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Local outbreaks of *Operophtera brumata* and *Operophtera fagata* cannot be explained by low vulnerability to pupal predation

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Abstract. One of the unresolved questions in studies on population dynamics of forest Lepidoptera is why some populations at times reach outbreak densities, whereas others never do. Resolving this question is especially challenging if populations of the same species in different areas or of closely-related species in the same area are considered.

The present study focused on three closely-related geometrid moth species, autumnal *Epirrita autumnata*, winter *Operophtera brumata* and northern winter moths *Operophtera fagata*, in southern Finland. There, winter and northern winter moth populations can reach outbreak densities, whereas autumnal moth densities stay relatively low.

We tested the hypothesis that a lower vulnerability to pupal predation may explain the observed differences in population dynamics. The results obtained do not support this hypothesis because pupal predation probabilities were not significantly different between the two genera within or without the *Operophtera* outbreak area or in years with or without a current *Operophtera* outbreak.

Overall, pupal predation was even higher in winter and northern winter moths than in autumnal moths. Differences in larval predation and parasitism, as well as in the reproductive capacities of the species, might be other candidates.

Keywords. *Epirrita autumnata*; forest Lepidoptera; *Operophtera brumata*; *Operophtera fagata*; outbreak; population dynamics; pupal predation.

INTRODUCTION

Understanding population dynamics of insects involves the important question of why some populations at times reach outbreak densities, whereas others never do (Wallner, 1987; Tanhuanpää *et al.*, 2002). Differences in life-history and ecological traits might explain general patterns of insect population dynamics (Hunter, 1991, 1995; Tammaru & Haukioja, 1996) but they probably cannot explain regional variation in population dynamics within species or between species having very similar traits. The potential

mechanisms for such regional differences comprise environmental conditions and genetic differences, as well as multitrophic interactions (Berryman, 1988; Cappucino & Price, 1995).

Although delayed density-dependent interactions with host plants and specialized natural enemies are the most frequently suggested factors for causing forest insect population cycles, which often culminate in outbreak densities for a few successive years (Berryman, 1988; Ruohomäki *et al.*, 2000), predation by generalists may act as a principal force in maintaining low population densities (Mason, 1987; Klemola *et al.*, 2002). In particular, pupal predation is considered to have a regulating influence on many lepidopteran populations (East, 1974; Bauer, 1985; Cook *et al.*, 1994; Elkinton *et al.*, 1996; Tanhuanpää *et al.*, 1999; Raymond *et al.*, 2002).

Well-known examples of outbreaking forest pest species are the autumnal moth *Epirrita autumnata* (Borkhausen), the winter moth *Operophtera brumata* (Linnaeus) and the northern winter moth *Operophtera fagata* (Scharfenberg) (all Lepidoptera: Geometridae). In northern Fennoscandia, autumnal moths have a well-documented history of outbreaks (Tenow, 1972; Klemola *et al.*, 2006; Tenow *et al.*, 2007), whereas outbreaks have never been observed in southern Fennoscandia (Tenow, 1972; Haukioja *et al.*, 1988; Ruohomäki *et al.*, 2000). By contrast, winter and northern winter moths have been reaching outbreak densities in southern, eastern and northern Fennoscandia (Tenow, 1972; Hogstad, 1997, 2005; Tikkanen *et al.*, 1998; Tikkanen & Roininen, 2001; Ims *et al.*, 2004). A recent outbreak of winter and northern winter moths was observed in 1997-2000 in a birch forest on the south-western coast of Finland with peak densities in 1998-1999 (Niemistö *et al.*, 2004).

Differences in larval and pupal predation rates have been suggested as the most likely explanation for the low population densities of autumnal moths in southern Fennoscandia compared with the high-amplitude cycles in the north (Tanhuanpää *et al.*, 1999, 2001; Klemola *et al.*, 2002). Therefore, we hypothesized that a low vulnerability to pupal predation in winter and northern winter moths might be the reason why they can reach outbreak densities in southern Finland, whereas autumnal moths cannot. To test this hypothesis, we exposed pupae of autumnal, winter and northern winter moths to the natural predator community in southern Finland, both in areas where winter and northern winter moth outbreaks (hereafter called *Operophtera* outbreaks) have occurred or have been absent. We conducted one experiment in 1999, when the *Operophtera* outbreak was still ongoing (Niemistö *et al.*, 2004) and one in the same locations in 2004, when the outbreak was already over.

MATERIALS AND METHODS

Study species

Autumnal, winter and northern winter moths are nocturnal geometrids [wingspan (mean [range]) of Finnish specimens: autumnal moth male: 34.1 (29.5-37.5) mm; autumnal moth female 33.1 (29.5-38.0) mm; northern winter moth male: 31.8 (28.0-36.5) mm; winter moth male: 27.2 (23.5-32.5) mm; winter and northern winter moth females are virtually wingless; Mikkola *et al.* 1985]. They are obligatorily univoltine and eggs overwinter and hatch at host plant budburst. The polyphagous larvae feed on foliage during their five larval instars and then pupate in the soil. In southern Finland, the three moth species feed on birches (*Betula pubescens* Ehrh. and *Betula pendula* Roth; Fagales: Betulaceae), pedunculate oak (*Quercus robur* L., Fagales: Fagaceae) and bird cherry (*Prunus padus* L., Rosales: Rosaceae), with outbreaks most commonly occurring in birch forests (Niemistö *et al.*, 2004); for eastern Fennoscandia, see also Tikkanen *et al.* (1998) and Tikkanen & Roininen (2001). Averaged across southern Finland, the flight period of adults starts on 3 September for autumnal moths and on 30 or 29 September for winter and northern winter moths, respectively (Mikkola *et al.*, 1985).

All developmental stages of autumnal, winter and northern winter moths are attacked by various predators such as ants, beetles, spiders, insectivorous birds and small mammals (voles and shrews) (Frank, 1967b; Tanhuanpää *et al.*, 1999, 2001, 2003; Ruohomäki *et al.*, 2000; Enemar *et al.*, 2004; Hogstad, 2005). Furthermore, several parasitoid species are known to attack these geometrid species. Different studies have found at least one egg parasitoid, one egg-larval, one larval-pupal and approximately 15 larval and five pupal species (Glavendekic & Gruppe, 1992; Ruohomäki, 1994; Ruohomäki *et al.*, 2000; Klemola *et al.*, 2007; Klemola, 2009; K. Ruohomäki & T. Klemola, unpublished data).

For the experiment conducted in 1999, winter and northern winter moths were collected in 1998 as pupae from the soil within the *Operophtera* outbreak area and were transferred to the laboratory at the University of Turku. Adults of each species were mated in the laboratory, although only northern winter moths successfully laid eggs from which a new generation could be raised. Therefore, in the experiment conducted in 1999, only autumnal and northern winter moth pupae were used. Because of their scarcity in the field, autumnal moth pupae were obtained by larval rearing (see below) from our laboratory stock, originating from parents collected as larvae from several localities 20-30 km northeast of Turku in 1998.

For the experiment conducted in 2004, adult winter moth females were collected either in copula or not from tree trunks in Ruissalo, Turku (60°26'N, 22°10'E) in the

autumn of 2003 and were allowed to lay eggs in the laboratory, from which a new generation was raised in 2004. In this year, no northern winter moth females could be found from nature. Thus, only autumnal and winter moth pupae were used in this year of the experiment. Autumnal moth pupae were again obtained from our laboratory stock, originating from parents collected as larvae from several localities 20-30 km northeast of Turku in 2003.

In both experimental years, moth larvae were reared from egg to pupa on birch foliage in the laboratory and were allowed to pupate singly in transparent plastic vials (48 mL) filled with moist potting soil as pupation substrate. The potting soil included glitter to enable an easier retrieval of the cocoons after the exposure period (Tanhuanpää *et al.*, 1999).

Experimental design

The experiment was conducted in two separate areas near Pori in south-western Finland in 1999 and 2004. One area (Harjavalta; 61°18'N, 22°08'E, approximately 30 km southeast of Pori) was outside the *Operophtera* outbreak area, whereas the other area (Reposaari; 61°37'N, 21°27'E, approximately 25 km northwest of Pori) was inside the outbreak area (Niemistö *et al.*, 2004). The outbreak area was dominated by birch forest, whereas a mixed coniferous forest prevailed in the non-outbreak area. Within each area, the experimental setup was replicated at three sites, which were the same in both study years. The sites were arranged in a triangular layout, with inter-site distances in the range 7.8-12.1 km in the outbreak area and 6.6-13.2 km in the non-outbreak area. Each site comprised two plots, which were located 100-140 m apart.

In each plot, the pupae were buried into the ground in three parallel lines with an inter-line distance of 10-15 m. In each line, five autumnal and five winter or northern winter moth pupae (depending on experimental year) were alternately buried 1-1.5 m apart. In 1999, there were two exceptions to this pattern because insufficient northern winter moth pupae were available that had built a proper cocoon. Therefore, in four lines, two within and two outside the outbreak area, only two northern winter moth but eight autumnal moth pupae were buried. Thus, in total, there were 192 autumnal moth and 168 northern winter moth pupae in 1999. In 2004, there were 180 pupae of each species (autumnal and winter moth). The pupae were buried into the soil at the natural pupation depth of approximately 4 cm by poking a small hole into which the pupa was dropped and then covered by moss/litter. The location of each pupa was marked in a fixed compass direction with a wooden stick (length 20 cm) at a distance of 10 cm from the pupa. In 1999, the pupal exposure lasted from 22 June to 26 August and, in 2004, from 17 June to 12 August, matching approximately the timing of the natural

pupal occurrence of autumnal moths. Both the method and the pupal densities used were similar to those employed in previous experiments (Tanhuanpää *et al.*, 1999).

At the end of the exposure time, the pupae were re-collected and transferred to the laboratory at the University of Turku, where their fates were checked. Invertebrate predation was identified based on specific feeding marks on the pupa (Frank, 1967a,b; Tanhuanpää *et al.*, 1999). Vertebrate predation was assumed to have occurred when the pupa had disappeared totally (Tanhuanpää *et al.*, 1999; Klemola, 2009; Heisswolf *et al.*, 2009) because vertebrate predators usually either consume the pupa totally or take it away to consume it later in a different place (Frank, 1967b). Vertebrates also eat pupae that have been already partially consumed by invertebrates. Consequently, the status of invertebrate predation was unknown for pupae that had been subsequently predated by vertebrates and these cases were treated as missing values in the statistical analyses of invertebrate predation probability. There were only four cases of pupal parasitism (three autumnal moth pupae and one northern winter moth pupa in Reposaaari 1999), which are not further considered in the present study. In 1999, one autumnal and four northern winter moth pupae were dead at the time of re-collection and the fate of three autumnal and ten northern winter moth pupae could not be assessed. In 2004, the fate of ten autumnal and nine winter moth pupae could not be assessed. These cases were omitted from the statistical analyses.

Statistical analysis

Pupal predation probability was analysed with generalized linear mixed-effects models (the GLIMMIX procedure in SAS, version 9.1; SAS Institute, Cary, North Carolina) with a binomial error structure and a logit link function. Invertebrate, vertebrate and total predation were analysed separately. In all models, area [outbreak area (Reposaaari) or non-outbreak area (Harjavalta)], genus [non-outbreaking (*Epirrita*) or outbreaking (*Operophtera*)], year [current outbreak (1999) or no current outbreak (2004)] and all their interactions were used as fixed effects. Site nested within area and year was used as a random effect to account for the replicated experimental design within each area and for the different experimental years. Because random variables were included, the denominator degrees of freedom for the type III F-tests of fixed effects were computed using the method of Kenward & Roger (1997). Model-derived parameter estimates are given as back-transformed least-squares means accompanied by their 95% confidence limits.

Table 1: Results of generalized linear mixed-effects models on the survival of geometrid moth pupae depending on area [outbreak area (Reposaari) or non-outbreak area (Harjavalta)], genus [non-outbreaking (*Epirrita*) or outbreaking (*Operophtera*) in southern Finland] and year [with (1999) or without (2004) a current *Operophtera* outbreak]. F-values, degrees of freedom (d.f.) and P-values of type III tests of fixed effects are given.

Explanatory factor	Invertebrate predation			Vertebrate predation			Total predation		
	F	d.f.	P	F	d.f.	P	F	d.f.	P
Area	0.11	1, 7.9	0.754	19.21	1, 9.2	0.002	0.97	1, 7.8	0.354
Genus	6.92	1, 223	0.009	3.37	1, 675	0.067	8.00	1, 675	0.005
Year	0.63	1, 7.9	0.450	1.11	1, 9.2	0.319	0.08	1, 7.8	0.786
Area × Genus	1.72	1, 223	0.191	1.20	1, 675	0.273	2.48	1, 675	0.116
Area × Year	0.01	1, 7.9	0.930	2.33	1, 9.2	0.160	0.83	1, 7.8	0.391
Genus × Year	3.57	1, 223	0.060	1.94	1, 675	0.164	0.13	1, 675	0.717
Area × Genus × Year	3.42	1, 223	0.066	3.43	1, 675	0.065	0.01	1, 675	0.925

RESULTS

Some large differences were found in the estimated mean predation probabilities of moth pupae between genera, areas and years (Figure 1). The invertebrate predation probability was very low in *Epirrita* pupae in 1999 in the *Operophtera* outbreak area, whereas it was approximately one order of magnitude higher in *Operophtera* pupae in the outbreak area in the same year and outside the outbreak area in 2004. In the outbreak area, the estimated vertebrate predation probability was approximately 20% lower for *Epirrita* pupae in 2004 compared with *Epirrita* pupae in 1999 and with *Operophtera* pupae in both study years.

Statistically, however, the differences in invertebrate and vertebrate predation probabilities of *Epirrita* and *Operophtera* pupae, depending on whether the pupae were exposed within or outside the *Operophtera* outbreak area or in a year with or without a current *Operophtera* outbreak, were not significant (see three-way interactions in Table 1). Combined as total predation probabilities, the differences in invertebrate and vertebrate predation seemed to cancel each other out because there were clearly no differences between groups (Table 1). In addition, all pupal predation probabilities within each of the two moth genera were not statistically significantly influenced by area or year (see area × genus and genus × year interactions in Table 1).

The invertebrate predation probability was significantly greater overall in *Operophtera* compared with *Epirrita* pupae (Figure 2, Table 1), although there were no differences between areas or years (Table 1). Furthermore, the probability of vertebrate predation was significantly greater overall in the outbreak area than outside of it (Figure 2, Table 1), although it did not differ between genera or years (Table 1). Fi-

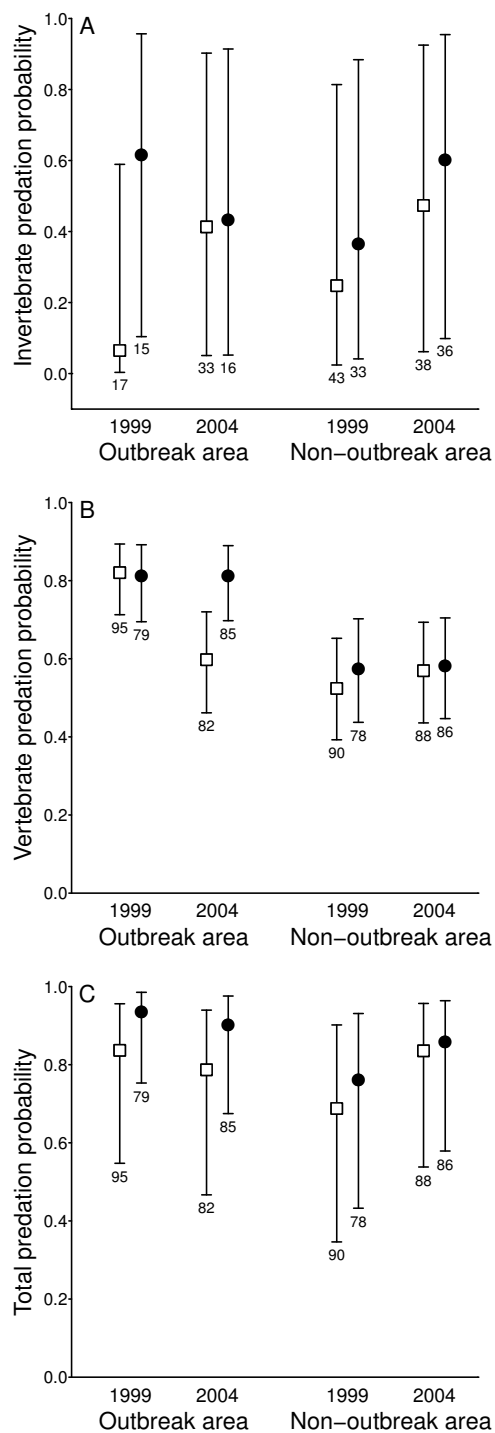


Figure 1: Model-derived parameter estimates for (A) invertebrate, (B) vertebrate and (C) total predation probability of pupae of the two geometrid moth genera *Epirrita* (white squares) and *Operophtera* (black circles) within and outside the *Operophtera* outbreak area both in a year with (1999) and without (2004) a current *Operophtera* outbreak. Back-transformed least-squares mean values accompanied by their 95% confidence limits are shown. Sample sizes are given below each bar.

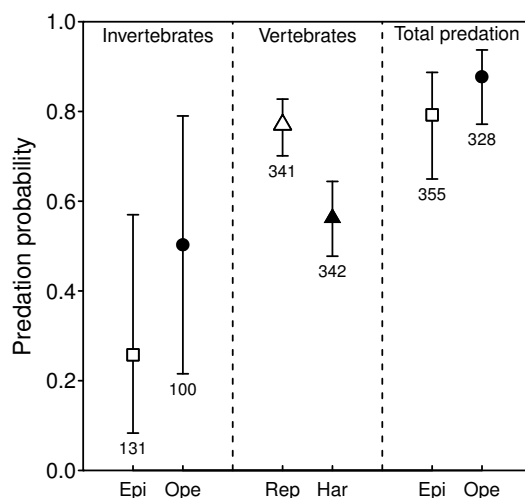


Figure 2: Model-derived parameter estimates for invertebrate predation probability depending on genus [non-outbreaking (Epi, *Epirrita*; white squares) or outbreaking (Ope, *Operophtera*; black circles) in southern Finland], vertebrate predation probability depending on area [outbreak area (Rep, Reposaaari; white triangle) or non-outbreak area (Har, Harjavalta; black triangle)] and total predation probability depending on genus (Epi, Ope). Back-transformed least-squares mean estimates accompanied by their 95% confidence limits are shown. Sample sizes are given below each bar.

nally, *Operophtera* pupae had a significantly greater probability of predation from all causes than *Epirrita* pupae (Figure 2, Table 1), although this was not affected by area or year (Table 1).

DISCUSSION

The predation of experimentally exposed geometrid moth pupae of the genera *Epirrita* and *Operophtera* did not support the hypothesis that a reduced vulnerability to pupal predation might explain why *Operophtera* species (i.e. winter and northern winter moths) can reach outbreak densities in southern Finland, whereas *Epirrita* (i.e. autumnal moth) population densities stay relatively low and stable there. Only some general differences in predation were observed between genera and areas, with greater invertebrate and total predation in *Operophtera* than in *Epirrita* in both areas and years, and greater overall vertebrate predation in the outbreak area compared with the non-outbreak area in both genera and years. Thus, the outbreaking species suffered more from pupal predation than the non-outbreaking species, which makes it unlikely that escape from the regulatory influence of generalist pupal predators allows the *Operophtera* species to reach outbreak densities in the study area.

Previous studies on population dynamics in autumnal moths have suggested that pupal predation by generalists may be responsible for the differences in population

dynamics between southern and northern populations, with more stable, low-density fluctuations in the south compared with outbreak dynamics in the north (Haukioja *et al.*, 1988; Tanhuanpää *et al.*, 1999; Klemola *et al.*, 2002). In these studies, it is argued that both a longer duration of the pupal period and a more diverse and abundant natural predator community lead to greater pupal mortality in the south, which is assumed to restrict the possibility of reaching outbreak densities in southern autumnal moth populations. This hypothesis is suitable for explaining the north-south gradient from cyclic to more stable population dynamics in autumnal moths. However, despite their even longer pupal period (Mikkola *et al.*, 1985), it does not appear to apply for the winter (*O. brumata* and northern winter moth *O. fagata*, which can reach outbreak densities also in southern Finland and at the same latitude on the Russian side of the border (Tikkanen *et al.*, 1998; Tikkanen & Roininen, 2001). Thus, it could be assumed that these species might be less vulnerable to pupal predation and may manage to escape the regulatory influence of generalist predators even in southern Finland.

The results obtained in the present study, however, do not support this hypothesis but suggest the opposite situation. In some cases, there were virtually no differences in pupal predation between *Epirrita* and *Operophtera* but, most of the time, *Operophtera* pupae suffered more from predation than *Epirrita*. This is particularly notable because naturally-occurring *Operophtera* pupae would have been in the soil for approximately another 4 weeks (Mikkola *et al.*, 1985; pupae of both species were collected at the same time for practical reasons), such that final predation rates would most likely have been even greater. Furthermore, there were no pronounced differences in pupal predation probabilities between the two *Operophtera* species that were used in the different study years, which makes it unlikely that the use of only one species per experimental year led to a bias in the results obtained in the present study.

For invertebrate predation, the difference in predation probability was comparable with our observations from autumnal and winter moth populations in northern Finland, where winter moth pupae suffered from three-fold greater invertebrate predation rates than autumnal moth pupae (Klemola, 2009; Heisswolf *et al.*, 2009). Probably as a result of their thicker and harder cuticle, autumnal moth pupae are most likely consumed by fewer invertebrate species and require also longer handling times for the species that are able to feed on them (Frank, 1967a,b).

Vertebrate predation was almost the same for *Epirrita* and *Operophtera* pupae in both areas and years, except in the outbreak area in the year when the *Operophtera* outbreak was already over. There, the estimated vertebrate predation was approximately 20% less for *Epirrita* than for *Operophtera* pupae. Similarly, the overall vertebrate predation probabilities were approximately 20% less within the non-outbreak area compared with the outbreak area. Although we have no explanation for the differences in

vertebrate predation probability between the two genera, one possible reason for the differences between the two study areas might be that the areas were covered by different forest types, which might affect the composition of the vertebrate predator community. Reposaari, the outbreak area, was dominated mainly by birch trees, whereas, in Harjavalta, the non-outbreak area, a mixed coniferous forest prevailed. Consequently, also the invertebrate predator community would probably differ between the two forest types (Raymond *et al.*, 2002). However, there was no evidence of any difference in invertebrate predation between the two areas. Thus, the reasons for the regional patterns in vertebrate predation, as well as other specific characteristics that made Reposaari prone to winter and northern winter moth outbreaks, remain to be elucidated in further studies.

Finally, another very important result obtained in the present study was that total predation rates were very high (> 69% for all groups) even during the *Operophtera* outbreak, when the natural *Operophtera* pupal densities were very high within the outbreak area (K. Ruohomäki & M. Käär, personal observations). There, the estimated total predation probability of *Operophtera* pupae was 93%. Assuming that the generalist predator population densities do not follow the density changes in the moth populations but rather show a functional response to prey density (Hanski, 1992), it would be expected that the predators become saturated at high pupal densities and more and more pupae escape predation. On the basis of the results of the present study, however, the natural predator community appears to be capable of coping even with very high pupal densities in southern Finland, whereas saturation appears to be reached at much lower pupal densities in northern Finland (Heisswolf *et al.*, 2009). It might be possible that the material used for the pupal cocoons (i.e. potting soil mixed with glittering powder) led to a slightly greater predation than the natural rate of pupal predation, although this does not affect the comparison between genera in the present study because the method employed was the same for all individuals. In the experiment conducted in northern Finland (Heisswolf *et al.*, 2009), a different method was used, although the predation rates obtained there are comparable with other northern experiments where the glittering powder method was used (K. Ruohomäki & T. Klemola, unpublished data).

Which other hypotheses might then be considered as potential explanations for the *Operophtera* outbreaks in southern Finland? Although pupal predation does not appear to be a suitable candidate mechanism, other kinds of predation might generate the observed patterns in population dynamics. Tanhuanpää *et al.* (2001) studied predation by generalists in autumnal moth larvae, which was not considered in the present study. They were able to show that predation by birds had a considerable impact on larval survival, which might, in addition to larval parasitism, be needed to decrease the moth

population density to that which allows density-dependent regulation by pupal predation. Similarly, in a study by Roland (1994) suppression by parasitoids was required for pupal predators to be able to regulate winter moth populations. Thus, further studies should test whether differences in larval predation and parasitism between autumnal, winter and northern winter moth populations in southern Finland could explain the occurrence of outbreak densities in the latter two species.

Another possible mechanism could comprise a difference in the species' reaction to induced host plant defences (Haukioja & Neuvonen, 1987; Hanhimäki & Senn, 1992; Klemola *et al.*, 2008). If autumnal moth fecundity was reduced more by plant defence chemicals than the fecundity of winter and northern winter moths, autumnal moth population abundance could be restricted to a low density, whereas the other two species might still be able to increase their population densities to outbreak levels. For this scenario, however, a very species-specific reaction to host plant defences and an immense decrease in fecundity or survival would be needed, which does not appear to be very likely (Haukioja & Hanhimäki, 1985; Mutikainen *et al.*, 2000; Klemola *et al.*, 2008; A. Heisswolf, N. Klemola, T. Klemola, unpublished data). Furthermore, because winter moths can reach outbreak densities on several different tree species (Tikkanen *et al.*, 1998; Tikkanen & Roininen, 2001), such species-specific responses are even less likely.

A third alternative worthy of closer investigation in future studies comprises the possible differences in the reproductive capacities of *Operophtera* and *Epirrita* and how reproduction depends on climate and host tree. If *Operophtera* species grow comparatively better than *Epirrita* in the south and reach larger sizes, they may be able to produce more eggs and might thus escape their enemies even in the south. No detailed data are yet available in this respect, although there is evidence to suggest that *O. brumata* females might be larger in southern populations (Tikkanen *et al.*, 2000) than in northern Fennoscandia (Klemola, 2009). However, because pupal mass also depends on the rearing conditions, more detailed studies using identical rearing conditions are necessary to assess the specific size differences and reproductive capacities of northern and southern *Operophtera* and *Epirrita* populations.

In conclusion, the results obtained in the present study show that local outbreaks of winter and northern winter moths in southern Finland cannot be explained by low vulnerability to pupal predation. Other potential candidate mechanisms, such as larval predation and parasitism, induced species-specific host plant defences and reproductive capacity, need to be examined in future studies aiming to elucidate whether they might contribute to the observed differences in population dynamics of these geometrid moth species in southern Finland.

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