starting year as a random effect to control for unknown (e.g. climatic) effects associated with year.

All the GLMMs for density dependences were fitted with the GLIMMIX procedure of SAS version 9.3., using maximum likelihood estimation based on the Laplace approximation (Stroup 2013). Because values of the dispersion parameter (Pearson’s χ^2 divided by df) were always reasonably close to 1, and in most cases slightly less than 1, there was no evidence of overdispersion. For each response variable, the candidate models were compared and ranked by their values of Akaike information criterion corrected for small samples (AICc). These assessed the performance of models based on goodness-of-fit and a penalty for the number of estimated parameters (Burnham and Anderson 2002). The penalty component played a minor role here, as all the candidate models were parsimonious. Because abundance indices as explanatory variables were strongly correlated among each other (due to the fact that autumnal moth abundance equalled pooled abundance in the beginning and that successive years of the same cycle phase caused autoregressive processes), only one abundance index at a time was entered into the model to avoid problems in statistical and inferential interpretation (Graham 2003). For the same reason, we did not want to emphasize one particular model and abundance index as a definite ‘winner’, but rather looked for broader divisions between the autumnal moth’s own and pooled abundances, and on the other hand, between direct and delayed density dependences. To help readers to do the same, we have tabulated parameter estimates of abundance indices from all models in Online Resource 2, although predictions of the best-ranked models only are illustrated with figures. For clarity, graphs were produced with the NOBLUP option, which does not use the predictors of the random effects in computing the predicted values with their confidence intervals.

Predictive powers of survival rates of exposed eggs and pupae, as well as those of their parasitism levels, were analysed on the population growth rate of the autumnal moth by simple linear regressions. The response variable, annual population growth rate [$\log_e(N_{t+1}/N_t)$], was based on larval abundances (N_t) estimated before (year t) and after (year $t + 1$) the pupal or egg exposure in the field.

Differences in the probability of predation and parasitism between autumnal and winter moth pupae were tested

with binary GLMMs with Species, Year and their interaction as fixed explanatory factors. Hierarchical random effects were Study plot nested within year and Transect nested within study plot and year. Abundance indices of the moths were not used, because only 5-years of data (i.e. half a cycle) were collected for the winter moth. Only uncaged pupae were considered throughout. Furthermore, the Kenward–Roger approximation was specified, as recommended on certain conditions for non-Gaussian mixed models (Stroup 2013). The Kenward–Roger method applies SE and denominator *df* correction for the fixed effects facilitating accurate *F*-tests (Kenward and Roger 1997). The between-species analyses were conducted using the residual pseudo-likelihood estimation technique of the GLIMMIX procedure.

Results

Abundance of moth larvae

Outbreaks of autumnal moths were recorded at the Hana area between the mid- to late 1980s and in the early 2000s (Fig. 1). In 2013, the density reached the outbreak level again. The cycle peak in mid-1990s was truncated at a lower density that was apparent only when the data were plotted on a logarithmic scale (Fig. 1b). This was a ‘true’ peak in the sense that it occurred simultaneously with large-scale outbreaks of the autumnal moth elsewhere in northern Fennoscandia (Ruohomäki et al. 1997; Tenow et al. 2007).

During the period (2001–2011) over which egg and pupal survival surveys were done, the larval abundance of the autumnal moth was consistent with two nearby sites that have been monitored for a longer time (Fig. 1). The autumnal moth cycle peaked in 2002–2003, when the larvae caused practically 100 % defoliation of mountain birches. Thereafter, the abundance of the autumnal moth decreased rapidly, hit the trough in 2007–2009 and started a new increase. The winter moth cycle peaked in 2005–2007 and crashed in 2008–2010. Overall, a bimodal geometrid outbreak occurred at the survey site in the six consecutive summers of 2002–2007 (Fig. 1).

Pupal predation and parasitism

Density dependence in predation and parasitism of autumnal moth pupae

Figure 2 illustrates the relationships between the percentage distributions of recorded-fate categories of autumnal moth pupae. Clear reciprocal, year-to-year variation was recorded between the proportions of successful moth

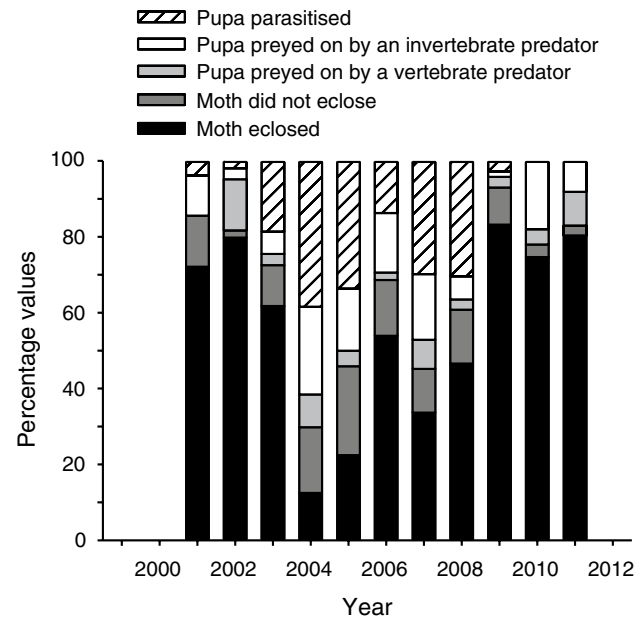


Fig. 2 Percentage distribution of recorded fates in the survival study of autumnal moth pupae conducted in the Hana study site during summers 2001–2011. Study design remained unchanged, apart from the abandonment of the caging treatment after 2007. For consistency, the distribution is given only for freely (i.e. no protective mesh cage) buried pupae also in 2001–2007

eclosion and pupal parasitism (Fig. 1a, Online Resource 3), whereas pupal predation by both invertebrates and larger predators (assumed to be mainly vertebrates) varied relatively little during the study period (Fig. 2). A positive relationship was apparent between the proportions of pupae parasitised and moths that survived the field exposure but did not enclose successfully (Fig. 1b, Online Resource 3). Information on observed pupal parasitoids and potential predators can be found in Online Resource 4.

The high year-to-year variation in the moth eclosion (range 12.5–83.2 %, mean \pm SE, 56.5 ± 7.5 %; these descriptive statistics for freely buried pupae only; see also Fig. 3a) was inversely related to several moth abundance indices (Table 1a, Online Resource 2). The highest-ranked model judged by the smallest AICc value included the interaction between autumnal moth abundance 2 years earlier and the caging treatment as a significant explanatory factor. Accordingly, predicted probability values for the moth eclosion in relation to the selected abundance index (autumnal moth $t-2$) were drawn with specific slopes and intercepts for both free and caged pupae (Fig. 4a). As can be seen, the eclosion of the free pupae, but not that of the caged pupae, was inversely dependent on the moth abundance. Other highly ranked models similarly included past moth abundances (autumnal moth $t-3$, pooled $t-1$ and pooled $t-2$) as

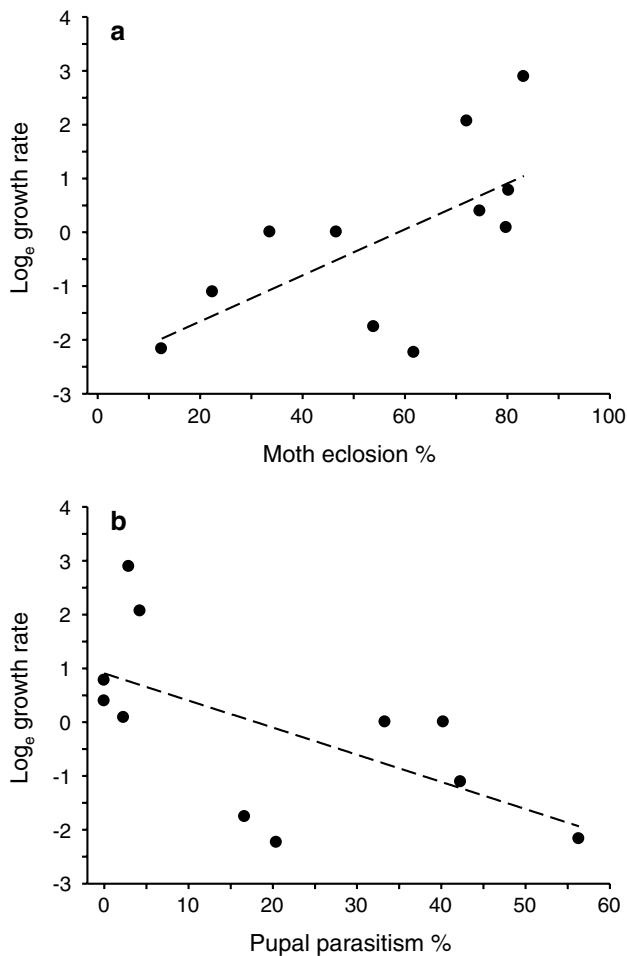


Fig. 3 The annual population growth rate [$\log_e(N_{t+1}/N_t$; where N_t is larval abundances in year t)] of the autumnal moth regressed on the percentage of eclosed moths (**a**), or on the percentage of parasitism of the pupae exposed to natural enemies in the Hana study site (**b**). For consistency, data are based on freely buried pupae only. Note different scales in *x*-axes. Slope (*b*) estimates (95 % confidence limits) and test statistics: moth eclosion, $b = 0.043$ (0.004–0.081), $t_1 = 2.5$, $P = 0.033$, $r^2 = 41.2$ %; pupal parasitism, $b = -0.051$ (–0.099 to –0.002), $t_1 = -2.4$, $P = 0.043$, $r^2 = 38.0$ %

significant explanatory factors. In these models, slope estimates were significantly negative also for the caged pupae. The probability of eclosion, in general, was higher for the caged than free pupae in all the models analysed (see example in Fig. 4a).

Yearly percentage parasitism of the pupae varied considerably during the study (range 0–56.3 %, mean \pm SE, 19.9 ± 6.1 % for freely buried pupae in data validated for further analyses, see Materials and methods and Fig. 3b). Several abundance indices had statistically significant, positive slope estimates (Table 1b, Online Resource 2). The highest ranked GLMM included the delayed effect of the pooled moth abundance (pooled $t-1$) in interaction with the caging treatment (Fig. 4b).

Among the models ranked next, explanatory factors included again the past moth abundances (pooled $t-2$ and autumnal moth $t-3$). The probability of parasitism was slightly lower for caged pupae, as is also illustrated in Fig. 4b.

Yearly pupal predation by invertebrate predators varied but always remained at a moderate level (range 1.4–25.3 %, mean \pm SE, 12.0 ± 2.3 % for freely buried pupae), and it did not show any evidence of density dependence (Table 1c, Online Resource 2; Fig. 4c). However, the main effect of the caging treatment was significant in all the models; the probability of predation by invertebrates was lower for the caged pupae than for free pupae (Fig. 4c).

Totally lost pupae that were interpreted as been taken by larger predators did not reveal any density-dependent effects (Table 1d, Online Resource 2; Fig. 4d). Here only free pupae were considered, because none of the cage-protected pupae entirely disappeared. The yearly proportion of totally lost pupae was low (range 0–13.5 %, mean \pm SE, 5.2 ± 1.2 %) throughout the study.

Overall, the annual population growth of the autumnal moth seemed to be affected by survival during the pupal stage (Fig. 3a). Regarding the strongest density-dependent mortality factor, the host population growth tended to decrease when the percentage of pupal parasitism increased (Fig. 3b).

Comparisons between autumnal and winter moths during 2007–2011

Because no single autumnal moth pupa (Fig. 2), and only one winter moth pupa, was parasitised in the two last study summers, the between-species analysis of parasitism was restricted to data from summers 2007–2009. Parasitism did not differ between autumnal and winter moth pupae (species, $F_{1,164.5} = 1.3$, $P = 0.25$; species \times year, $F_{2,88.7} = 2.4$, $P = 0.097$; Fig. 5a), but decreased (year, $F_{2,18.7} = 14.1$, $P < 0.001$) from 2007 onwards, being virtually zero in 2010–2011.

Winter moth pupae consistently had slightly higher levels of invertebrate predation than autumnal moth pupae throughout the study years (species, $F_{1,263.2} = 4.4$, $P = 0.038$; species \times year, $F_{4,112.5} = 0.2$, $P = 0.94$; Fig. 5b). In addition, significant among-year variation occurred in invertebrate predation of moth pupae (year, $F_{4,30.6} = 8.8$, $P < 0.001$).

Totally lost pupae were consistently more common among winter than among autumnal moth pupae (species, $F_{1,108.2} = 47.9$, $P < 0.001$; species \times year, $F_{4,102.0} = 1.3$, $P = 0.27$; Fig. 5c). The among-year variation was relatively minor and consistent between the moth species (year, $F_{4,25.1} = 2.0$, $P = 0.13$).

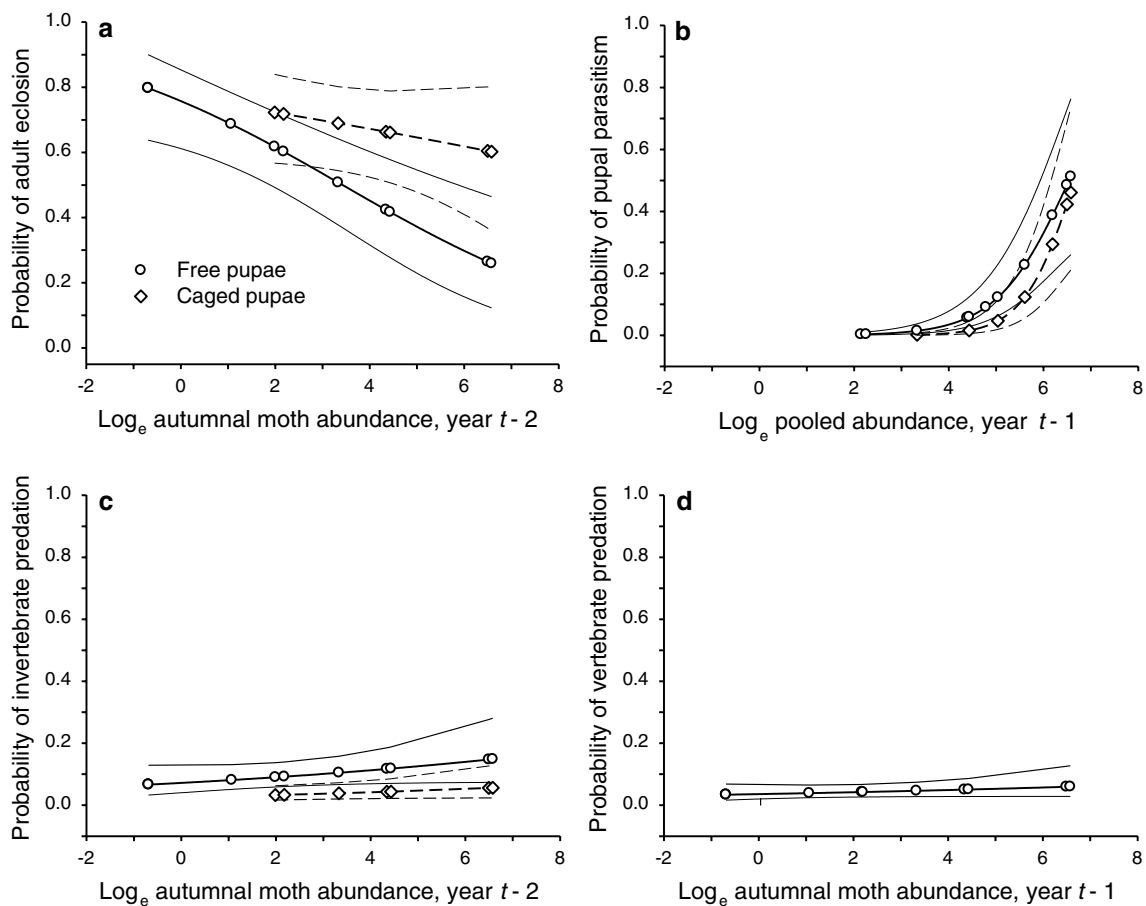


Fig. 4 Logistic regression curves (with 95 % confidence limits) predicting the probability of successful eclosion of adult moths (a), pupal parasitism (b), invertebrate predation (c) and vertebrate predation (d) in relation to a moth abundance index that was ranked the

best in the model comparison (see Table 1, Online Resource 2). Axis scales are the same in all graphs, although the explanatory variable and its distribution vary

Egg predation and parasitism

Density dependences in predation and parasitism of autumnal moth eggs

The proportions of autumnal moth eggs that hatched successfully and eggs that were parasitised varied in a reciprocal manner among years (Fig. 6). Although egg parasitism was not recorded during the first three exposures, even logical maximum values for these years (i.e. assuming that all unhatched eggs were parasitised) seem to fit well to the general pattern (Fig. 2a, Online Resource 3). Proportions of eggs that disappeared (one egg per stick) or were assumed to be depredated by informed predators (both eggs per stick disappeared) varied relatively little during the study period (Fig. 6). Parallel to the study with pupae, the proportions of eggs parasitised and the eggs that remained intact but did not hatch successfully later were positively related (Fig. 2b, Online Resource 3). Information on egg parasitoids and potential predators can be found in Online Resource 4.

The probability of the eggs hatching was highly variable and inversely related to density (range 5.4–84.0 %, mean \pm SE, 43.3 ± 10.4 % in data validated for further analyses, see Materials and methods) (Figs. 6, 7a, 8a; Table 2a, Online Resource 2). The highest ranked GLMMs included delayed effects of moth abundance, especially those including past abundance of autumnal moth alone (autumnal moth $t-3$ and autumnal moth $t-2$) (Fig. 8a), although the slopes were steeper for the models including pooled abundance (especially pooled $t-1$).

With the winters of 2004/2005–2010/2011 included in the analysis, the yearly percent parasitism of the exposed eggs varied greatly (range 0–45.1 %, mean \pm SE: 25.6 ± 7.1 %) (Figs. 6, 7b). Several abundance indices had statistically significant slope estimates (Table 2b, Online Resource 2). Among the highest ranked models, those including pooled abundance as an explanatory factor had generally steeper positive slopes than the models with the abundance of autumnal moth alone. The model with the pooled abundance of both moth species without a time lag

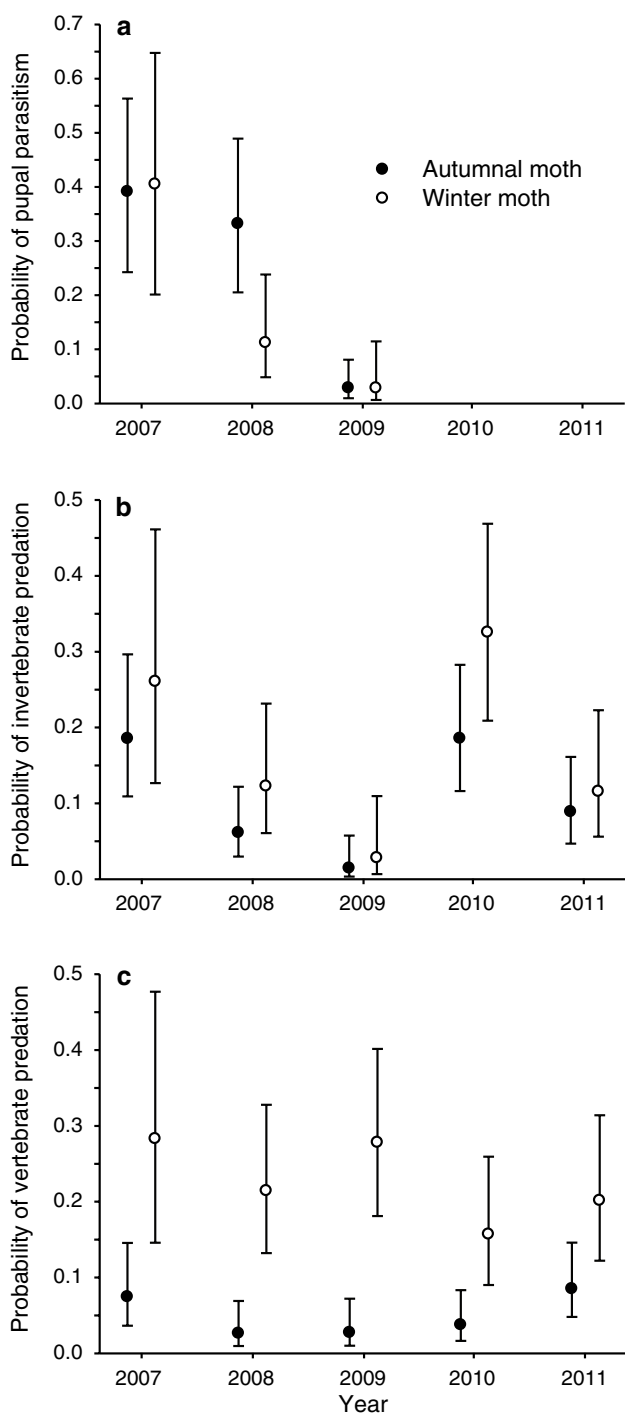


Fig. 5 Estimated marginal means (with 95 % confidence limits) of the species-specific probability of pupal parasitism (a), invertebrate predation (b) and vertebrate predation (c) in 2007–2011. Estimates are from binary GLMMs with species, year and their interaction as fixed explanatory factors (random effects are described in “Materials and methods”). Only data for 2007–2009 were included in analyses of pupal parasitism, because of zero parasitism in other years. Note different scales on y-axes

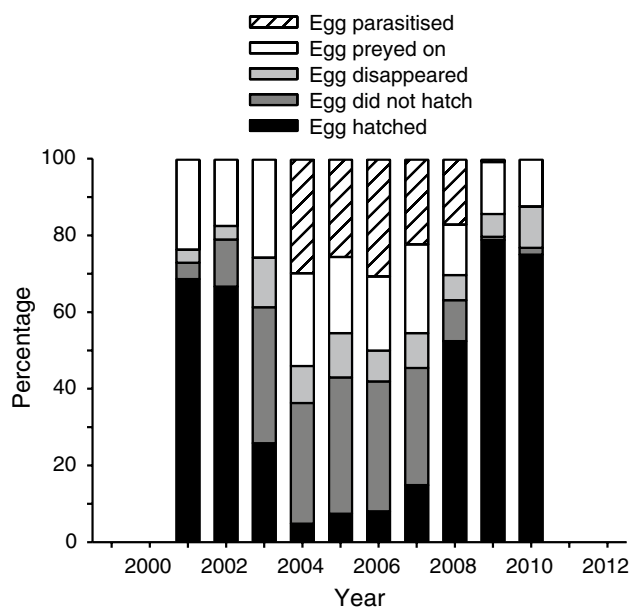


Fig. 6 Percentage distribution of recorded fates in the survival study of autumnal moth eggs conducted in the Hana study area during winters 2001/2002–2010/2011. Stacked bars are for different years according to the initiation of the egg exposure in autumn. This position on the x-axis refers to year *t*, which was used in statistical analyses. Study methods were the same throughout, but egg parasitism was not recorded before the exposure initiated in autumn 2004

(pooled *t*) yielded the lowest AICc, and predicted probability values from this model indicated high egg parasitism at high moth densities (Fig. 8b). The five next best models (pooled *t*–1, autumnal moth *t*–3, autumnal moth *t*–2, pooled *t*–2 and autumnal moth *t*–1) included some sort of delayed density dependence.

Assumed predation on eggs by informed predators was delayed density dependent in a weak manner only (Table 2c, Online Resource 2; Fig. 8c). The models with own past abundances of autumnal moth (autumnal moth *t*–1 and autumnal moth *t*–2) as explanatory factors ranked the best, albeit the slopes were slightly steeper in the models including the pooled abundance (pooled *t*–1 and pooled *t*).

The disappearance of the eggs was density dependent with only one abundance predictor (pooled *t*–2) (Table 2d, Online Resource 2). According to this model, slightly more eggs disappeared at high abundance of the moths in the past (Fig. 8d). The yearly proportion of disappeared eggs was rather invariable (range 3.4–12.9 %, mean ± SE, 8.1 ± 1.0 %), and very interestingly, only half or less than the proportion assumed to be taken by informed predators (range: 12.5–25.8 %, mean ± SE, 19.3 ± 1.6 %) throughout the study (Fig. 8c, d).

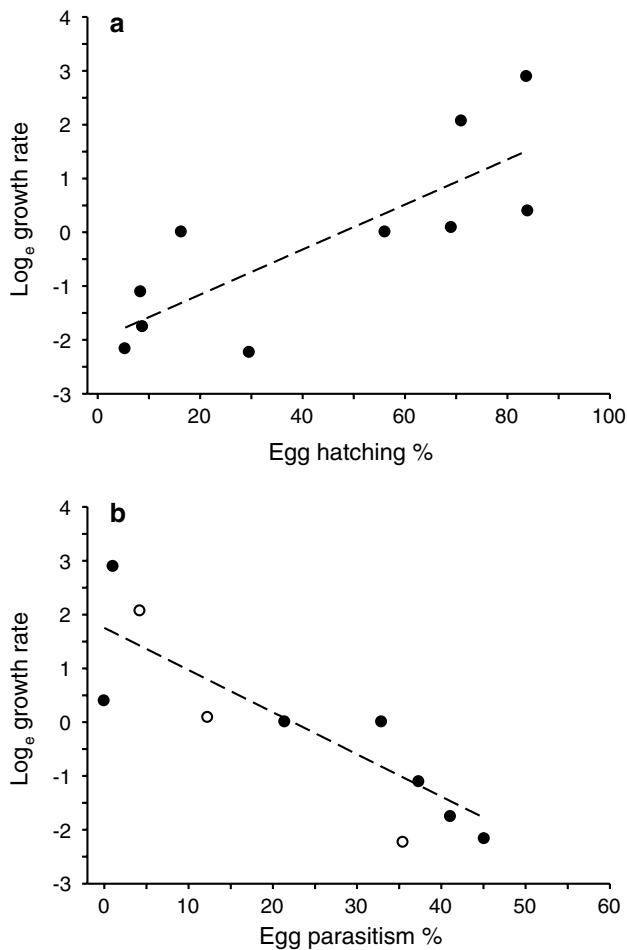


Fig. 7 The annual population growth rate [$\log_e(N_{t+1}/N_t)$] of the autumnal moth regressed on the percentage of hatched eggs (**a**), or on the percentage of parasitism of the eggs exposed to natural enemies across winter in the Hana study site (**b**). Note different scales on *x*-axes. Slope (*b*) estimates (95 % confidence limits) and test statistics: egg hatching, $b = 0.042$ (0.016–0.067), $t_1 = 3.8$, $P = 0.005$, $r^2 = 64.1$ %; egg parasitism, $b = -0.078$ (–0.130 to –0.026), $t_1 = -3.9$, $P = 0.012$, $r^2 = 75.1$ %. **b** Circles denote starting years 2001–2003, when egg parasitism was not recorded; here the maximal possible values are presented, equal to the proportion of unhatched eggs (if less, the circles move *leftwards*). These three data points were not included in the regression analysis

Survival during the egg stage was significantly related to the annual population growth of the autumnal moth (Fig. 7a). Egg parasitism, as the strongest density-dependent mortality factor, had an apparent effect on the host population growth (Fig. 7b).

Comparisons between autumnal and winter moths 2007–2011

Only parasitised eggs were counted for the winter moth. In the winter 2007/2008, 14 eggs were parasitised from 218 exposed ones. Corresponding figures were 21/64 eggs, 0/76

eggs and 0/39 eggs for study winters 2008/2009, 2009/2010 and 2010/2011, respectively. Methodological differences, such as variable egg number in sticks and disregarded estimation of disappearance and unaccountable mortality of winter moth eggs, restricted comparison to autumnal moth eggs. Nevertheless, some consistency can easily be seen: virtually zero parasitism was observed for both species during the last two study winters (see Fig. 6 for the autumnal moth).

Discussion

Density-dependent survival and parasitism of sedentary life stages

Survival rates of autumnal moth eggs and pupae, indicated by the successful hatching of larvae and eclosion of adults, respectively, from field-exposed individuals, were inversely related to past larval densities. Survival of both stages was substantially lower during and just after the bimodal moth outbreak in 2003–2008 as compared to ‘background levels’ that prevailed during low density years before and after the massive outbreak. It should be noted that the survival was still high during the first outbreak year (2002), showing delayed rather than direct feedback to the moth density. The survival of both life stages of autumnal moth contributed to the population growth rate: marginally so in the pupal stage, but more strongly so in the egg stage. Thus, density-related mortality factors during the sedentary life stages are able to account for cyclic population dynamics of the autumnal moth.

The most important mortality factors were egg and pupal parasitoids, which reciprocally explained the low survival rates. Both rates of parasitism also predicted subsequent growth rate of the host population size with egg parasitism having a stronger effect than pupal parasitism. In contrast to parasitism, all types of predation showed either no or only very weak, although delayed, relationships to density. Accordingly, the action by hymenopteran egg and pupal parasitoids can be seen to be typical for specialists of these geometrids, whereas all predators, irrespective of being vertebrates or invertebrates, acted more like generalists in our study system (Andersson and Erlinge 1977; Klemola et al. 2002). Levels of parasitism of pupae did not differ between autumnal and winter moths when both species were simultaneously examined. A fairly similar temporal pattern was also observed in egg parasitism of both species. All parasitoid species identified in this study were common for both host species (Online Resource 4). In addition, levels of parasitism of the autumnal moth were also related to the pooled abundance of the two moths (Online Resource 2), rather than the autumnal moth’s abundance alone. The levels of both egg and pupal parasitism of the autumnal

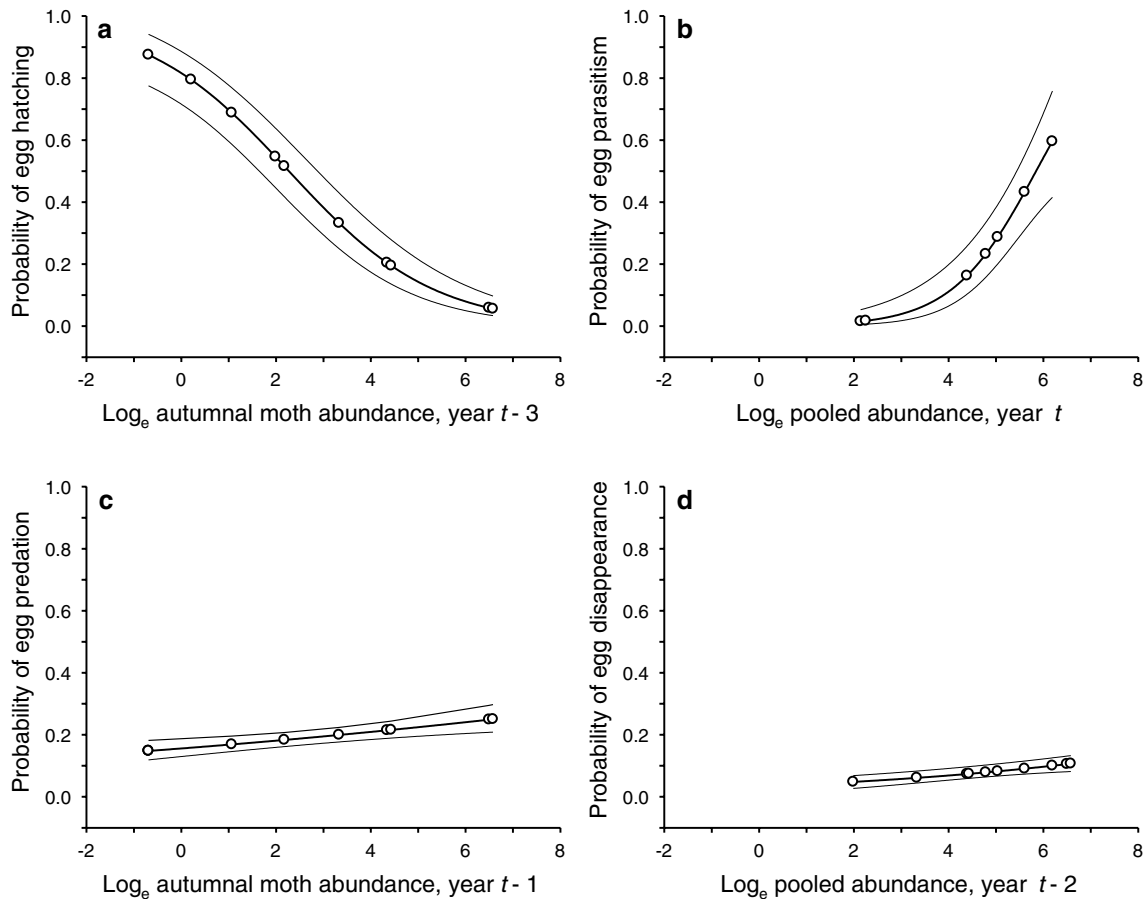


Fig. 8 Logistic regression curves (with 95 % confidence limits) predicting the probability of successful hatching of eggs (a), egg parasitism (b), egg predation (c) and egg disappearance (d) in relation to a

moth were pronounced halfway through the survey as larval abundance was declining, but diminished close to zero at the end when larval abundance increased again. In the exposures conducted during 2003–2008, levels of both types of parasitism exceeded 30 % and peaked at approximately 50 %. This implies a significant joint effect on the moth population. If we assume a moderate 30 % mortality in a host population that is serially but independently inflicted by both egg and pupal parasitoids, approximately half (51 %) of the over-wintered population in the egg stage would be killed by parasitoids before the next egg-laying period. If this were increased to the still realistic level of 50 % parasitism for each guild, 75 % would be killed. For the impact of all three parasitoid guilds, including also larval parasitoids (see below), the corresponding levels would be 65.7 and 87.5 %, respectively.

In addition to direct losses from parasitism, considerable levels of mortality of eggs and pupae occurred without an obvious external cause. Because unidentified causes of mortalities of the eggs and pupae were associated with the levels of egg and pupal parasitism, respectively, one can argue that

moth abundance index that was ranked the best in the model comparison (see Table 2, Online Resource 2). Axis scales are the same in all graphs, although the explanatory variable and its distribution vary

some eggs and pupae were parasitised, or somehow affected by parasitoids [e.g. by a harmful reaction of the own immune system, by host stinging without oviposition, or by some other form of ‘pseudoparasitism’ (Hegazi and Khafagi 2000; Münster-Swendsen 2002)], and thereby killed, although no adult parasitoid ever emerged or parasitoid larva could be identified from host remnants. Naturally, many other mortality factors, e.g. unspecified pathogens temporally correlated with the parasitism, could also explain our observations.

Although the egg parasitism was best related to non-delayed, pooled moth abundance (pooled t), the models with past moth abundances ranked close behind. The observed ranking of the candidate models might be due to the three first winters when we judged unhatched eggs as dead, but missed their parasitism. However, assuming that the association between the proportions of eggs that remained unhatched and observed egg parasitism is real, a delayed increase of parasitism relative to the moth abundance would be indicated for the missed winters as well [see Egg did not hatch category (years 2001–2003), Fig. 6, in relation to the moth abundance given in Fig. 1].

Observed rates of the survival, parasitism and predation were based on autumnal moth eggs and pupae produced under parasitoid-free conditions in the laboratory but transferred to the field site for exposure to natural enemies. We could not estimate the rates from wild eggs and pupae, because they are impossible to find during the low density phase of a population cycle. For this same reason, larval abundance was used as a proxy for the abundances of sedentary life stages. Furthermore, parasitism and predation do not necessarily act independently of each other and predators may prey preferentially either on parasitised or unparasitised hosts (Roland 1988, 1990). As a result, the values of parasitism and predation cannot be directly applied to wild eggs and pupae in nature. However, because our study methods remained the same year after year, we have confidence in the observed density-dependent patterns in the data, including inter-specific differences in comparisons of the two moth species.

During the study, parasitism in the larval stage of the autumnal moth remained at the moderate level (~50 % at maximum, less in most years) in the semi-oceanic Hana study area (Klemola et al. 2007; K. Ruohomäki, unpublished data). This seems to contrast to truly continental sites, for example Kevo in northernmost Finland (80 km south-west from Hana) and Abisko in northern Sweden (see Online Resource 1), where larval parasitism has been recorded to be close to 100 % in the decrease phases of the population cycle (Tanhuanpää et al. 2002; Klemola et al. 2010). In contrast, the pupal parasitism that played a role in Hana has, at least fairly recently, been negligible in the continental sites (Tanhuanpää et al. 1999; Heisswolf et al. 2009; Klemola et al. 2009). In the future, a comparison of the egg and pupal parasitism is also required between truly continental and truly oceanic populations (e.g. in the Tromsø region; see Online Resource 1) of the moths. Patterns of larval parasitism, and consequently the importance of larval parasitoids to cyclic population dynamics, seem to fundamentally differ between these geographical areas of northern Fennoscandia (Tanhuanpää et al. 2002; Hagen et al. 2010; Klemola et al. 2010; Schott et al. 2010, 2012). Comprehensive egg parasitism studies have not been carried out within the outbreak range of the autumnal moth, but Ammunét et al. (2012) found some exposed eggs to be parasitised by *Telenomus cf. laeviceps* in a study site located rather close to Hana, but none in the continental Kevo. Altogether these findings suggest that not only do different parasitoid species dominate in different areas or during different outbreaks in the same area (Tenow 1972; Ruohomäki et al. 2000; Vindstad et al. 2010), but that there may also be differences in the importance of different parasitoid guilds (i.e. egg parasitoids vs. larval parasitoids vs. pupal parasitoids) depending on the locality and time.

Predation on pupae and eggs

We did not find density dependence in predation rates of the deployed pupae by invertebrate predators, although rather high among-year variation was observed. On average, every tenth autumnal moth pupa was attacked by an invertebrate predator. Earlier, Heisswolf et al. (2009) found that the natural invertebrate predator community seems to become saturated at rather low densities of autumnal and winter moth pupae, emphasizing that invertebrate predators can be characterized as generalists, for which moth pupae are available only during a rather short period with regard to the whole life cycle of a predator, and consequently, for which the response to moth densities is likely to be functional rather than numerical.

The most interesting finding regarding invertebrate predation was that winter moth pupae were attacked with a consistently higher probability than autumnal moth pupae. In Hana, the between-species difference was only moderate compared to our two earlier studies (Heisswolf et al. 2009; Klemola et al. 2009), where in both cases winter moth pupae suffered about threefold higher predation rates by generalist invertebrates than did autumnal moths. Smaller pupal size, and hence especially lower thickness and hardness of the pupal cuticle, could be a reason for the greater vulnerability of winter moth pupae compared to larger autumnal moths; mandibles of all invertebrates are not powerful enough to penetrate the pupal wall of the moths (Frank 1967a, b).

The fact that our caging treatment totally prevented autumnal moth pupae from disappearing also indicates that some larger ground-dwelling predators, such as small mammals (Frank 1967a, b; East 1974; Roland 1994), preyed upon pupae. Because pupae that totally disappeared left no hint about the predator, we cannot exclude larger invertebrate predators either (see below). Predation assumed to be caused by these larger predators remained constantly at a low level, and, most importantly, did not show any density-dependent effects. Totally lost pupae, however, indicated that winter moths (~22 %) suffered a constantly much higher rate of vertebrate predation than autumnal moths (~5 %). This was surprising because larger (approximately 80 mg) pupae of the autumnal moth should be energetically more profitable for voles and shrews compared to pupae (40 mg) of the winter moth. Therefore, it is tempting to argue that maybe a larger assemblage of smaller invertebrate predators could remove small winter moth pupae and eat them elsewhere. This view is indirectly supported by the fact that freely buried autumnal moth pupae suffered higher rates of invertebrate predation than caged pupae, suggesting that some of the invertebrate predators present were too large to enter cages but probably were capable of carrying freely buried autumnal

moths, let alone winter moth cocoons, away from the original spot in the ground. Nonetheless, the pronounced difference in totally lost pupae between moth species seems to be a specific feature of the current study, since other studies have not reported such a strong bias towards winter moths (Hansen et al. 2009; Heisswolf et al. 2009; Klemola et al. 2009).

Both invertebrate and vertebrate predators seem to prefer winter moth pupae to autumnal moth pupae. This may contribute to diverging population dynamics of the two species in Hana by postponing the density increase of the winter moth compared to that of the autumnal moth in the low density phase (Klemola et al. 2009; Ammunét et al. 2014). On the other hand, pupal predation is hardly responsible for asynchronous crashes of the population cycles, and more research is needed to understand the mechanisms behind the phase-lagged population dynamics of winter and autumnal moths in northern Fennoscandia (Klemola et al. 2008, 2009).

Increasing moth density caused a weak increase both in the assumed egg predation by informed predators and in the disappearance rate of the autumnal moth eggs. Due to almost flat slope estimates, however, any regulative impact can hardly be attributed to egg predation alone. If anything, weakly density-dependent egg predation might act synergistically with egg parasitism. In this regard, it does not even matter whether we correctly categorized predation events, or whether the eggs now judged to be dislodged were also depredated or vice versa. Based on a simple probability calculation, it seems that some informed predators were commonly taking the two adjacent eggs of the same egg stick. Most likely, these predators were invertebrate generalists (e.g. spiders, ants, beetles, bugs), or possibly small passerine birds, which may eat moth eggs when they encounter them (Nuessly and Sterling 1994; Tanhuanpää et al. 2003).

Outside Fennoscandia predatory effects by small mammals on pupae have received considerable attention since the 1950s (e.g. Varley and Gradwell 1960; Klomp 1966). A particular focus has been on the effect on a low density level (Roland 1988, 1994; Elkinton et al. 1996, 2004; Dwyer et al. 2004) and/or synchronization of moth populations in spatially disjunct locations (Liebhold et al. 2000; Haynes et al. 2009). However, we are not aware of cases where egg or pupal predators are concluded to be agents driving population cycles of forest Lepidoptera.

Conclusion

Our long-term study demonstrated that increasing egg and pupal parasitism with increases of current and past moth densities reduced the survival of the autumnal moth to low

levels. Predation of eggs and pupae was low and weakly density dependent at best. In the continental populations studied, larval parasitism (up to nearly 100 %) seems a dominant factor related to cyclic population dynamics of the autumnal moth (Tanhuanpää et al. 2002; Klemola et al. 2010). At least during this study, in contrast, egg and pupal parasitoids were common in the semi-oceanic Hana region. This highlights the variation in trophic-level interactions associated with local conditions and raises the question: can this variation be explained by a continental-oceanic transect?

Parasitoids of different guilds could have a strong joint impact on host populations, if they exhibit similar density-dependent feedback mechanisms. Here, the patterns found were indeed amazingly similar between the two guilds of parasitoids we studied. The parasitism rates in both egg and pupal stages of the autumnal moth were associated with declines in the host population growth rate and thus showed such delayed negative feedbacks to the moth density that they are capable of contributing to the cyclic population dynamics of the autumnal moth in northern Fennoscandia. However, because causalities of observed density-dependent relationships cannot be inferred from correlations with mortality, experimental approaches in the field are needed. With parasitoids that is a challenging task (Klemola et al. 2010). Our more general message is that egg and pupal parasitoids should not be overlooked when causal explanations are sought for the population cycles of forest Lepidoptera.

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