No Impact of Pupal Predation on the Altitudinal Distribution of Autumnal Moth and Winter Moth (Lepidoptera: Geometridae) in Sub-Arctic Birch Forest

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ABSTRACT We tested the hypothesis that pupal predation by shrews underlies the altitudinal distribution pattern of the geometrid moth species *Operophtera brumata* L. (winter moth) and *Epirrita autumnata* Bkh (autumnal moth) in a sub-arctic birch forest in northern Fennoscandia. In particular, we predicted more intense pupal predation at low altitudes where the two moth species normally do not reach outbreak densities. Predation of pupae of both moth species was estimated along 10 parallel altitudinal transects, spanning from sea level to the altitudinal tree-limit in a coastal birch forest in northern Norway. Shrew abundance and the abundance and population growth rate of the two moth species were assessed in the same transects. Our study provided no support for the hypothesis that pupal predation by shrews can account for the altitudinal distribution of the two moth species. Despite high densities of common shrews (*Sorex araneus* L.) and an observed predation rate of ~90%, there was no difference in the rate of pupal predation either between the two geometrid species or between the various altitudes. These results narrow down the range of possible explanations for the altitudinal distribution pattern of these insects in northern birch forests.

In Fennoscandia, the two geometrid moth species *Epirrita autumnata* Bkh (Lepidoptera, Geometridae) and *Operophtera brumata* L. (Lepidoptera, Geometridae) show population outbreak cycles with a period of 9–10 yr in northern and sub-arctic birch (*Betula pubescens* Ehrh.) forests (Tenow 1972, Tenow et al. 2001, Haukioja 2003), whereas lowland, southern populations are nonoutbreaking and relatively stable (Ruohomäki et al. 2000, Klemola et al. 2002). Natural enemies, in particular specialized larval parasitoids, have a delayed density-dependent numerical response, have often been proposed to be the decisive factor underlying cyclic outbreak dynamics in herbivorous insects (Berryman 1996, Turchin et al. 2003). In contrast, hosts of generalist predators with a direct density-dependent functional response are thought to keep nonoutbreaking populations in check (Klemola et al. 2002).

Tanhuanpää et al. (1999) highlighted the role of insectivorous small mammals, most notably shrews (*Sorex* spp.), as major predators on geometrid pupae. By deploying laboratory-reared *E. autumnata* pupae to the field, they showed that pupal predation by small mammals was consistently high and density dependent in southern stable populations, whereas it was significantly lower and without any sign of density dependence within the outbreak range in northern Fennoscandia. Thus, these findings indicate that the nature of pupal predation may be decisive for determining where geometrids may escape the regulatory action of natural enemies.

In the oceanic sector of the sub-arctic birch forest, along the northwestern coast of northern Norway, it has been noted that geometrid outbreaks with severe defoliation of trees usually are limited to a zone close to the altitudinal tree line (Tenow 1972, Bylund 1999). Moreover, *O. brumata* has been reported to have outbreaks at somewhat lower altitudes than *E. autumnata*, but rarely at the sea level (Tenow 1972, Hågvar 1972). In this study, we investigated whether predation on geometrid pupae could determine the altitudinal distribution pattern of the two geometrid species in coastal sub-arctic mountain birch forest in northern Norway. We did this by recording the level of pupal predation in both geometrid species along 10 parallel altitudinal transects from sea level to the upper altitudinal tree line. We predicted that pupal predation would act to limit the abundance and regulate population growth of the two geometrid species within the altitudes they normally do not exhibit outbreaks, i.e., in particular at the lowest altitudes.

Materials and Methods

Study Species. *Epirrita autumnata* and *O. brumata* lay eggs during the autumn on tree trunks and twigs and the eggs overwinter and hatch in spring. In northern Fennoscandia, the eggs hatch around the timing of budburst in birch (Mjaaseth et al. 2005), which is the primary food plant of the two species in the region.

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The solitary, spring feeding larvae undergo five instars for 1–1.5 mo before they pupate in the ground. At our study site in northern Norway, the pupal stage lasts ≈2.5 mo for *E. autumnata* and ≈3 mo for *O. brumata,* with eclosion and mating happening in September for *E. autumnata* and in October for *O. brumata.*

Study Area and Study Design. The study was carried out in 2003 and 2004 at Reinøya in northern Norway (70°00′ N, 19°49′ E) in a northeasterly oriented slope (mean slope, 23.3°), where the mountain birch forest forms a fairly homogenous belt from sea level and up to the forest limit at ≈240- to 250-m elevation. Ten parallel altitudinal transects, spaced at 200-m intervals from sea level to the forest limit, were established. Each transect had four stations at the following altitudes: 30, 100, 170, and 240 m. The length of transects varied between 514 and 628 m. A detailed description of the study area is given in Mjaaseth et al. (2005).

The abundance of shrews on the 40 sampling stations was estimated on 29–30 May 2003, before recruitment of young of the year, and then again on 30–31 August, toward the end of the reproductive season and the end of the pupal period for *E. autumnata.* This was done by placing four multiple capture live traps (Ugglan special, Grahnab, Sweden) at each transect station, so that there was one trap in each of the corners of a 15 by 15-m quadrate centered on the sampling station. Each trap was baited with fish and was checked for 2 d. All small mammals entering the live traps were recorded. This included also some northern red-backed voles (*Myodes rutilus* Pallas). However, the common shrew (*Sorex araneus* L.) was the only abundant vertebrate pupal predator in the area. Therefore, in the following analyses, we used only the data on shrews.

The density of autumnal and winter moth was estimated at all transect stations by counting the number of larvae on 10 branches of an arm length size. Each branch was taken from a different tree within a radius of 50 m from the sampling station mark. The branch was thoroughly shaken in a large plastic box, and the larvae of each type were counted. This census method gives a reliable estimate of local larval density (Hagen et al. 2003, Ims et al. 2004, Mjaaseth et al. 2005, Hagen et al. 2006). Larval densities were estimated in both 2003 and 2004 to test for an effect of shrew abundance and pupal predation on the population growth of the two geometrids and for an association between abundances of shrews and geometrids in space within year (i.e., in 2003).

Pupae for the predation study (see below) were obtained by sampling larvae in the field and rearing them to pupae in the laboratory. Larvae were collected in late June to early July in 2003 and kept in 1-liter plastic boxes with lids in groups of 15. The larvae were fed fresh birch leaves every other day until pupation. The boxes used to rear the larvae contained dirt/sand as pupation substrate with some moss on top for moisture. To ensure that the pupae were alive at onset of the predation study, they were released from the cocoons. In total, 451 live *O. brumata* pupae and 459 live *E. autumnata* pupae were obtained.

The pupal predation study was initiated on 28–29 July 2003, by burying 10 pupae of each geometrid species (i.e., totally 20 pupae) on each of the 40 sampling stations. The 20 pupae were placed in two 5-m parallel lines, separated by 1 m, with one pupa of each species along each line at 1-m intervals. At each position along the line, one pupa of each species was buried 2 cm below the surface, 10 cm from a brightly colored stick: one species in the north and the other in the south direction. The two species positions in the north and south direction were changed every other station. To know exactly where the two pupae were placed, we used a wooden cross, 20 cm in diameter, with a hole in the middle that could be placed over the brightly colored stick. The cross was placed parallel to the line, and one pupa was placed at the end of each of the other two arms of the cross (i.e., exactly 10 cm from the line at a straight angle). The cross was used also during collection of the pupae to avoid potential bias related to not finding the pupae (i.e., falsely classifying pupae as being predated). A similar method was used by Tanhuanpää et al. (1999) in their study of shrew predation on autumnal moth pupae.

Collection of transplanted pupae for determination of predation rates was carried out on 24–25 August 2003, which was before the onset of the flight period of *E. autumnata* at our study site in this year. In cases where the pupae were entirely gone, it was concluded that the predator had removed them and eaten them elsewhere, which is common in shrews (Hanski and Parviainen 1985, Tanhuanpää et al. 1999). In cases where we found partly eaten pupae, i.e., pupal shells, these were collected in plastic tubes and brought back to the laboratory to evaluate whether these cases represented shrew predation. As a point of reference, we fed captive *S. araneus* intact pupae of both moth species and recorded the patterns of damage on the leftovers, i.e., the pupal shells. The pupal shell was either split in approx. two equal halves, or a large hole was torn in the pupal shell. On this basis, the pupal fragments found in the predation study were individually classified as being eaten by shrews or something else.

Statistical Methods. Variation in shrew density in relation to altitude was explored using analysis of variance (ANOVA), with altitude as factor variable. The same procedure was used to study variation in density of geometrid larvae in relation to altitude and change geometrid density from 2003 to 2004 (i.e., population growth rate) in relation to altitude. Pearson correlation analyses and Spearman rank correlation analyses were used to test for correlations between the two geometrid species in their patterns of density variation, population growth, and degree of pupal predation at the 40 sampling stations. Degree of pupal predation in relation to altitude was further modeled using logistic regression analysis. All analyses were carried out using the statistical software R (R Development Core Team 2005).
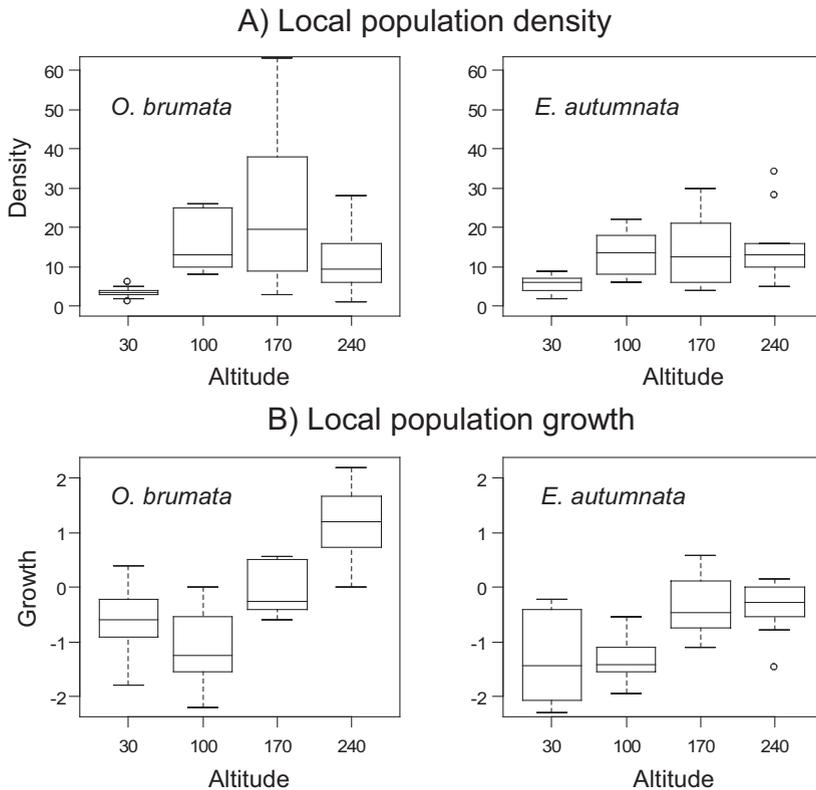
A) Local population density

B) Local population growth

Fig. 1. Boxplots of local larval abundances and population growth rate in relation to altitude for the two geometrid species. (A) Larval abundance per transect sampling station in July 2003. (B) Population growth rates at the scale of transect sampling stations from July 2003 to July 2004 based on larval densities.

Results

Larval Population Density and Growth Rate. Altitude was both a significant predictor of larval density in 2003 [ANOVA on $\log(N_{2003} + 1)$, *O. brumata*: $R^2 =$ 0.47, df = 3,36, $P < 0.0001$, *E. autumnata*: $R^2 = 0.33$, df = 3,36, $P = 0.0021$] and of the rate of change in larval densities between 2003 and 2004 {ANOVA on $\log([N_{2004} + 1]/([N_{2003} + 1)$, *O. brumata*: $R^2 = 0.62$, df = 3,36, $P < 0.0001$, *E. autumnata*: $R^2 = 0.43$, df = 3,36, $P < 0.0001$}. The altitudinal distribution of larval densities in 2003 was quite similar for the two moth species (Fig. 1A), with the lowest density at the lowest altitude (30 m). At the other altitudes, there was much variation between transect stations, especially at 170 m. *O. brumata* exhibited more local variation than *E. autumnata* and had the highest maximum densities (Fig. 1A). The altitudinal pattern in the rate of change between the years (i.e., population growth rate) was also quite similar among the species, with the lowest, and generally negative, growth rate at the two lowest altitudes (Fig. 1B). The variation in larval densities and growth rate between transect stations, when corrected for altitude (i.e., using the residuals from the ANOVA models), was correlated between the species (larval densities in 2003: Pearson $r = 0.59$, $P < 0.0001$, population growth rate: Pearson $r = 0.60$, $P < 0.0001$).

Density of Shrews. The common shrew *S. araneus* was the most common small mammal (76.4% of the captures), and the only specialized insectivore trapped at the transect stations. Although only three shrew individuals entered the traps in May in 2003, a total of 249 individuals were trapped in the end of August the same year. At the end of August, shrews were caught at all stations but in highly variable numbers (range: 1–12 individuals). Local shrew density was not related to the local density of moth larvae in 2003 ($R^2 = 0.002$), nor was rate of change in larval densities between 2003 and 2004 related to local variation in shrew densities in 2003 ($R^2 = 0.015$). Although only a relatively small amount of the variation in local shrew abundance was accounted for by altitude (ANOVA, $R^2 = 0.16$, df = 3,36, $P = 0.09$), there was a tendency for shrew abundance to be lowest at 100 m (Fig. 2).

Predation on Moth Pupae. Of the 800 pupae placed out at the transect stations $\approx$10% (10.0% autumnal moth and 10.5% winter moth) were recovered alive, <10% of the pupae (9.8% autumnal moth and 6.0% winter moth) had been eaten on site (as evidenced by remains of pupae shells compatible with shrew predation), and the remainder of the pupae was not recovered (80.2% autumnal moth and 83.5% winter
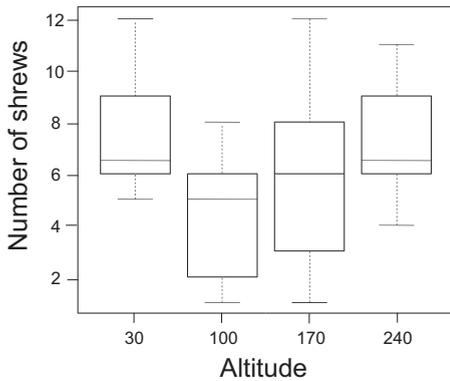
Fig. 2. Boxplot of number of common shrews caught per transect station in September 2003.

Table 1. Altitude-specific quasi-likelihood estimates with 95% confidence intervals of proportion pupae that had been eaten by predators on site (predation in situ), proportion removed, and those found alive (survival) at the end of the experiment

Altitude (m)	Predation in situ	Removed	Survival
30	0.06 [0.02,0.13]	0.83 [0.71,0.90]	0.12 [0.07,0.20]
100	0.13 [0.07,0.21]	0.77 [0.65,0.85]	0.11 [0.06,0.19]
170	0.07 [0.03,0.15]	0.87 [0.76,0.93]	0.06 [0.03,0.13]
240	0.07 [0.03,0.14]	0.82 [0.70,0.89]	0.12 [0.07,0.20]

There were initially 200 pupae on each altitude (i.e. 20 on each transect station).

moth) and thus had most likely been removed by predators. The spatial variation in both removal rate and in situ predation rate was correlated between the two moth species (Spearmann rank correlation, removal rate: $r_s = 0.63$, $P < 0.0001$, in situ predation rate: $r_s = 0.50$, $P = 0.0018$). Because of the very similar and spatially correlated predation rate, the data for the two moth species were lumped in the further analyses of possible determinant of predation.

We assumed that the most complex, ecologically realistic predation rate model, given our data and study design, included the following three predictor variables: shrew abundance, natural abundance of moth larvae (assuming shrew functional response), and altitude (assuming that other food sources for shrews varied with altitude). We modeled local (i.e., station-specific) predation rate as a binomial proportion in a generalized linear model framework. Considering first total predation (the proportion of pupae removed or found eaten on site), the most complex model did not fit the data because of extrabinomial variance (goodness-of-fit test: $\chi^2 = 66.8$, df = 34, $P < 0.001$). Because of this overdispersion, quasi-likelihood models were used for evaluating the effects of the predictor variables. None of the predictor variables had any effects on total predation rate ($P > 0.35$). Considering the proportion of pupae that had been eaten on site (i.e., predation in situ), we found no statistically significant effects of shrew abundance, altitude, or natural abundance of the two moth species ($P > 0.20$). The small variation in predation rates between the four altitudes is evident from Table 1.

Discussion

An outbreak zone close to the altitudinal three-limit is common for the autumnal moth in the sub-arctic, coastal birch forest (Tenow 1972, 1996; Bylund 1999; Tenow et al. 2007). In comparison, winter moth outbreaks usually take place in the middle sections of forest slopes (Hågvar 1972, Tenow 1972). In the most recent outbreak, further northeast of the current study area, a distinct defoliation zone caused by *O.*

brumata was observed close to the altitudinal tree limit (Hagen et al. 2007). Both moth species apparently rarely attain outbreak densities at the lowest altitudes, close to the sea level (Tenow 1972, Tenow et al. 2007). Although these altitudinal patterns in abundance and population dynamics are likely to have a climatic origin (Hagen et al. 2007), this has not yet been substantiated by empirical evidence. First, a direct effect of winter climate in terms of differential egg survival is unlikely, because lethal temperatures of −35 to −36°C (Bylund 1999) are never approached in the coastal birch forest in northern Norway. Low winter temperature may, however, cause altitudinal gradients in *E. autumnata* because of different rates of egg survival in northern inland areas (Neuvonen et al. 1999, Virtanen and Neuvonen 1999). Second, Mjaaseth et al. (2005) recently studied growth and development of larvae of both species in the same altitudinal gradient as used in this study and failed to find any evidence for altitudinal effects on development rates. Thus, a closer study of other possible explanations, with a focus on indirect rather than direct climate effects, for instance, caused by trophic interactions, is warranted.

Shrews (*Sorex* spp.) are major predators of insect pupae (Neuvonen 1988, Hanski 1992), and maximum predation rates >90% per month have been recorded (Hanski and Parviainen 1985). When operating in a direct density-dependent manner (Ruohomäki et al. 2000, Klemola et al. 2002), such high predation rates on pupae can at least theoretically prevent population outbreaks in insects. Tanhuanpää et al. (1999) compared pupal predation between outbreaking (northern) and nonoutbreaking (southern) populations of autumnal moth in Finland. They found that the predation rates were relatively low and density independent in northern continental birch forest and relatively high and density dependent in the southern mixed coniferous forest. Tanhuanpää et al. (1999) concluded that a north–south contrast in shrew abundance contributes to the large-scale geographic dichotomy in the population dynamics of *E. autumnata* in Fennoscandia. Building on their results and interpretations, we therefore hypothesized that differential shrew predation similarly might explain the more small-scale phenomenon of contrasting population dynamics in relation to altitude in northern coastal birch forest. In particular, we suspected that geometrid outbreaks are not found at the lower sections of altitu-

dinal forest slopes because of more intense predation by shrews. Our hypothesis was substantiated by previous reports of increasing common shrew abundance with decreasing altitude (Steven 1955) and distance to coast (Hansson et al. 1978) in northern Fennoscandia.

The premises for testing the "pupal predation hypothesis" seemed to be fulfilled in our study. With regard to the two geometrid moth species, the premise of an altitudinal pattern with lower abundances at the lowest altitude (i.e., 30m) was clearly supported. Moreover, both moth species were declining quite steeply between the 2 yr at the two lowest altitudes, whereas the populations where stable or even increasing at the two higher altitudes (Fig. 1). With regard to pupal predators, the abundance of common shrews was locally very high, and high enough to inflict high rates of pupal mortality. Similar high pupal predation rates, including a large proportion of removed pupae caused by small mammals, have been reported from previous studies (Buckner 1969, Hanski and Parviainen 1985, Hanski 1992). In fact, the estimated predation rate in this study, in the northern coastal birch forest, was higher than that Tanhuanpää et al. (1999) found for mixed coniferous forest in southern Finland. However, neither the observed abundance of common shrews nor the estimated pupal predation rates, based on the predation study, could account for the clear altitudinal pattern in moth abundance and population dynamics shown in our study. Shrew abundances and pupal predation rates were uniformly high across the entire altitudinal gradient and were unrelated to local density of moths, i.e., there was no density dependence. Thus, our results clearly suggest that pupal predation, although likely to be high enough to limit population growth, had no causal role in determining the altitudinal distribution of the two geometrids. We therefore reject the hypothesis that pupal predation is a decisive factor for regulating low altitude moth populations in northern coastal birch forest. Note that this conclusion is general and in no way limited to pupal predation by shrews, because our study actually measured overall pupal predation. Certainly, at least to some degree, generalist invertebrate predators, such as carabid beetles and ants (and possibly others), must have contributed to the high disappearance of pupae in our experiment and thus also the overall predation pattern used to draw inferences. To assess the relative importance of various pupal predators was, however, beyond the scope of our study.

Among other causal factors that remain to be studied in relation to the altitudinal pattern of geometrid moth population dynamics in the northern birch forest are insect parasitoids. Parasitoids are believed to be important determinants of the population dynamics in both winter moth (Roland and Embree 1995) and autumnal moth (Ruohomäki et al. 2000, Klemola et al. 2002). In the present context, the altitudinal pattern of parasitoid attack, which may be temperature dependent (Virtanen and Neuvonen 1999), should be explored in both moth species. Moreover, the synchrony of hatching of eggs and bud burst in host trees is regarded to be a very climate sensitive stage in the life cycle of folivorous Lepidoptera (Kerslake and Hartley 1997, Hunter and Elkinton 2000, Vanbergen et al. 2003, Tikkanen et al. 2006). That is, whether the degree of phenological match between herbivore and host trees differs across altitudes needs closer study. In any case, we believe that the clearly patterned population dynamics of the two sympatric birch forest geometrids relative to altitudinal in coastal sub-arctic birch forest offers unique opportunities for further studies of relationship between climate and population outbreaks in herbivorous insects.

Acknowledgments

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