

# Spatial and temporal variation in flight morphology in the butterfly *Melitaea cinxia* (Lepidoptera: Nymphalidae)

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Some studies on insects have found a relationship between habitat structure and investment in dispersal-related traits. In this study we compared the morphology of the butterfly *Melitaea cinxia* from five sites on the large Baltic island Öland that differed markedly in degree of fragmentation and size. Both wild-caught adults and individuals reared in a split-plot design were compared. We found significant site differences in size-adjusted thorax mass and total body mass. Male thorax mass was on average larger among the sites with the highest degree of habitat fragmentation. However, due to significant sex–site interactions, males and females may have adapted differently to the habitat fragmentation. Using museum specimens, we also analysed changes in morphology, finding an increase in size (measured as head and thorax width) over time. Thorax width appears to have increased among females and decreased among males. Possible explanations include increasing fragmentation of the landscape and changes in population density. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, 77, 445–453.

**ADDITION KEYWORDS:** dispersal – flight ability – flight design – Glanville fritillary – habitat fragmentation – landscape structure – mobility

## INTRODUCTION

Insect migration can be greatly influenced by habitat characteristics (Southwood, 1962, 1981). Consequently, one might expect the migratory level of populations to differ between habitats with varying degrees of fragmentation. The effects of fragmentation on dispersal-related traits have received attention in recent years (Leimar & Norberg, 1997; Thomas, Hill & Lewis, 1998; Hill, Thomas & Lewis, 1999b; van Dyck & Matthysen, 1999; Thomas, 2000).

It has been suggested that morphological traits associated with flight can adapt to the level of fragmentation (Berwaerts *et al.*, 1998; Thomas *et al.*, 1998; Hill *et al.*, 1999b). A fragmented habitat could select for increased flight ability (Taylor & Merriam, 1995) since movement between fragments requires longer flight distances. Similarly, increased flight ability may be expected in recently colonized, perhaps previously uninhabitable areas (den Boer, 1970) or

following an expansion in range (Hill, Thomas & Blakeley, 1999a). On the other hand, as the distance between patches increases, so does the cost of moving between them; with some degree of isolation, therefore, there may be selection against flight-related traits (Dempster, King & Lakhani, 1976; Dempster, 1991; Leimar & Norberg, 1997).

Adaptations in flight morphology may also be found among migratory butterflies. Roff (1991) found that for British Papilionoidea, migratory butterflies on average were larger (measured as wingspan) than non-migratory ones. A similar pattern was found for other insects as well. Roff (1991, 1992) hypothesized that this would be expected for bioenergetic reasons, since the distance an insect can fly ought to increase with body mass. However, Dixon & Kindlmann (1999) suggested that this might not be the general case. Contrary to Roff's prediction, Dixon & Kindlmann (1999) found that, among aphids, migrants were smaller than non-migrants.

Many insects including butterflies use flight for tasks that are not related to dispersal (sometimes referred to as 'trivial movements' (Southwood, 1962)

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or 'station keeping' (Dingle, 1996)). Since these kinds of flight behaviour (e.g. mate locating or foraging behaviour) can affect flight morphology, it is not obvious what factors lie behind a certain flight design. Changes in the importance of trivial flight could potentially confound the effect of habitat fragmentation on flight morphology (van Dyck & Matthysen, 1999). Comparisons between species show that both ecological and behavioural factors can affect flight morphology. Wickman (1992) found that flight design was related to mating system (perching and patrolling) among 44 species of temperate butterflies. Males of perching species had larger thorax/body mass ratios, higher wing loadings and higher wing aspect ratios than patrolling species. A relationship between mate-locating strategies and flight design has also been demonstrated in within-species comparisons on *Pararge aegeria* (van Dyck, Matthysen & Dhondt, 1997). In a comparison of several neotropical butterflies it has been demonstrated that palatability, and thus the need to evade predatory birds by flight, is related to morphology and flight behaviour (Chai & Srygley, 1990; Srygley & Chai, 1990a,b; Marden & Chai, 1991). Palatable butterflies have more of their mass allocated to flight muscles and tend to have shorter wings and smaller wing areas than unpalatable ones. Thus, factors such as altered predation pressure or a shift in the mating system, which occur in parallel with a change in habitat structure, could influence flight morphology.

In this study we have measured morphological traits of five *Melitaea cinxia* populations from the Baltic island Öland (Sweden). The sites were selected to represent different habitat types in terms of degree of isolation/fragmentation and size. If landscape structure is important in determining the flight design of *M. cinxia*, one might expect that individuals from large and continuous areas of habitat have a lower flight ability compared to those from a fragmented habitat. One reason for this is that the latter might need to fly between habitat patches in order to utilize the same area of habitat as the former. We have also analysed museum specimens of *M. cinxia* collected from Öland between 1918 and 1973. This habitat has gradually become more fragmented and as a consequence the optimal flight design of *M. cinxia* may have shifted during this period.

## MATERIAL AND METHODS

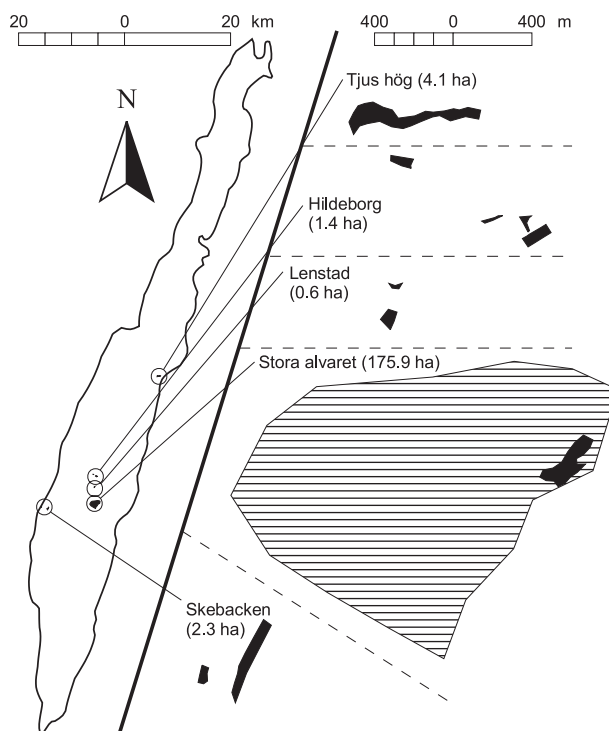
### STUDY SPECIES

The Glanville fritillary, *Melitaea cinxia* (Linnaeus 1758) (Lepidoptera: Nymphalidae), is found along the coast in the southern part of Sweden and on the large islands Öland and Gotland in the Baltic sea. Its distribution has decreased both in Sweden and in many

parts of western and northern Europe during the past 30 years (Hanski & Kuussaari, 1995). The habitat is typically restricted to scrub/woodland clearings, dry slopes and hillsides (Nordström, 1955; Henriksen & Kreutzer, 1982), where the larval host plants grow (mainly *Plantago lanceolata* and *Veronica spicata*). The eggs are laid in large batches on the host plant. When the gregarious larvae hatch they spin a communal web around the plant and feed until they have entered the fourth or fifth instar (Wahlberg, 2000). At that stage they diapause inside the web and start feeding again in the early spring. After completing the sixth instar they pupate. The adults emerge at the beginning of June and the flight period may extend to the beginning of July.

### STUDY AREA

Specimens of *M. cinxia* were collected from five sites on Öland (Hildeborg, Lenstad, Skebacken, Stora alvaret and Tjus hög, see Fig. 1). Large areas of Öland are given over to 'alvar', a type of landscape which often provides a suitable habitat for *M. cinxia*. Alvar land has been shaped by sheep grazing and is characterized



**Figure 1.** Left, locations of the *Melitaea cinxia* sampling sites on Öland. Right, the habitat patches of each site, in greater detail. For Stora alvaret, the sampled area (marked black) was much smaller than the actual area of continuous habitat (hatched). Both of the host plants, *Plantago lanceolata* and *Veronica spicata*, are present in each site.

**Table 1.** Sample sizes of males and females for wild-caught and reared butterflies. The reared butterflies were raised in pots with all larvae from a common web and two pots per web

Site	Wild-caught		Reared			
	Females	Males	Females	Males	Webs	Pots
Hildeborg	11	9	25	19	8	16
Lenstad	13	20	25	16	7	14
Skebacken	24	12	20	25	8	16
Stora alvaret	13	17	25	22	8	16
Tjus hög	7	7	23	22	8	16

by limestone outcrops, a lack of taller vegetation and a rather dry shallow soil. The site Stora alvaret is part of a large alvar area and may well be the largest continuous area of *M. cinxia* habitat in Sweden (shaded in Fig. 1). Tjus hög is an elongated strip of fairly continuous habitat containing alvar and pasture-land that covers a relatively large area. Skebacken, Hildeborg and Lenstad consist of smaller patches that are scattered within each site and are surrounded by scrub/woodland. Some 30 years ago, Hildeborg and Lenstad contained more open areas and most of the patches within these sites were connected by open habitat. Within each site, movement between patches is likely since the distances are well within the recorded dispersal distance of *M. cinxia* (cf. Hanski, 1999). However, there is probably very little exchange of individuals between sites, because of the large distances between them. Neither are there any known *M. cinxia* populations closer than 2 km to any of these sites.

#### MEASUREMENT METHODS

Among the traits we measured were mass (total, thorax, abdomen and wing) and dimension (head width, thorax width and length). The thorax mainly contains flight muscles (Srygley & Chai, 1990a) and relative thorax mass could therefore be a good indicator of flight performance, although wing size, thorax shape, and body size have also been suggested (Dempster *et al.*, 1976; Betts & Wootton, 1988; Dudley, 1990; Marden & Chai, 1991; Roff, 1991; Wickman, 1992; van Dyck *et al.*, 1997; Srygley & Kingsolver, 1998).

All masses were measured on dried butterflies using the same balance (Precisa 205 A SCS). The thorax (excluding legs), and the abdomen and wings of dissected butterflies were weighed separately while the total body mass was measured on undissected butterflies.

Dimensions were measured using a stereoscope with a graticule micrometer, at a magnification of  $\times 25$ . To allow a better view, the wings and the tegulas were removed prior to measuring thorax length. For the museum butterflies (see below), care had to be taken to avoid damaging the specimens and these were not dissected. Head width was measured at the widest lateral distance between the outer borders of the eyes. Thorax length was measured from the caudal end to the cephalic end of mesoscutum, along the centre-line. Thorax width was measured at the widest part of the mesoscutum.

#### WILD-CAUGHT BUTTERFLIES

Adult butterflies were captured during the summer of 1997 and killed immediately after capture using ethyl acetate (sample sizes in Table 1). The age of each individual was estimated from the condition of the wings, using a ranked scale varying from one (perfect) to six (badly tattered and worn).

#### REARED BUTTERFLIES

During the autumn of 1997 we collected larvae from all sites (sample sizes in Table 1). The larvae were hibernating inside wintering webs and several were collected from each web. During the spring of 1998 the larvae were put in  $18 \times 18$  cm square plastic pots with planted *P. lanceolata*. We used two pots per web with 16 larvae in each pot. The pots were kept outdoors in a random grid pattern to achieve a split-plot design with pots as blocks (a pot contained only one site but both sexes). A few times the pots were exchanged when the larvae had eaten all the *P. lanceolata*. Three individuals or less from each pot were randomly selected for morphological measurements and the adults were frozen at  $-70^\circ\text{C}$  the day after emergence (the remaining adults were used in another study).

**Table 2.** Body size and relative thorax size was analysed for the wild-caught and the reared butterflies using head width, total dry mass and thorax mass. Abdomen and thorax mass decrease with age, therefore age class was included as a covariate for the wild-caught butterflies. To compensate for overall body size, head width was used as a covariate in the analysis of thorax mass. For the reared butterflies, raised in a split-plot design, pot has been used as a random factor nested in site. *N*-values are found in Table 1

Effect	Wild-caught			Reared		
	df	<i>F</i>	<i>P</i>	df	<i>F</i> /Chi <sup>2</sup> *	<i>P</i>
ln (head width)						
site	4	4.50	0.002	4	0.65	0.63
pot(site)	–	–	–	1	10.55*	0.001
sex	1	29.15	<0.001	1	76.40	<0.001
sex × site	4	0.45	0.77	4	0.21	0.93
ln (total mass)						
age class	1	38.24	<0.001	–	–	–
site	4	4.58	0.002	4	1.56	0.19
pot(site)	–	–	–	1	0.25*	0.62
sex	1	34.77	<0.001	1	1564.94	<0.001
sex × age class	1	6.82	0.010	–	–	–
sex × site	4	1.98	0.10	4	2.84	0.025
ln (thorax mass)						
ln (head width)	1	79.13	<0.001	1	152.64	<0.001
age class	1	33.32	<0.001	–	–	–
site	4	7.57	<0.001	4	1.35	0.26
pot(site)	–	–	–	1	9.31*	0.002
sex	1	14.97	<0.001	1	919.95	<0.001
sex × age class	1	11.63	<0.001	–	–	–
sex × site	4	3.69	0.007	4	4.04	0.004

#### MUSEUM BUTTERFLIES

Specimens of *M. cinxia* were obtained from the Swedish Museum of Natural History (Stockholm) and used for morphological measurements. The 45 males and 32 females had all been collected on Öland between 1918 and 1973 by different collectors.

As a complement to the museum butterflies, fifth or sixth instar larvae were collected from Stora alvaret during the spring of 1997. The larvae were raised individually on *P. lanceolata* plants at a temperature of 21.5°C; 18 females and 30 males of the adults were killed with ethyl acetate, pinned through the thorax (using pin size 00) and mounted on a spreading board. When the butterflies had dried, measurements were taken in the same way as for the museum specimens.

#### STATISTICS

All statistical tests were performed with SAS (2001). For linear models involving only fixed factors we used the 'GLM' procedure and for tests involving both fixed and random factors (i.e. mixed models) we used

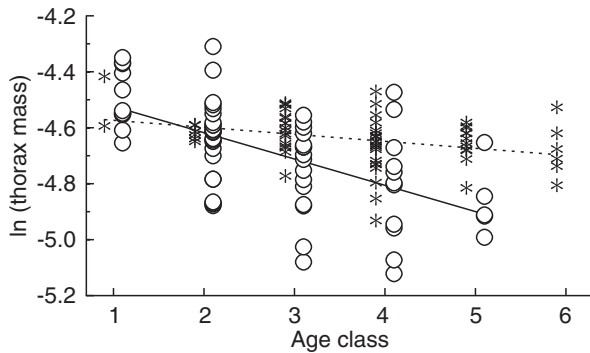
'MIXED'. Chi-square statistics were used to test the effect of the random factors, and SAS type III sums of squares the effect of the fixed factors.

To illustrate the result of some analyses, adjusted means (Underwood, 1997) have been used in figures, where the dependent variable is adjusted for the effect of one or more covariates. Dimensions and masses in tests, figures and tables are in millimetres and grams.

## RESULTS

#### DECREASE OF THORAX MASS WITH AGE

It is known that butterfly thorax mass may decrease with age (Karlsson, 1994, 1998; Stjernholm & Karlsson, 2000). For the wild-caught *M. cinxia* we found negative relationships between age and thorax mass, adjusted for size and site differences (Table 2; Fig. 2). These relationships were also significant for each sex analysed separately (females:  $R^2 = 0.64$ ,  $P < 0.001$ ; males:  $R^2 = 0.62$ ,  $P = 0.015$ ). Consequently, age has been used as a covariate in the analyses involving total and thorax mass (Table 2). The size-



**Figure 2.** Thorax mass of different age classes of female (○) and male (\*) wild-caught *Melitaea cinxia*, adjusted for size (head width) and site differences. The decrease in thorax mass with age is significant for both sexes (see text) and the rate of decrease differs significantly between them (Table 2).

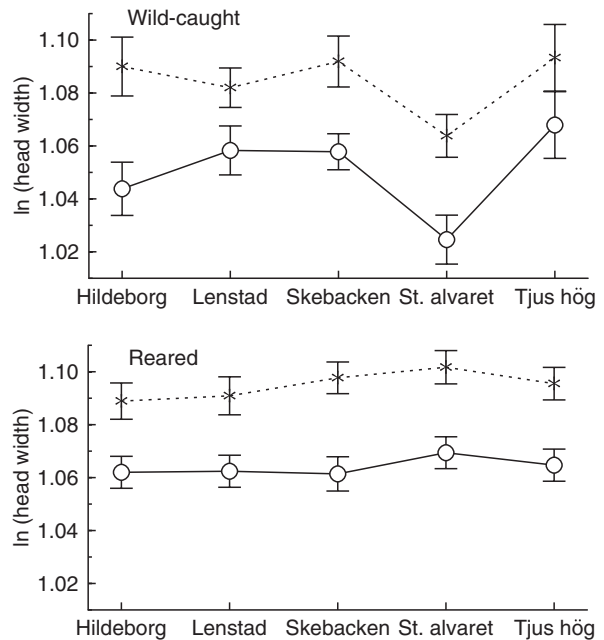
adjusted thorax mass decreased faster for females than for males, as verified by the significant sex–age interaction in Table 2. Similar to Karlsson (1994), there tended to be a positive relationship between age and the ratio of thorax mass to total mass ( $R^2 = 0.81$ ,  $P = 0.052$ ), caused mainly by abdomen mass decreasing faster than thoracic mass with age. When analysing each sex separately this relationship was only significant for the males ( $R^2 = 0.10$ ,  $P = 0.009$ ).

#### BETWEEN-SITE COMPARISONS

We used head width (Fig. 3) and total dry body mass (henceforth total mass; Fig. 4) to compare body size between sites. For the wild-caught butterflies (WB) these (adjusted for age) differed significantly between sites (Table 2). Among the reared butterflies (RB), there was a significant interaction between sex and site in the analysis of total mass (Table 2), although head width did not differ significantly among sites.

To assess whether between-site variation in thorax mass was not due simply to variation in body size we attempted to adjust thorax size for variation in body size. In order to devise a measure of thorax size in relation to body size that would be applicable to both WB and RB, head width was used as a covariate in the analysis of thorax mass (Table 2). For WB, thorax mass differed significantly between sites and there was also a significant interaction between sex and site (Table 2; Fig. 5). Among RB there was a significant interaction between sex and site in thorax mass (Table 2 and Fig. 5).

For both RB and WB, significant site differences were also found for abdomen mass. It should be stressed that since thorax and abdomen together



**Figure 3.** Female (○) and male (\*) head width. There are significant differences between populations of the wild-caught butterflies but not of the reared butterflies (see Table 2).

comprise the major part of the body mass, their sizes are unlikely to be independent of each other.

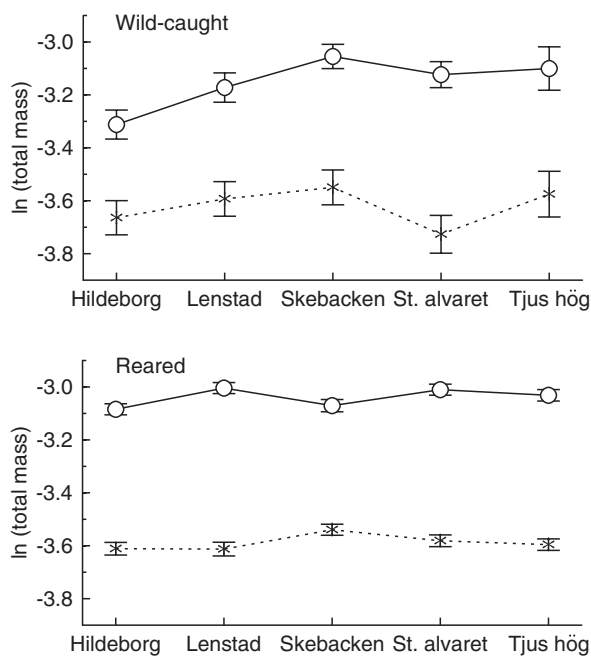
Other morphological measures were also analysed. Concerning the ratio thorax width : length (Dempster *et al.*, 1976), no differences were found between sites for either WB or RB. Among RB no significant site differences were found for thorax width, thorax length and wing mass (adjusted for body size). However, for WB significant site differences were found for thorax width.

#### CHANGES OVER TIME

Changes in body shape between 1918 and 1997 were studied on mounted specimens from the museum collection and RB from 1997. A significant increase in  $\ln$  (head width) over time was found for both males and females (Table 3; Fig. 6). This increase remained significant also when excluding RB from the analysis ( $F = 4.56$ ,  $P = 0.036$ ). In the analysis of size adjusted thorax width (Table 3), a significant interaction was found between sex and year of capture, indicating that the thorax width of *M. cinxia* has changed during this period and that it has changed differently for males and females. As seen in Figure 7, female thorax width, adjusted for size using  $\ln$  (head width), has increased relative to male thorax width during this time period. The sex by year of capture interaction remains significant when excluding RB ( $F = 7.35$ ,  $P = 0.008$ ).

**Table 3.** Analyses of head width and thorax width measured on mounted butterflies from museum specimens (captured between 1918 and 1973) and the reared butterflies from 1997 (cf. Figs 6 and 7). In order to control for body size, head width was used as a covariate in the analysis of thorax width

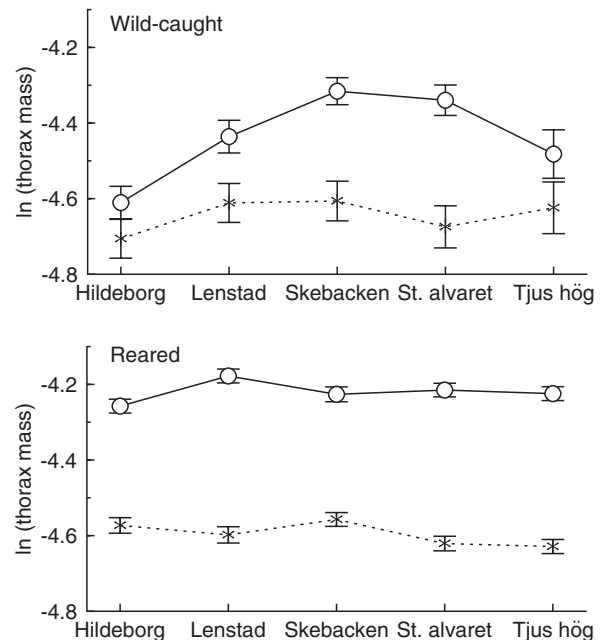
	df	F	P
ln (head width), $R^2 = 0.39$			
sex	1	48.76	<0.001
year of capture	1	28.67	<0.001
error	126		
ln (thorax width), $R^2 = 0.24$			
ln (head width)	1	23.10	<0.001
sex	1	8.43	0.004
year of capture	1	0.54	0.47
sex $\times$ year of capture	1	8.79	0.004
error	124		



**Figure 4.** Total dry body mass of female (O) and male (\*) *Melitaea cinxia*. The masses of the wild-caught butterflies has been adjusted to the youngest age class. There are significant differences between populations of both the wild-caught and the reared butterflies (see Table 2).

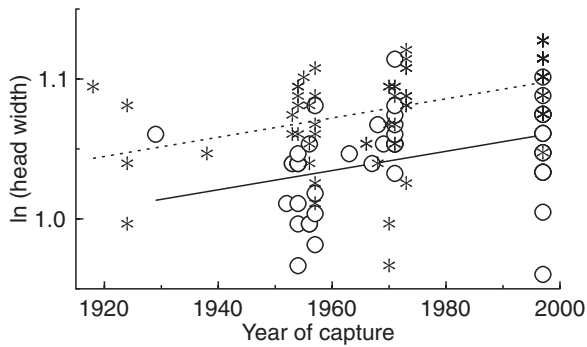
## DISCUSSION

Our results revealed both spatial and temporal variation in *M. cinxia* morphology. The analyses of total body weight and relative thorax mass of the reared butterflies suggest that some of the variation between



**Figure 5.** Thorax mass of female (O) and male (\*) *Melitaea cinxia* adjusted for size, using ln (head width). The thorax masses of the wild-caught butterflies have been adjusted to the youngest age class. There are significant differences between populations of both the wild-caught and the reared butterflies (see Table 2).

sites was due to genetic differences (another possibility is that the variation was caused by environmental differences during the first larval instars, before the larvae were collected). We did not find any distinct patterns for the fragmented vs. unfragmented sites, which may suggest that factors other than habitat fragmentation are important in determining the flight design of *M. cinxia*. The significant interactions we found between sex and site suggest that factors specific to each sex play a role in determining the morphology. This could for instance be male mate locating behaviour, which is known to impact butterfly flight morphology (Wickman, 1992; van Dyck *et al.*, 1997). Our results from the wild-caught butterflies show, when contrasted with those of the reared butterflies, that the environmental influence on morphology is considerable (Figs 3–5). High phenotypic variation will lower selection coefficients and could thus be another reason for a lack of genetic differences between fragmented and unfragmented sites. Yet another possibility is that the gene flow between the populations is high enough to counteract local adaptations. In such a case an overall change in habitat structure might have a stronger effect on flight morphology. Since the landscape on Öland has changed during the 20th century, the change over time

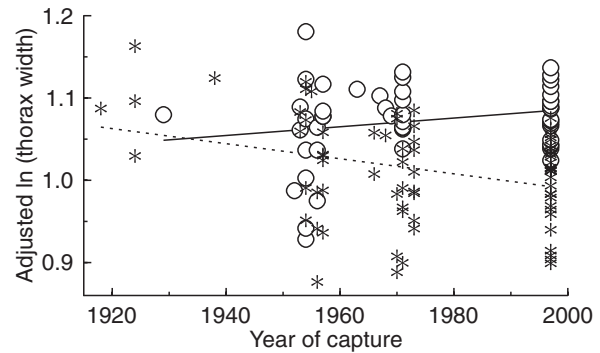


**Figure 6.** Head width of female (○) and male (\*) *Melitaea cinxia* increased significantly over time (see Table 3). Because of the measurement resolution, several values of head width are the same; for the reared butterflies (1997) several values are superimposed.

we found for the museum specimens could be an adaptation to the landscape structure.

There is some empirical evidence that butterfly thoraxes (that mainly contain flight muscles) may be relatively heavier in fragmented habitats (Hill *et al.*, 1999b); similar observations have been recorded for damselflies (Taylor & Merriam, 1995). In a fragmented habitat, where individuals may need to fly between patches, it might be favourable to have good flight ability. In our rearing study, the males had large relative thorax masses in the fragmented sites Hildeborg, Lenstad and Skebacken (Fig. 5), which could indicate an adaptation to higher flight ability. However, this was not the case for the females. Although the largest female relative thorax mass was found for the smallest site (Lenstad), there were only small differences among the other sites. The sexes differ quite a lot in flight behaviour and it could be that optimal flight design differs for the sexes in habitats with different landscape characteristics (e.g. fragmentation and size). Males generally are more active in flight than females, and they probably cover large distances during a sunny day in their search for females. In a fragmented habitat, males may need to visit several patches in order to find females and it could be that the requirements on male flight ability are high compared to those on females. Concerning body mass, which also has been suggested to be related to flight ability (Roff, 1991, 1992), we found a significant interaction between sex and site. However, there seems to be little agreement between body mass and habitat size/fragmentation for either sex (Fig. 4).

It seems reasonable that a great deal of the variation among the wild-caught butterflies was due to environmental differences between the sites. An environmental influence on morphology is further supported by a significant effect of breeding pot found



**Figure 7.** The size-adjusted thorax width has changed differently for female (○) and male (\*) *Melitaea cinxia* during 1918–97 (see Table 3). Thorax width was adjusted for size using  $\ln(\text{head width})$ .

for several measures of the reared butterflies (Table 2). Although we have no data on the nature of the environmental factors causing these effects, the most likely candidates would be variation in the amount and quality of larval host plants or in local temperature and insolation during larval development. Given the population dynamics of *M. cinxia*, with often large fluctuations in population size (Hanski, 1999), larval food shortages as a result of high larval densities will be fairly common. Thus, the small adults captured at Stora alvaret (Fig. 3) very likely suffered food shortage during larval development. Such responses to food availability are of course typical for insects in general. It is much less clear how one might interpret the variation in size and age-adjusted thorax mass (Fig. 5). One possibility is that this represents some kind of phenotypic plasticity in thorax investment. There is then the possibility that the local populations could differ in their norms of reaction, since in our rearing study we controlled for the environmental effects in a split-plot design.

Concerning the decrease of thorax mass with age (Fig. 2), our findings agree with the patterns seen in other butterfly species, for instance *Pararge aegeria* (Karlsson, 1994), *Speyeria mormonia* (Karlsson, 1994) and *Pieris napi* (Karlsson, 1998; Stjernholm & Karlsson, 2000). Together with *M. cinxia*, what these species have in common is that the adults feed on nitrogen-poor diets and it seems that older females use resources from the thorax (flight muscles) for egg production (Karlsson, 1998). Although the absolute thorax mass decreases with age, the abdomen mass decreases even more rapidly, so that the relative thorax mass instead increases with age. Thus, in spite of the thorax mass decrease, flight performance may remain unchanged or possibly increase with age (*cf.* Karlsson, 1994).

During the second half of the 20th century, large parts of the *M. cinxia* habitat on Öland have been lost or altered due to changed agricultural usage. It is thus possible that the changes over time in morphology indicate adaptations to an altered and/or more fragmented landscape. Possibly, an increased body size could correspond to a higher flight endurance (Roff, 1991, 1992), which may be advantageous in a more fragmented landscape. Although, we did not find a relationship between body size and habitat fragmentation in our site comparisons, an overall change in landscape structure would probably have a stronger impact. The result that thorax width changed in different directions for the two sexes could thus be related to behaviours that differ between the sexes, e.g. mate locating strategies. A large male thorax size is generally associated with a perching strategy (the males sit and wait for females) as opposed to patrolling (the males actively fly in search for females). Generally, *M. cinxia* has been classified as a perching species (Wickman, 1992). The decrease in male thorax width that we observed could thus indicate a change from a perching to a patrolling strategy, although it is not obvious why a change to a more fragmented habitat would favour the latter. An overall reduction in population density could be one explanation. In this way, landscape changes would influence morphology indirectly, by way of an influence on the social interactions of the butterflies.

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