Ecological Entomology (2003) **28**, 659–665

Density-dependent melanism in sub-arctic populations of winter moth larvae (*Operophtera brumata*)

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Abstract. 1. The aim of this 4-year observational study was to test for the presence of direct and delayed density-dependent larval melanism in the geometrid moth species *Operophtera brumata* (winter moth) in northern Norway.

2. Data from many populations with a wide range of population densities in time and space facilitated statistical analyses that could separate the effects of current and past density. The data also included different phases of the 10-year population cycle of this species so that eventual non-linear density effects due to population phase could be detected.

3. The results showed that the prevalence of melanism had a strong positive, linear relation to population density within years, whereas there was no evidence for a delayed effect from the year before or dependency on the phase of the population cycle.

4. In combination, these results limit the range of possible explanations of larval melanism in this outbreaking species. The possible reasons why winter moth larvae might benefit from crowding-induced melanism are discussed.

Key words. Birch forest, Lepidoptera, outbreak species, phase-dependent, population cycles.

Introduction

Density-dependent melanism, i.e. the phenomenon that individuals at high population densities develop into a dark-coloured phenotype, has been documented in a number of insects (Long, 1953; Kunimi & Yamada, 1990; Goulson & Cory, 1995; Reeson *et al*., 1998; Barnes & Siva-Jothy, 2000; Reeson *et al*., 2000). In many of these cases, melanism seems to be a direct counter-measure to density-dependent responses of natural enemies (predators, parasites, disease) (Kunimi & Yamada, 1990; Reeson *et al*., 1998; Barnes & Siva-Jothy, 2000; Wilson *et al*., 2001). Melanin strengthens the insect cuticle's ability to withstand penetration of fungi, bacteria, and parasitoids (St Leger *et al*., 1988; Hajek & St Leger, 1994; Wilson *et al*., 2001). Moreover, melanin is toxic to microbes (Ourth & Renis, 1993), and the enzymes involved in the production of melanin are also involved in the various immune responses directed against parasites and pathogens (Poinar, 1974; Götz, 1986; Hung & Boucias, 1992; Beckage *et al*., 1993). Thus, crowding-induced melanism may well reflect an investment in immune defence; however, there are also alternative mechanisms that might underlie density-dependent melanism. For instance, the coloration of larvae may serve as camouflage, and there is a possibility that the background colour of the foliage on which the herbivorous larvae forage may turn darker or provide less protection at outbreak densities (S. B. Hagen *et al*., pers. obs.). Moreover, decreased foliage at outbreak densities might expose the larvae to more UV radiation against which pigmentation offers protection (Gunn, 1998). Finally, there is evidence that melanism may play a role in temperature regulation, with darker phenotypes absorbing more sun energy, yielding faster growth in cold climates (Goulson, 1994; Hazel, 2002).

In the boreal and sub-arctic forests of North America and Fennoscandia, the geometrid moth species *Operophtera brumata* (winter moth) and *Epirrita autumnata* (autumnal moth) demonstrate pronounced population fluctuations with a period of 9–10 years (Tenow, 1972; Haukioja *et al*., 1988; Hogstad, 1997; Ruohomäki *et al*., 2000). Several

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hypotheses have been proposed to explain these cycles, from natural enemies and induced plant defence, to maternal and genetic effects (for recent reviews see Ruohomäki *et al*., 2000; Klemola *et al*., 2002). Although the effects of crowding on phenotype have been the subject of some studies (e.g. Haukioja *et al*., 1988 for *E. autumnata*, which is a non-melanic species), there is an aspect that has received little attention in this connection, namely that winter moth larvae are extremely variable in coloration, from pale yellow or green to almost entirely black. In one sub-alpine population in central Norway, the proportion of melanic winter moth larvae was found to increase during an outbreak (Hogstad, 1996). However, because Hogstad (1996) focused on a single population, it was unclear whether the degree of melanism changed as result of changing conditions during the different phases of the outbreak (i.e. food resource quality or quantity) or whether it changed as a direct response to density. Assuming that a changing degree of melanism may be causally linked to mechanisms underlying population dynamics, a more detailed analysis of the relationship between patterns of melanism and population dynamics is warranted. Pattern-oriented analyses focusing on different aspects of density-dependent responses have proved to be rewarding in studies of cyclic populations (for reviews see Berryman, 1996; Stenseth, 1999). The issues concerning density-dependence that in particular have been highlighted in recent analyses on cyclic mammal populations are whether the responses are direct (i.e. dependence of current year density) or delayed (i.e. dependence of past year density), and eventually whether the density-dependent responses work in a linear or non-linear fashion (Stenseth, 1999). A non-linear response would be expected if the effect of population density depends on the phase of the cycle; i.e. whether a population is at its peak, is declining, or increasing (Stenseth, 1999). If such phenomena are also expressed as responses in the degree of melanism in cyclic winter moth populations it could help to direct future research on the causes of these cycles.

Thus, the primary goal of the work reported here was to investigate if and how the degree of larval melanism was related to larval density, focusing on the aspects of direct vs. delayed and linear vs. non-linear responses. The 4-year observational study covered the peak, crash, and low phase of several spatially asynchronous populations with a large temporal and spatial variation in local larval densities. Thus, the data provided an excellent opportunity to separate the different aspects of density-dependent responses.

Methods

Study areas

The study was carried out in late June to early July 1999–2002 in the coastal districts of Troms county, northern Norway (69°30′ to 70°03′N). The study area is characterised by an oceanic, sub-arctic climate, with relatively mild winters (average January temperature −5 to 0 °C) and cool, wet summers (average July temperature 10 to 15 °C). Twelve spatially separated study sites with mature birch were selected to represent typical winter moth habitats. All sites were at similar altitude, approximately 100–150 m above sea level, which is the altitude where winter moth outbreaks typically occur (Tenow, 1972). The 12 sites were arranged in six pairs with one site on the mainland or a large island and one site on a nearby, small- to medium-sized island (Fig. 1). All of the islands were true islands surrounded by sea, except on locality (Rekvik), which is a forest island isolated from the continental forest by treeless alpine habitats. The straight-line distance between the continent and the island within a pair ranged from 4 to 9 km and always included a stretch of more than 1.5 km of open sea (or mountain habitat in the case of Rekvik), which probably constitutes an efficient barrier for ballooning winter moth larvae (Edland, 1971). The straight-line distance between the two nearest sites from two different pairs ranged from 13 to 42 km. This probably is sufficiently far to ensure little or no exchange of individuals, because ballooning is believed to have little effect beyond the forest stand scale in forest Lepidoptera (Ruohomäki *et al*., 2000). Thus, for the purpose of this study, the various study sites could be assumed to inhabit separate winter moth populations.

Study design

At each of the 12 study sites, sampling of larvae for determination of cuticular melanism and local population density was done according to a transect design. The transects were 1.8 km long and had 10 permanent sampling stations positioned at regular intervals, approximately 200 m apart, at the same altitude (see above). At each sampling station, larvae were sampled from 10 arm-length birch twigs, collected haphazardly from different trees within a radius of 20 m. Each branch was beaten thoroughly with a stick over a large plastic box and the larvae were counted and subjectively classified into three ordinal categories based on their degree of melanism: (1) non-melanic (pale yellow or green larvae with pale head capsules) (2) melanic (very dark larvae with black stripes and black head capsules), or (3) intermediate (larvae being somewhere in between these two extremes of coloration). Control checks of beaten branches by subsequently scrutinising every leaf for the presence of remaining larvae revealed that the method was efficient for the purpose of obtaining a reliable index of larval density. Both transects in each pair of sites were sampled during a single day and all sites/transects were sampled during one week. Care was taken to perform the sampling when most of the larvae were in their third or fourth instars to avoid overlooking first instar larvae or losing fifth instar larvae that had pupated. Sampling time therefore varied somewhat from late June to early July depending on the relative progress of larval development in the different years. This slight difference in the timing of sampling of the various transects does not matter in this

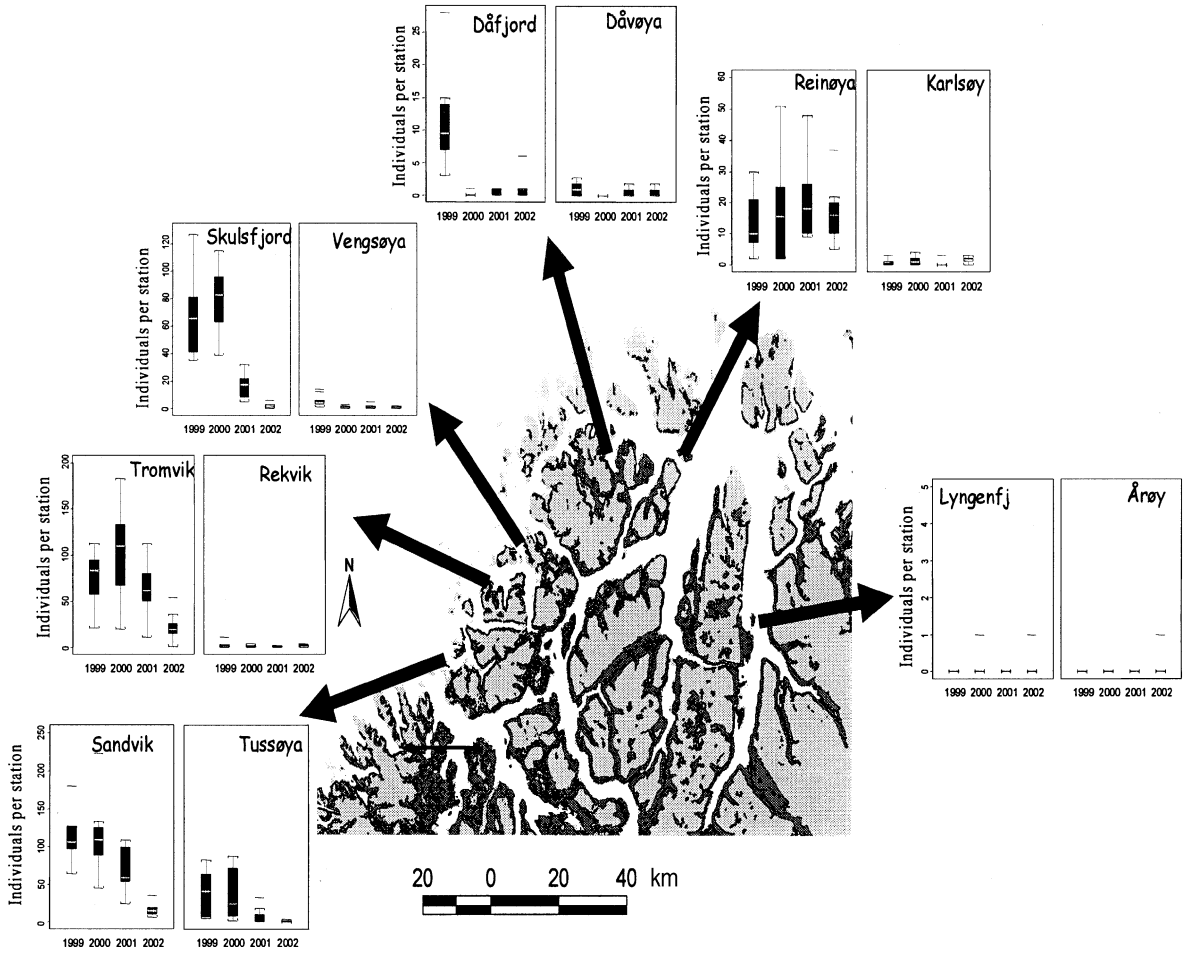

Fig. 1. Variation in the number of winter moth larvae independent of coloration within and between the 12 named study sites (transects) during the 4 years. The box plots describe the distribution of station-specific densities among the 10 stations per site and year. Box specifications: line within boxes = median; boxes = quartiles; whiskers = 1.5 inter-quartile distance; lines beyond = outliers.

context, because degree of melanism does not appear to depend on instar (Hogstad, 1996).

Statistical procedure

Sources of variation in the proportion of non-melanic, intermediate, and melanic larvae were investigated using logistic regression analysis (Agresti, 1990). In addition to the focal variables local population density within year and the year before, a related aim was to investigate whether the relation between density and melanism was consistent in time and space by including study site and year as additional predictor variables. Different approaches exist for logistic regression when the categories are ordered (ordinal regression; Greenland, 1994). The approach considered here is the simplest one based on analysing cumulative proportions, i.e. both the proportion non-melanic/(non-melanic + intermediate) and the proportion (non-melanic + intermediate)/(non-melanic + intermediate + melanic), which enabled the consistency of the relation between the degree of melanism and population density to be checked. This was considered to be important because the results might depend on the subjective cut points used to classify the degree of melanism (a continuous variable) in the field. Model selection based on the two Information Criteria AIC and BIC (Burnham & Anderson, 1998; Miller, 2002), the latter being more conservative, was used to strike the balance between variance (too many parameters) and bias (to few parameters) when selecting variables to be included in the statistical models. To ensure robust results, model selection was conducted on sampling stations with 10 larvae or more ($n = 8729$ caterpillars in total), and the small-sample correction for the AIC was used, but the selected models were also fitted to the entire data set ($n = 9119$ caterpillars in total) to check that the main relationships hold for even lower densities. Goodness-of-fit (GOF), which describes how well a statistical model describes the data, was assessed on the basis of the residual deviance divided by the number of degrees of freedom for the most

complicated model, which is a reliable assessment of GOF provided that sample sizes are adequate (e.g. Agresti, 1990). As evidence for overdispersion was found, i.e. more residual variation than would be expected from a binomial variance, both the AIC and the BIC were adjusted, and the $QAIC_C$ and QBIC for model selection were used:

$$QAIC_C = \frac{\text{Deviance}}{\hat{c}} + 2K + \frac{2K(K+1)}{n-K-1}$$

$$QBIC = \frac{\text{Deviance}}{\hat{c}} + \log(n)K$$

where $\hat{c}$ is the overdispersion correction factor, K is the number of parameters, and n the sample size. $\hat{c}$ was estimated using the residual deviance divided by the number of degrees of freedom for the most complicated model. Parameter estimates and their standard errors were calculated using quasi-likelihood approaches for the binomial family. Plots of residuals and influential values (as measured by Cook's distances) were used for the most complicated model as well as for the selected model(s). In particular, the linearity of the relationship between the density of moth larvae and the cumulative proportions (on a logit scale) was carefully investigated, using partial residual plots (Cook & Croos-Dabrera, 1998) and generalised additive models (Hastie & Tibshirani, 1990). All analyses were done using the computer software R (Ihaka & Gentleman, 1996).

Results

There was considerable variation in the density of *O. brumata* larvae both within and among the 12 study sites (transects) during the 4 years (Fig. 1, Table 1). Many of the populations appeared to be in different phases of the population cycle. While some moth populations had already crashed at the onset of study in 1999 and remained low for the next 3 years, other populations were at peak/outbreak densities and crashed during the study period (Fig. 1). The large spatio-temporal variability in cyclic phase and local population density provided an excellent opportunity for statistically separating the effect of current density from the effect of density the year before (i.e. delayed or phase-dependent effect) on the degree of larval melanism.

Using the material from all 4 years, a fit was obtained for the most complex model containing year, area, population density, and the interactions between these variables as well as all nested subsets of this baseline model. Based on the

Table 1. Variation in the abundance of winter moth larvae of each colour morph (N = non-melanic, I = intermediate, M = melanic) within and among the 12 named study sites (transects) during the 4 years. Numbers are mean values with range in parentheses.

	1999			2000			2001			2002		
Study site	N	I	M	N	I	M	N	I	M	N	I	M
Sandvik	14.7 (5–24)	87.5 (50–158)	8.8 (2–14)	19.5 (10–29)	87.6 (29–185)	5.7 (1–23)	29.8 (21–41)	30.4 (3–62)	8.4 (0–25)	10.2 (6–16)	4.5 (0–15)	0.4 (0–4)
Tussøy	1.2 (0–3)	33.9 (1–77)	1.9 (0–6)	8.3 (1–14)	24.8 (0–77)	2.1 (0–11)	4.0 (0–22)	1.4 (0–6)	0.8 (0–4)	0.4 (0–3)	0.0 (0–0)	0.0 (0–0)
Tromvik	4.5 (0–13)	64.5 (9–104)	6.1 (0–14)	10.1 (1–28)	71.5 (12–148)	20.6 (0–85)	15.2 (3–28)	35.9 (3–71)	10.0 (0–35)	10.2 (1–19)	6.6 (0–17)	4.7 (0–18)
Rekvik	1.5 (0–8)	0.5 (0–3)	0.0 (0–0)	1.1 (0–4)	0.0 (0–0)	0.0 (0–0)	0.8 (0–2)	0.0 (0–0)	0.0 (0–0)	1.5 (0–4)	0.0 (0–0)	0.0 (0–0)
Skulsfjord	3.8 (0–15)	59.3 (20–115)	5.9 (2–11)	9.7 (3–21)	59.2 (19–86)	9.1 (2–21)	12.2 (5–21)	3.2 (0–10)	0.5 (0–2)	1.3 (0–5)	0.1 (0–1)	0.0 (0–0)
Vengsøy	4.7 (1–11)	0.7 (0–3)	0.1 (0–1)	0.8 (0–3)	0.0 (0–0)	0.0 (0–0)	1.2 (0–5)	0.0 (0–0)	0.0 (0–0)	0.6 (0–2)	0.0 (0–0)	0.0 (0–0)
Dåfjord	7.5 (3–16)	2.9 (0–10)	0.7 (0–2)	0.0 (0–0)	0.1 (0–1)	0.0 (0–0)	0.1 (0–1)	0.3 (0–3)	0.0 (0–0)	1.1 (0–6)	0.0 (0–0)	0.0 (0–0)
Dåvøy	1.1 (0–3)	0.0 (0–0)	0.0 (0–0)	0.0 (0–0)	0.0 (0–0)	0.0 (0–0)	0.5 (0–2)	0.0 (0–0)	0.0 (0–0)	0.5 (0–2)	0.0 (0–0)	0.0 (0–0)
Reinøy	5.4 (2–11)	6.0 (0–21)	2.8 (0–7)	4.2 (1–9)	13.5 (1–45)	0.0 (0–0)	4.5 (2–7)	15.1 (2–37)	0.8 (2–35)	8.8 (5–13)	6.2 (0–18)	1.5 (0–7)
Karlsøy	0.7 (0–2)	0.2 (0–1)	0.0 (0–0)	1.0 (0–3)	0.2 (0–1)	0.0 (0–0)	0.3 (0–3)	0.0 (0–0)	0.0 (0–0)	1.3 (0–2)	0.1 (0–1)	0.1 (0–1)
Lyngenfj	0.0 (0–0)	0.0 (0–0)	0.0 (0–0)	0.0 (0–0)	0.2 (0–1)	0.0 (0–0)	0.0 (0–0)	0.0 (0–0)	0.0 (0–0)	0.1 (0–1)	0.0 (0–0)	0.0 (0–0)
Årøy	0.0 (0–0)	0.0 (0–0)	0.0 (0–0)	0.0 (0–0)	0.0 (0–0)	0.0 (0–0)	0.0 (0–0)	0.0 (0–0)	0.0 (0–0)	0.1 (0–1)	0.0 (0–0)	0.0 (0–0)

model selection criteria $QAIC_C$ and QBIC, two models could be used for further inference (Table 2). Both of these models indicated clear evidence of density-dependent melanism, with proportion non-melanic/(non-melanic + intermediate) and proportion (non-melanic + intermediate)/(non-melanic + intermediate + melanic) larvae decreasing linearly in response to increasing population densities within years (Fig. 2). The results were not affected either by outliers or by selecting all sampling stations irrespective of their densities: For proportion non-melanic/(non-melanic + intermediate), the estimated effect of population density were $b = -1.33$, $SE = 0.13$, $P < 0.001$ ($n > 10$ larvae) and $b = -1.32$, $SE = 0.09$, $P < 0.001$ ($n > 0$ larvae). Similarly, for proportion (non-melanic + intermediate)/(non-melanic + intermediate + melanic), the estimated effect of population density were $b = -0.97$, $SE = 0.19$, $P < 0.001$ ($n > 10$ larvae) and $b = -0.96$, $SE = 0.14$, $P < 0.001$ ($n > 0$ larvae). Hence, there was a highly consistent relation between the degree of melanism and population density, and consequently no evidence that the results depended on the subjective cut points used to classify the degree of larval melanism in the field. Evidently, the occurrence of melanism had a strong direct density-dependent component.

Delayed (or phase-dependent) effects of population density on occurrence of melanism was assessed in a separate but interrelated analysis using only the years 2000–2002, i.e. the years for which there were data on larval densities both the same year and the year before. For the proportion non-melanic/(non-melanic + intermediate), the estimated effect of population density the same year was $b = -0.96$, $SE = 0.21$, $P < 0.001$, whereas the estimated effect of population density the year before was $b = -0.02$, $SE = 0.17$, $P =$ NS. Likewise, for the proportion (non-melanic + intermediate)/(non-melanic + intermediate + melanic), the estimated effect of population density the same year was $b = -1.54$, $SE = 0.32$, $P < 0.001$, whereas the estimated effect of population density the year before was $b = -0.31$, $SE = 0.30$, $P =$ NS. Thus, this second analysis yielded no evidence of delayed (or phase dependent) effects, but rather verified the strong density-dependent effects within years found in the first analysis (see above).

Table 2. Results from model selection for (a) the proportion non-melanic/(non-melanic + intermediate) and (b) the proportion (non-melanic + intermediate)/(non-melanic + intermediate + melanic). The *best models* are in bold. The overdispersion factor $\hat{c}$ was taken as 2.71 for the analysis of (a) and 1.60 for the analysis of (b). y = year, s = site, d = larval density.

y	s	d	y:s	y:d	s:d	y:s:d	$QAIC_C$	QBIC
(a)								
x	x						176.36	147.43
x	x	x					37.58	11.28
x	**x**	**x**	**x**				**2.12**	**0.00**
x	x	x		x			38.63	19.99
x	x	x			x		34.65	23.33
x	**x**	**x**	**x**	**x**			**0.00**	**4.32**
x	x	x	x		x		8.14	18.46
x	x	x		x	x		32.55	28.20
x	x	x	x	x	x		8.79	24.64
x	x	x	x	x	x	x	29.21	59.64
(b)								
x	x						91.07	57.47
x	x	x					52.77	21.83
x	x	x	x				7.24	0.74
x	x	x		x			23.56	0.36
x	x	x			x		62.34	46.54
x	**x**	**x**	**x**	**x**			**0.00**	**0.00**
x	x	x	x		x		12.23	18.30
x	x	x		x	x		34.23	25.47
x	x	x	x	x	x		13.51	25.18
x	x	x	x	x	x	x	32.06	58.48

Discussion

There are several reasons why *O. brumata* larvae might benefit from crowding-induced melanism. In a number of insect species with phase-dependent polymorphism, it has been documented that the high-density (gregaria) phenotype is aposematic, i.e. warningly coloured and unpalatable to predators (see, e.g. Sword *et al.*, 2000). In fact, it has been speculated that density-dependent melanism in certain Lepidopteran larvae might have evolved as an anti-predator strategy in which crypsis is selected for at low population densities and aposematism is selected for at high population densities (Wilson, 2000). There is no evidence in support of this hypothesis, however (Wilson *et al.*, 2001), and on a general basis, it can be argued that this is not a likely explanation in the case of *O. brumata*. Firstly, aposematism usually involves warning colours, such as yellow or red in combination with black, and *O. brumata* larvae do not have such coloration. Secondly, many insectivorous birds feed almost exclusively on *O. brumata* larvae during the outbreaks in central Fennoscandia (Hogstad, 2000). Although these sorts of observations cannot be used to dismiss aposematism as a function of melanism (Sword *et al.*, 2000; Wilson, 2000), they suggest that aposematism is not an effective strategy in this species.

Another possibility is that the melanic larval phenotype offers a better camouflage at high population densities, whereas the non-melanic phenotype offers a better camouflage at low population densities. Large outbreaks of *O. brumata* damage trees to an extent that the colour of the leaves often changes from pale green to a brownish dark green colour (S. B. Hagen *et al.*, pers. obs.). This could potentially induce a strong selection against non-melanic larvae during increasing population densities and vice versa, because the larvae would appear conspicuously mismatched against the background and thus would be more easily detected by predators such as insectivorous birds. Hence, it could be that larval coloration is an adaptation to blend with the changing background coloration during the progress of an outbreak; however, the data presented in this study suggest that this is not a likely explanation either. The relation between density and melanism was linear even at densities that were much lower than what

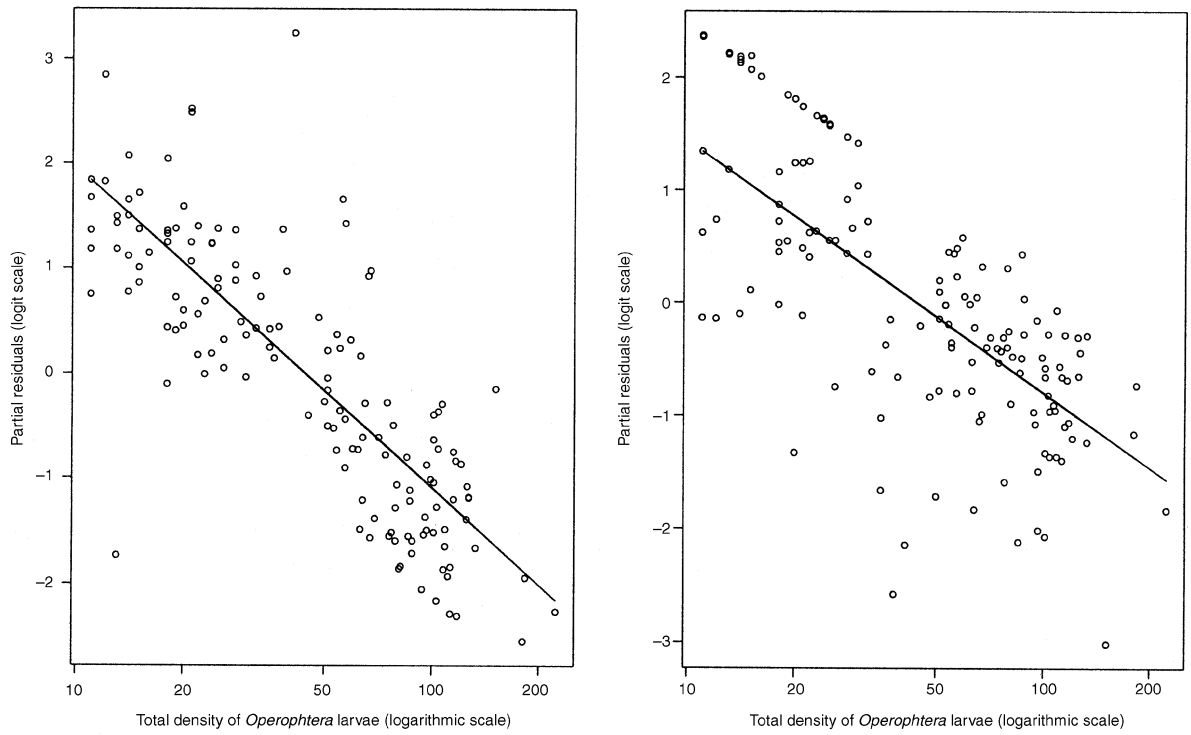

Fig. 2. The relationship between population density and the two proportions: non-melanic/(non-melanic + intermediate) (left) and (non-melanic + intermediate)/(non-melanic + intermediate + melanic) (right). The degree of melanism (the *y*-axis) is the partial residuals from the best fit of the models in Table 1, i.e. the effect of non-focal effects (year, site, and interaction terms) have been corrected for. Results for sampling stations with 10 or more larvae are shown.

would alter the coloration (the camouflage hypothesis) or the protective cover (the UV hypothesis) of birch foliage. After severe *O. brumata* damage, the darker *unhealthy* colour and the sparse foliage of the damaged forest may last for years after the density of larvae has dropped to almost zero (S. B. Hagen *et al.*, pers. obs.). Hence, if camouflage or protective cover were the point, a progressive matching would have resulted in a delayed density-dependent response, which was not found.

If the risk of being exposed to pathogens increases with density due to density-dependent pathogen transmission, then it is likely that insects will use the contact rate with other individuals of the same species as a cue to match their levels of investment in immune function to the perceived risk of transmission (Wilson *et al.*, 2001). The fact that the density-dependent melanism was strictly linear over the large range of densities included in this study, indeed suggests that larval contact rate is the proximate mechanism of melanism and, furthermore, that pathogen transmission risk may be the ultimate cause behind melanism then functioning as an investment in immune defence. Evidently, experimental studies are now needed to verify this.

In conclusion, this study has provided evidence for a linear, direct density-dependent degree of cuticular melanism in winter moth larvae based on data from a wide range of population densities and different phases of the population cycle in coastal, sub-arctic birch forest of northern Norway. It is suggested that melanism is induced proximally by contacts between larvae and that ultimately melanism may act as a defence mechanism against pathogens transmitted via contacts. There was no evidence for any phase-dependent or delayed density-dependent melanism. The presence of delayed density-dependent mechanisms has been claimed to be necessary for the generation of population cycles in geometrid moths (Klemola *et al.*, 2002). Both specialist parasitoids and induced chemical defence in the birch may exert their effects in a delayed manner (Ruohomäki *et al.*, 2000). The lack of a delayed effect of density on degree of melanisms in the present study may therefore suggest that the causes of melanism and cycles are not related. It is also worthwhile noting that *E. autumnata* occurs in sympatry and fluctuates in synchrony with *O. brumata* in several places in Fennoscandia (Tenow, 1972) but does not exhibit melanistic forms. The role of cuticular larval melanism in the population biology of the winter moth awaits further experimental studies.

Acknowledgements

We thank Ove Sørlibråten and Ragnhild R. Mjaaseth for assistance in the field. Financial support to S. B. Hagen from the Norwegian Research Council is greatly acknowledged.

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Accepted 15 May 2003