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Source: *Holarctic Ecology*, Vol. 14, No. 3 (Jul. - Sep., 1991), pp. 192-202

Published by: Blackwell Publishing on behalf of Nordic Society Oikos

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Latitudinal patterns in the size of European butterflies

Sören Nylin and Lena Svård

Nylin, S. and Svård, L. 1991. Latitudinal patterns in the size of European butterflies. – *Holarct. Ecol.* 14: 192–202.

The importance of seasonality in shaping latitudinal size patterns was investigated in 16 species of lycaenine and satyrine butterflies with distributions in Sweden and continental Europe. Species without shifts in voltinism within the study area generally displayed clear size clines, increasing in size from north to south within Sweden. These species were also larger in continental Europe than in Sweden. In northern temperate areas a linear model for mean size at different latitudes seems to be a reasonable approximation for most species in this category. The size patterns for three species with shifts from univoltinism to bivoltinism at latitudes within Sweden were more reminiscent of the “saw-tooth”-pattern predicted by theory for such cases. The results suggest that size patterns in European butterflies to a large extent is governed by the length of the favorable season at different latitudes, affecting selection for development time and size. Altitude and drought also affect the effective season length and may amplify or complicate latitudinal patterns.

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Introduction

Body size is a central feature in life-history patterns because of the constraints imposed by size and because of the tendency for other traits to scale with size (Barbault 1988). A good understanding of the selection pressures contributing to body size is, thus, a necessary prerequisite for an understanding of how life-histories evolve.

In most parts of the world, organisms live in seasonal environments. For many species, only one season is favourable in that it permits growth and reproduction. Therefore, the length of the favourable season and/or the amplitude in seasonal changes (factors which are often correlated with latitude) can be expected to have great impact on key life-history traits, including size and traits related to size.

Latitudinal patterns in the body size and clutch size of homeotherm animals, i.e. birds (e.g. Ashmole 1963, Ricklefs 1980, Murphy 1985) and mammals (e.g. Lindstedt and Boyce 1985, Geist 1987) have attracted much interest ever since Bergmann's rule (1847) was first proposed. The patterns have been documented exten-

sively and their causes discussed vigorously (McNab 1971, Geist 1987). It is now thought that seasonality is an important factor in shaping geographical size patterns among homeotherms, although the exact mechanism is under debate (e.g. Ricklefs 1980, Lindstedt and Boyce 1985, Murphy 1985, Geist 1987). In contrast, in poikilotherms, comparatively little is known about patterns or causes. Studies have been largely confined to between-species patterns (e.g. Lindsey 1966), to one or a few related species (most references below concerning insects, and references in Ray 1960) or to laboratory experiments on the physiological effects of temperature on body size (e.g. Ray 1960). There are few, if any, broad studies of within-species patterns.

Considerations of seasonality can be expected to be even more important in small, relatively stationary and locally adapted organisms with generation times similar to the period of seasonal fluctuation (e.g. many poikilotherm animals and plants) as among the typically large and long-lived homeotherm animals. Round the middle of this century, when ecogeographical rules were debated, two contending schools held, respectively, that Bergmann's rule is applicable also to poikilotherms (but

Accepted 28 June 1990

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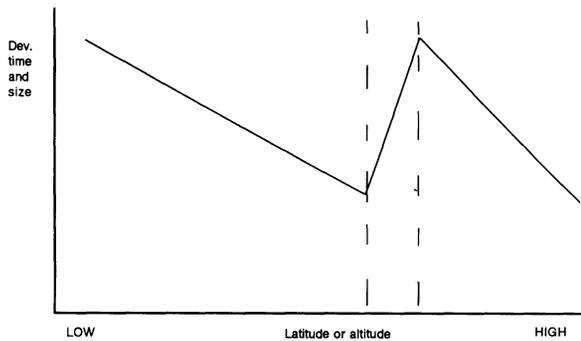


Fig. 1. A schematic illustration of how (according to the investigated model) size could be expected to vary with latitude or altitude as an effect of the length of the favorable season affecting selection on development time. Size can be expected to increase from north to south or from higher to lower altitudes, but the size cline should reverse at areas where shifts in generation number takes place, e.g. from univoltinism (right) to bivoltinism (left) (after Masaki 1973, 1978a,b, Roff 1980, 1983, Bradshaw and Holzapfel 1983).

for reasons unrelated to heat conservation) or that the converse pattern is typical (references in support of both views can be found in Ray 1960). The importance of seasonality was sometimes considered (e.g. Petersen 1947, Martof and Humphries 1959) but to our knowledge never tested. More recently, a simple and testable model has been suggested for the impact of seasonality on poikilotherms, specifically insects (e.g. Masaki 1973, 1978a,b, Roff 1980, 1983, Mousseau and Roff 1989). The assumptions of the model are: 1) that a longer development time should, everything else being equal, result in a larger or heavier mature insect (but is associated with increasing costs) and 2) that there is some advantage in being large. The amplitude of seasonal changes is not a factor in this model.

Roff (1980, 1983), who developed the mathematical framework of the model, suggested that r , the instantaneous rate of increase, is an inappropriate measure of fitness in seasonal environments, where the length of the season constrains growth and development, and can lead to highly erroneous predictions. This is especially true for organisms which can survive the unfavourable season in only one stage, e.g. the diapausing stage of insects. In such cases the yearly rate of increase, R_y , is the appropriate measure of fitness. A model maximizing R_y predicts that final body size should be larger in southern populations of a species than in the north, as a result of the longer favorable season (in terms of days or, rather, day-degrees) allowing a longer development time. Therefore, this model predicts the "converse Bergmann principle" (e.g. Park 1949) as the general pattern.

A pattern of more or less gradually increasing size to the south can then be expected in univoltine species or in the univoltine range of bi- or multivoltine species (Fig. 1). In the simplest form of the model the increase

in size with decreasing latitude could be linear. An additional generation will be favoured south of a latitude where the length of the season allows it. Theory then predicts a shift from large size in the southernmost parts of the area with univoltine insects to small size in the northernmost parts of the area with bivoltine insects. This is because a bivoltine life cycle, associated with a large potential increase in fitness, can take place further to the north if a shorter development time is selected for. The result would be a "saw-tooth" pattern of optimal sizes at different latitudes (Fig. 1). The theory also applies to shifts in season length and generation number caused by for instance altitude or seasonally predictable drought rather than latitude, which may complicate latitudinal patterns.

Many other selection pressures than those included in the model, as well as proximate environmental effects, could also potentially affect the final size of insects and other poikilotherms. Systematic studies are therefore needed before it can be decided whether the model has any general predictive value. We here report the results of an investigation of latitudinal size patterns in European Satyrinae and Lycaenidae (Lepidoptera) where we test the predictions of the theory and of some alternative theories generating different predictions.

Materials and methods

Study species

The European butterflies in Lycaenini (the "coppers") and Satyrinae were chosen as the subject of the study. The investigation was restricted to those species of Lycaenini (four in all: *Lycaena helle* Schiff., *L. phlaeas* L., *Heodes virgaureae* L. and *Palaeocrysophanus hippothoe* L.) and Satyrinae (12 species: *Coenonympha tullia* Müll., *C. arcania* L., *C. hero* L., *C. pamphilus* L., *Aphantopus hyperantus* L., *Maniola jurtina* L., *Erebia ligea* L., *Hipparchia semele* L., *Lasiommata megera* L., *L. maera* L., *L. petropolitana* F. and *Pararge aegeria* L.) which have distributions throughout a substantial part of Sweden as well as in continental Europe.

The phylogenetic relationships between these species are as follows: the four species in Lycaenini are probably closely related to each other. Following Miller (1968) the 12 species in Satyrinae can be grouped as follows: the four species of *Coenonympha* are related to *A. hyperantus* (included in the *Coenonymphini*) and (more distantly) to *M. jurtina*. The three species of *Lasiommata* are closely related to *P. aegeria*. *E. ligea* and *H. semele* have no close relatives among the investigated species.

13 species display constant voltinism within Sweden, usually a single generation per year, but in one case (*L. megera*) two per year (Dal 1978, Henriksen and Kreutzer 1982). Most of the former type of species are univoltine throughout Europe as well; exceptions are *L.*

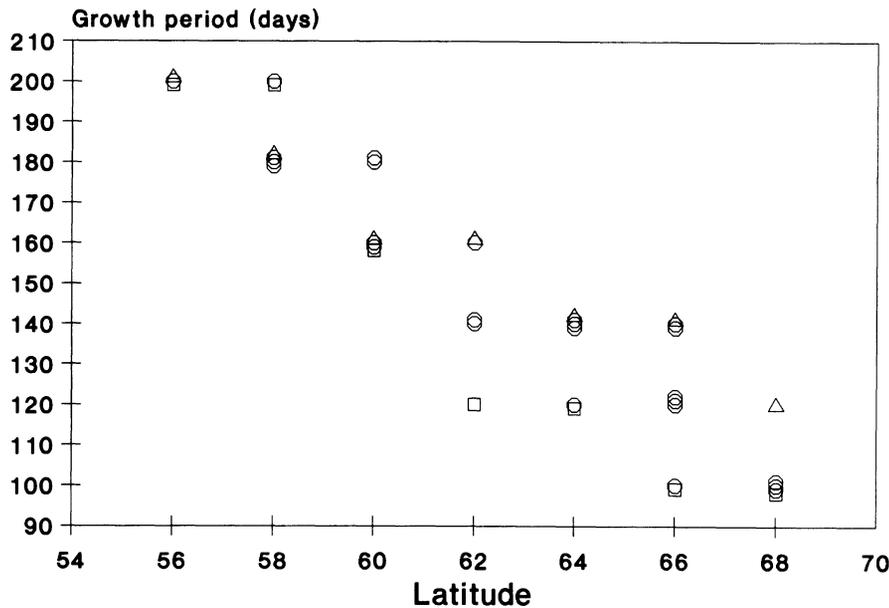


Fig. 2. The plant growth period (number of days with mean temperatures exceeding +6°C) at different latitudes within Sweden according to meteorological statistics (nearest higher 20-d isocline). The range and variation is shown by data points from the western border or coast (□), eastern border or coast (△) and additional data from each 1½ longitudinal degree across the country (○).

helle, *L. maera* and probably *L. petropolitana*. The latter species is, however, univoltine in most of its European range, including central Europe (cf. Dal 1978, Anonymous 1987, Chinery 1989). Finally, *L. phlaeas*, *C. pamphilus* and *P. aegeria* shift their voltinism from a single generation in northern Sweden to two or more further south within Sweden (Dal 1978, Henriksen and Kreutzer 1982).

Study area

The study focused on size variation within Sweden. This was done because sample sizes and the distribution of samples were adequate from this region whereas data from continental Europe was fragmentary. In combination with the heterogeneity of biotopes in continental Europe, and the differing distributions of species over those biotopes, this meant that data from south of Sweden could not be analyzed with any certainty. In particular, season length may not be well correlated with latitude in continental Europe, and the reasons behind such lack of correlations will differ for different species. A comprehensive analysis of these factors is beyond the scope of the present study and the material now available.

In contrast, Sweden is a region well suited to studies of latitudinal patterns, when such patterns are assumed to be caused by latitudinal and altitudinal variation in season length. This is because latitudinal and altitudinal patterns to some extent coincide within Sweden. North of 61°N altitude is almost everywhere > 200 m, climbing towards mountainous areas in the west, with large areas exceeding 500 m in these parts. Altitude is lower than 200 m only near the Baltic coast in the east. South of

61°N there are large regions with an altitude of < 100 m. Altitude exceeds 200 m only in the central part of the region between c. 57–58°N and nowhere exceeds 500 m.

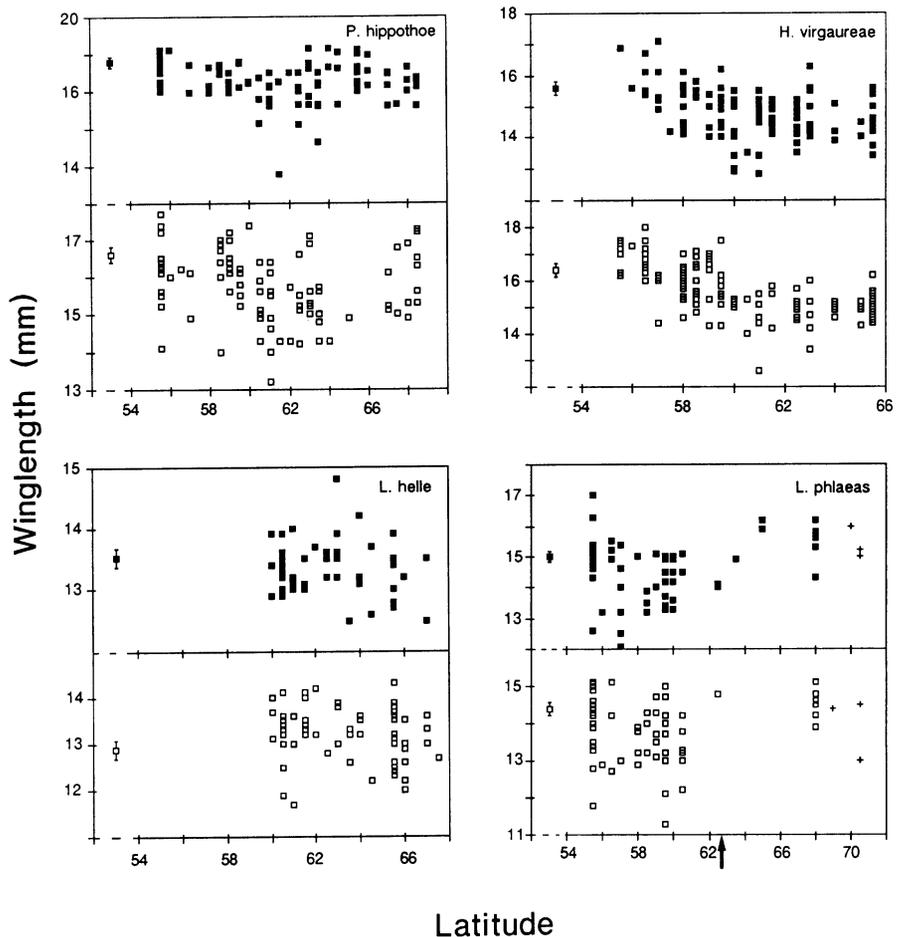
The effects of latitude and altitude together are reflected in climatic patterns such as mean temperatures. A biologically relevant measure is the length of the plant growth period, often defined as the number of days with mean temperatures exceeding +6°C. The range of the growth period at different latitudes within Sweden is depicted in Fig. 2.

Methods

We used museum specimens in order to obtain large samples from many species. There are several problems associated with studies of this type. Sample sizes from different localities can be very variable, due to abundance patterns as well as the irregular activities of collectors. Individuals could also vary considerably in size due to local environment effects (of starvation, microclimate or larger climatic difference, e.g. due to proximity to the coast or altitude) or genetic differences between populations which are not correlated with latitude. Any observed latitudinal pattern which despite these problems is consistent among species should be real and also reflect the true strength of the geographical patterns in nature better than laboratory breedings. Results from individual species should, however, be taken with caution.

Forewing length was used as an index for size. This measure is typically well correlated with other size or weight measures in butterflies, such as pupal weight (e.g. Jones et al. 1982). Winglengths were measured on all specimens of these species in the Swedish and Pa-

Fig. 3. Winglength at different latitudes for females (top, ■) and males (bottom, □) of *Palaeochrysopterus hippothoe*, *Heodes virgaureae*, *Lycaena helle* and *L. phlaeas* in Sweden. The leftmost dot in each figure represents the mean for continental Europe \pm S.E. For *L. phlaeas*, the northernmost latitude where the second generation occurs has been approximately marked with an arrow, and a few specimens from arctic Norway are shown as well (+).



learctic collections (excepting those from Asia and insects from the Baltic, British and Mediterranean islands) of the Museum of Natural History in Stockholm, and some additional specimens in collections belonging to the Dept of Zoology.

Sex, capture dates and sites were noted. This information was used to find the approximate latitude where a shift in voltinism takes place for a given species. The shifts are diffuse (probably genetically as well as environmentally variable) and it is, thus, not possible to give an exact latitude for them. For practical reasons we have used the Swedish coordinate system (used for labelling by the Museum of Natural History), ranging from 0 in the south of Sweden (55°N) to 32 in the north (about 69°30'N), in Figs 4–6 (Satyrinae). To simplify comparisons with data from other sources we have, however, calculated the slopes of the regression lines in mm per latitudinal degree in Tab. 2.

Samples from a larger number of latitudes were available only from Sweden, and so only these measurements were subjected to regression analysis. To test whether trends in size continued through continental Europe means of measurements from Sweden were

compared with means from the Palearctic collection (i.e. continental Europe). The differences in sample size from Sweden in the two analyses arose because of uncertain localities within Sweden for some specimens.

Results

General observations

In agreement with the prediction of the theory most species increased in size from northern to southern Sweden (Tabs 1 and 2, Figs 3–6). In 9 species out of 16 negative correlations between size and latitude were statistically significant in at least males (the sex for which data was most complete; Tabs 1–2). There were no significant positive correlations. The high proportion of observed negative slopes (significant or not) significantly deviated from the null hypothesis of a 50:50 ratio of positive and negative slopes in both sexes (Tab. 5).

Moreover, the majority of species were larger in continental Europe than in Sweden (Tabs 3 and 4). Again, only those results which showed a larger size in the

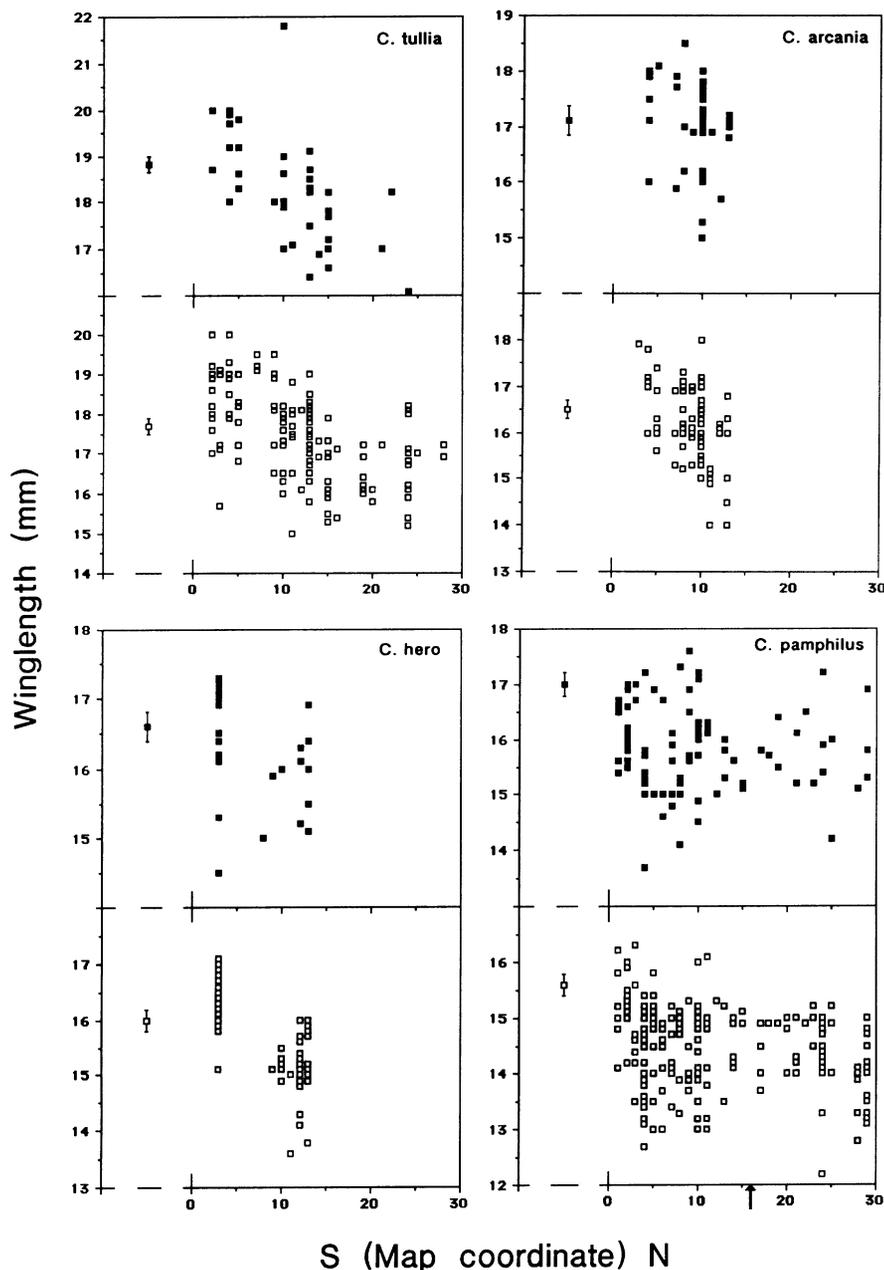


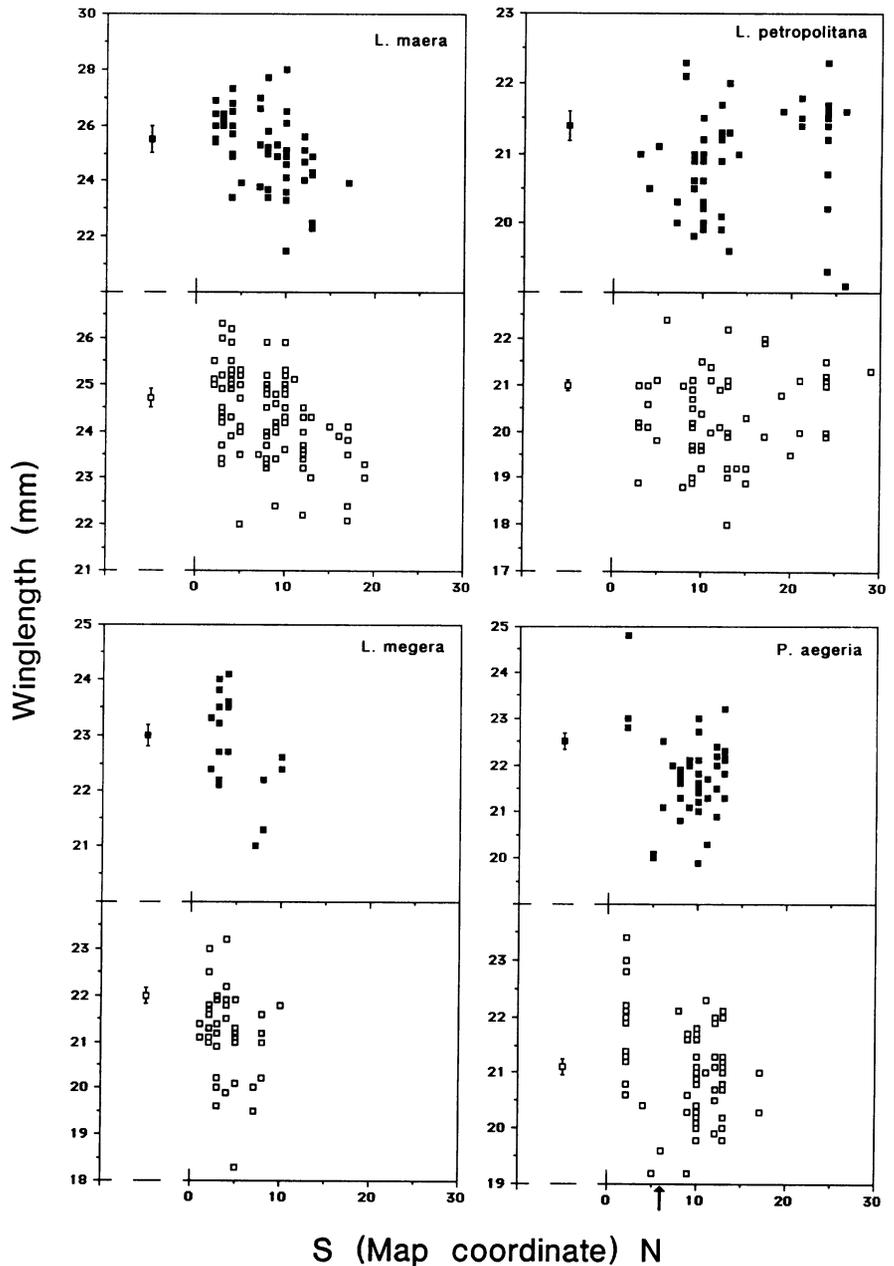
Fig. 4. Winglength at different latitudes for females (top, ■) and males (bottom, □) of four species of *Coenonympha* in Sweden. The leftmost dot in each figure represents the mean for continental Europe \pm S.E. For *C. pamphilus*, the northernmost latitude where the second generation occurs has been approximately marked with an arrow.

south were significant. The number of negative slopes (as inferred from differences in mean size) were significantly greater than expected from randomness in both sexes (Tab. 5). Thus, it can be concluded that European Lycaenini and Satyrinae show a latitudinal size trend, with increasing size to the south, as predicted by seasonality theory. For several species, a simple linear regression model accounted for 25–50% of the variation in size within Sweden (Tabs 1–2), despite the heterogeneity of the material.

Species with constant voltinism

As predicted by theory, most species which are univoltine within Sweden displayed negative size correlations with latitude within this area, although the slopes of the regression lines and the explanatory power (r^2) were often low due to large variation (Tabs 1 and 2). Likewise, species with constant univoltinism throughout Europe were typically larger in continental Europe than in Sweden (Tabs 3 and 4), and the same was true for *L. petropolitana* (Tab. 4) which is univoltine in at least

Fig. 5. Winglength at different latitudes for females (top, ■) and males (bottom, □) of three species of *Lasioommata* and the related *Pararge aegeria* in Sweden. The leftmost dot in each figure represents the mean for continental Europe \pm S.E. For *P. aegeria*, the northernmost latitude where the second generation occurs has been approximately marked with an arrow.



most of the studied European range. Trends which were not statistically significant in the first of these analyses generally were significant in the second (Tabs 1–4).

The same trends can be seen in a couple of somewhat different cases; *L. megera*, which is bivoltine in Sweden and apparently does not switch to a single generation in the northernmost parts of its distribution (Tab. 2, Fig. 5), and *E. ligea*, which has a two-year development, with two successive hibernations (Tabs 2 and 4, Fig. 6).

Species with shifting voltinism

Among the *Lycaeninae* the negative slope tended to be lower in males of the multivoltine *L. phlaeas* (and even reversed in females) than in the three univoltine species (Tab. 1; n.s.). When the size patterns among Swedish *L. phlaeas* is investigated more closely (Fig. 3) it can be seen that the non-existence of an obvious net trend in size within the borders of Sweden is due to the fact that after a possible initial increase in size going south from the very north of Sweden (and arctic Norway; Fig. 3)

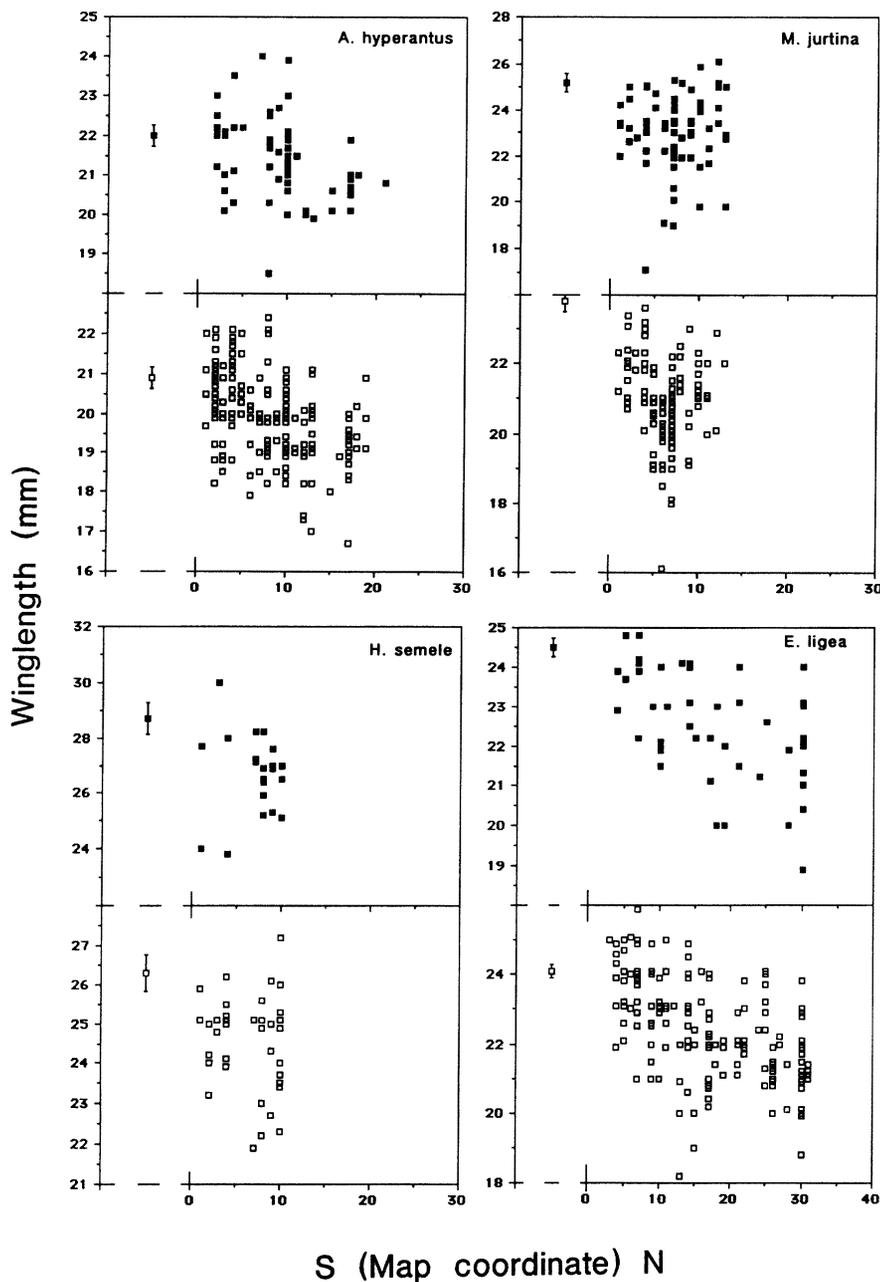


Fig. 6. Winglength at different latitudes for females (top, ■) and males (bottom, □) of *Aphantopus hyperantus*, *Hipparchia semele*, *Maniola jurtina* and *Erebia ligea*. The leftmost dot in each figure represents the mean for continental Europe ± S.E.

Tab. 1. Regressions of wing length on latitude in Sweden for four species of lycaenine butterflies with constant (C) or shifting (S) voltinism within Sweden.

Species and voltinism	Sex	N	Slope (mm degree)	r ²	p
<i>P. hippothoe</i>	+O ₁	92	-0.038	0.03	n.s
(C)		101	-0.047	0.03	n.s
<i>H. virgaureae</i>	+O ₁ +O ₂	136	-0.188	0.40	<0.001
(C)		105	-0.122	0.16	<0.001
<i>L. helle</i>	+O ₁ +O ₂	64	-0.054	0.05	n.s.
(C)		47	-0.025	0.01	n.s.
<i>L. phlaeas</i>	+O ₁	86	-0.021	0.01	n.s.
(S)		61	0.053	0.04	n.s.

Tab. 2. Regressions of wing length on latitude in Sweden for twelve species of satyrine butterflies with constant (C) or shifting (S) voltinism within Sweden.

Species and voltinism	Sex	N	Slope (mm degree)	r ²	p
<i>C. tullia</i>	♂ ♀ ♂ ♀ ♂ ♀ ♂ ♀ ♂ ♀ ♂ ♀	139	-0.194	0.29	<0.001
(C)		39	-0.307	0.40	<0.001
<i>C. arcania</i>		79	-0.352	0.27	<0.001
(C)		41	-0.161	0.07	n.s.
<i>C. hero</i>		67	-0.291	0.52	<0.001
(C)		27	-0.148	0.15	<0.050
<i>C. pamphilus</i>		206	-0.035	0.04	<0.010
(S)		91	-0.026	0.02	n.s.
<i>A. hyperantus</i>		194	-0.214	0.21	<0.001
(C)		61	-0.155	0.12	n.s.
<i>M. jurtina</i>		123	-0.185	0.03	n.s.
(C)		72	0.073	0.00	n.s.
<i>E. ligea</i>	190	-0.210	0.34	<0.001	
(C)	47	-0.179	0.28	<0.001	
<i>H. semele</i>	39	-0.088	0.01	n.s.	
(C)	22	-0.040	0.00	n.s.	
<i>L. megera</i>	40	-0.221	0.05	n.s.	
(C)	19	-0.300	0.17	n.s.	
<i>L. maera</i>	104	-0.227	0.23	<0.001	
(C)	54	-0.362	0.21	<0.001	
<i>L. petropolitana</i>	65	0.051	0.03	n.s.	
(C)	49	0.044	0.03	n.s.	
<i>P. aegeria</i>	82	-0.174	0.18	<0.001	
(S)	55	-0.042	0.00	n.s.	

the size cline seemed to level off or even reverse direction at intermediate latitudes within Sweden. Further to the south the size rapidly increased again.

A shift in voltinism takes place within the borders of Sweden, from a single generation in the very north to two in central and southern Sweden. The second generation first occurs at about 62°N (Fig. 3; this is more evident when the capture dates of individuals are taken into account). This means that size increased up to this point and was variable, with decreasing mean size, at latitudes where the shift in voltinism takes place. Thus, the observed size pattern in *L. phlaeas* is reminiscent of the "saw-tooth"-pattern described previously (Fig. 1). Judging from capture dates there seems to be two mechanisms behind the decrease in size at intermediate latitudes: a drastic decrease in size of individuals in the first generation (from diapausing larvae) and the occurrence

of a second generation with slightly smaller sizes than either the diapausing generation in the north or the second generation as it occurs further south.

Turning to the Coenonymphini, *C. pamphilus* seems to be a close parallel to *L. phlaeas*. The slope of the regression lines deviated only slightly from zero in the multivoltine *C. pamphilus* (not significantly in females; Tab. 2), which may be compared to the similar and related univoltine species of *Coenonympha* and *A. hyperantus* (Tab. 2). The shift in voltinism is even more diffuse than in *L. phlaeas* but again seems to take place at about 62°N, judging from capture dates, and a "saw-tooth" pattern can perhaps be deduced in this species as well.

A final species of this type is *P. aegeria*, which is the only species of the four in the "Pararge-group" (*P. aegeria*, *L. megera*, *L. maera* and *L. petropolitana*)

Tab. 3. Comparisons (t-tests) between winglengths of lycaenine butterflies (with constant (C) or shifting (S) patterns of voltinism within Europe) collected in Sweden and continental Europe (means ± S.E.).

Species	Sex	Sweden	N	Europe	N	p
<i>P. hippothoe</i>	♂ ♀	15.8±0.1	(92)	16.6±0.2	(25)	<0.001
(C)		16.5±0.1	(101)	17.6±0.2	(24)	<0.001
<i>H. virgaureae</i>	♂ ♀	15.6±0.1	(136)	16.4±0.2	(29)	<0.001
(C)		14.8±0.1	(105)	15.6±0.2	(24)	<0.001
<i>L. helle</i>	♂ ♀	13.2±0.1	(64)	12.9±0.2	(6)	n.s.
(S)		13.3±0.1	(47)	13.5±0.2	(11)	n.s.
<i>L. phlaeas</i>	♂ ♀	14.0±0.1	(86)	14.4±0.2	(32)	n.s.
(S)		14.6±0.1	(61)	15.0±0.1	(39)	n.s.

Tab. 4. Comparisons (t-tests) between winglengths of satyrine butterflies (with constant (C) or shifting (S) patterns of voltinism within Europe) collected in Sweden and continental Europe (means \pm S.E.).

Species	Sex	Sweden	N	Europe	N	p
<i>C. tullia</i>	♂	17.5 \pm 0.1	140	17.7 \pm 0.2	34	n.s.
(C)		18.3 \pm 0.2	40	18.8 \pm 0.2	11	n.s.
<i>C. arcania</i>	♂	16.2 \pm 0.1	80	16.5 \pm 0.2	48	n.s.
(C)		17.0 \pm 0.1	43	17.1 \pm 0.3	20	n.s.
<i>C. hero</i>	♂	15.7 \pm 0.1	71	16.0 \pm 0.2	18	n.s.
(C)		16.2 \pm 0.1	29	16.6 \pm 0.2	8	n.s.
<i>C. pamphilus</i>	♂	14.4 \pm 0.1	210	15.6 \pm 0.2	44	<0.001
(S)		15.8 \pm 0.1	93	17.0 \pm 0.2	25	<0.001
<i>A. hyperantus</i>	♂	20.1 \pm 0.1	245	20.9 \pm 0.3	18	<0.001
(C)		21.9 \pm 0.2	91	22.0 \pm 0.3	8	n.s.
<i>M. jurtina</i>	♂	20.9 \pm 0.1	124	23.8 \pm 0.4	35	<0.001
(C)		23.2 \pm 0.2	73	25.2 \pm 0.4	28	<0.001
<i>E. ligea</i>	♂	22.3 \pm 0.1	202	24.1 \pm 0.2	57	<0.001
(C)		22.5 \pm 0.2	51	24.5 \pm 0.3	15	<0.001
<i>H. semele</i>	♂	24.6 \pm 0.2	49	26.3 \pm 0.5	8	<0.001
(C)		26.7 \pm 0.3	26	28.7 \pm 0.6	13	<0.001
<i>L. megera</i>	♂	21.2 \pm 0.1	42	22.0 \pm 0.2	27	<0.001
(S)		22.7 \pm 0.2	21	23.0 \pm 0.2	20	n.s.
<i>L. maera</i>	♂	24.3 \pm 0.1	105	24.7 \pm 0.2	35	<0.050
(S)		25.2 \pm 0.2	57	25.5 \pm 0.3	24	n.s.
<i>L. petropolitana</i>	♂	20.3 \pm 0.1	70	21.0 \pm 0.1	24	<0.001
(S?)		20.9 \pm 0.1	54	21.4 \pm 0.2	18	<0.050
<i>P. aegeria</i>	♂	21.2 \pm 0.1	84	21.1 \pm 0.2	38	n.s.
(S)		21.8 \pm 0.1	56	22.5 \pm 0.2	23	<0.001

which has a shift in voltinism within Sweden. Again, the slopes of the regression lines were comparatively slight (Tab. 2), perhaps because the relationship between latitude and size is not linear but rather a “saw-tooth”-pattern (Fig. 5). However, this pattern was less clear than in the two former cases as very few specimens originated from the latitudes where the shift in voltinism evidently takes place.

A few species have a constant number of generations within Sweden but additional generations further south (*L. helle*, *L. maera* and probably *L. petropolitana*). Perhaps due to the many factors affecting size differences between Sweden and continental Europe, no consistent difference is evident between such species and those with constant voltinism (cf. Tabs 1–2, 3–4). See also below, and above concerning *L. petropolitana*.

Tab. 5. The number of negative or positive slopes of the regressions of wing length on latitude in Tabs 1–2, and inferred from Tabs 3–4, as compared to the null hypothesis of a 50:50 ratio. p = probability of result as given by χ^2 tests (goodness-of-fit).

Table	Sex	Slope		χ^2	p
		-	+		
1–2	♂	15	1	12.2	<0.001
1–2		13	3	6.2	<0.05
3–4	♂	14	2	9.0	<0.01
3–4		16	0	16.0	<0.001

Effects of factors not correlated with latitude

As already noted, there was considerable variation in size due to factors not correlated with latitude. More interestingly, when mean sizes from Europe are compared with actual data points from Sweden (as in Figs 3–6) it can be seen that the differences in mean size (Tabs 3–4) were mostly due to small sizes of individuals from central and northern Sweden. In contrast, insects from southern Sweden often seemed to be of the same size as, or even larger than, the mean for European insects. This suggests that the size trends in some cases may reverse again south of Sweden. This could occur for several reasons, different for different species. Some species occur in the Alps and other mountainous regions where the season may be shorter than in southern Sweden. Others are found in warm, dry habitats where summer drought can affect the length of the actual growth season. Some species also shift to more generations per year south of Sweden (see above). Concerning the present material samples from continental Europe were too fragmentary to permit interpretation in any of the species.

Variations in slope

Above we tentatively compared the slopes of the regression lines for different species, in an attempt to show differences in how strongly size is affected by latitude. This is obviously a risky procedure, e.g. due to differ-

ences in sample size and variation. Nevertheless, such comparisons could potentially be of considerable interest, and we would like to draw attention to a few possible research areas: 1) The already mentioned difference in slope between species with constant and shifting generation numbers (suggested by Tabs 1–2). 2) Comparisons between species with different (constant) number of generations. For instance, the univoltine *H. semele* can perhaps best be compared to *L. megera*, with which it shares the open, warm habitats and the geographical distribution in Sweden (mainly southern coastal areas). None of the regressions involved were significant (at least partly due to the small range of latitudes), but it can be noted that the slope tended to be steeper in both sexes of *L. megera* (Tab. 2, Fig. 6; n.s.). This could relate to the fact that this species should be much more time-constrained due to its two generations per year at the same localities as the single generation of *H. semele*. 3) The evident difference between the sexes in several species, most notably *M. jurtina* (Tabs 1–2). The similar size patterns for males and females (Figs 3–6) and the correlated slopes ($r^2 = 0.404$, $p < 0.01$; Tabs 1–2) suggest that such differences may be mostly artefacts (due to incomplete data from females) but in individual cases they could potentially result from sexually different outcomes of trade-offs involving size, or from sexual differences in the life-cycle. 4) The possibility that larger species should be more time-constrained and, thus, display greater slopes. Since, univoltine species are often larger than multivoltine, this effect could contribute to differences between the two types of species. However, mean sizes (in Sweden) and slopes of the regression lines were not correlated in this manner (Tabs 1–4).

Discussion

The prediction by the theory under study is one of increasing size to the south (unless other climatic factors affect season length, and with reversed size clines where shifts in voltinism occur). Theories typically predicting the opposite general size trend include: 1) those related to Bergmann's rule (1847), predicting large size in cold climates to achieve or conserve higher body temperatures, or for unspecified reasons, 2) theories invoking the amplitude of seasonal changes as the selective factor (organisms should be large when the amplitude is great, to promote survival through the unfavourable season) and 3) some theories based on proximate environmental effects, such as effects of temperature on growth (Ray 1960) or effects of starvation. The predictions of several of these theories, especially the third type, are dependent on the studied organisms.

For the presently studied species the general predictions from theories invoking proximate environmental effects should be larger size to the north. Invertebrates often become large adults when reared at low

temperatures (Ray 1960) and this is true at least for some butterflies (Gilbert 1984, Nylin et al. 1989), although the effect is by no means universal (Ratte 1985). Concerning starvation, for the studied species this should be more probable in more southern (warmer and drier) habitats where the foodplants may perish.

Blau's (1981) thermoregulatory theory (adult insects are small in cool but variable environments, to be able to heat up rapidly) could conceivably predict the same general size trend as the theory under study. We do not want to rule out the possibility that size patterns are caused or influenced by selection not on generation length but on the size of a developmental stage, perhaps the adult as suggested by Blau (1981). However, Kingsolver and Watt (1983) argued convincingly that thermoregulatory adaptations based on variations in temperature probably are marginal phenomena.

Thus, the results presented here strongly support the theory that season length is the main factor regulating butterfly size. The fact that this trend is observed also in multivoltine species is no contradiction of the theory, since for such species the predicted size differences are dependent on the exact latitudes compared (Roff 1980, 1983). Closer examination shows that size patterns in the multivoltine species are consistent with theory. The data is not complete enough to confirm the presence of "saw-tooth"-pattern in these species, but nevertheless hint at their existence. No other theory predicts such patterns.

Additional support is given by the results of Petersen (1947). Petersen did extensive research on the geographical variation of 16 butterfly species (Pieridae and Nymphalidae) in Sweden, Norway and Finland. He found that 10 species clearly increased in size to the south and away from mountainous areas. All except one are univoltine (in one case with two-year development) throughout the study area. Five species (among them *Pieris brassicae* L. and *P. rapae* L.) did not show any clear clinal variation in size. One species, *P. napi* L., varied in a more complicated way, consistent with a "saw-tooth"-pattern similar to that which is here suggested to occur in *L. phlaeas*, *C. pamphilus* and perhaps *P. aegeria*. Petersen's interpretation of these patterns is indeed similar to the theory discussed in the introduction.

The contrasting close similarity in size between the northern and southern Swedish populations of the migratory species *P. brassicae* and *P. rapae* found by Petersen (this similarity evidently extends to Italian populations; Nylin and Svård unpubl. data) supports one of the main prerequisites of the theory under study: that there is an important genetical component contributing to geographical size trends in butterflies. It is known that migratory behaviour works contrary to fine-tuned adaptations to local conditions, through increased gene flow and/or the necessity for "all-purpose" genotypes in such species. One example is given by the critical photoperiod for diapause in *P. brassicae* as compared to sta-

tionary species (Danilevskii 1965). The investigated butterfly groups, lycaenids and satyrines, are not considered very mobile (e.g. Shreeve 1981), thus, local adaptation should be possible.

Acknowledgements – We thank V. Wallenrud for measuring the butterflies. P. Lindskog at the Natural History Museum in Stockholm for his help with the museum collections, P.-O. Wickman and C. Wiklund for valuable discussions and P.-O. Wickman for letting us use his additional data on *Coenonympha*. Finally, D. Roff's suggestions improved the manuscript.

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