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Evolution of flight morphology in a butterfly that has recently expanded its geographic range

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Abstract Individuals colonizing unoccupied habitats typically possess characters associated with increased dispersal and, in insects, colonization success has been related to flight morphology. The speckled wood butterfly, *Pararge aegeria*, has undergone recent major expansions in its distribution: in the north of its range, *P. aegeria* has colonized many areas in north and east England, and in the south, it was first recorded on Madeira in 1976. We examined morphological traits associated with flight and reproduction in the northern subspecies *tircis*, and in the southern subspecies *aegeria*, from sites colonized about 20 years ago in northern England and on Madeira, respectively. Investment in flight was measured as relative wing area and thorax mass, and investment in reproduction as relative abdomen mass. All measurements were from individuals reared in a common environment and there were significant family effects in most of the variables measured. Compared with individuals from sites continuously occupied in recent history, colonizing individuals were larger (adult live mass). In the subspecies *tircis*, colonizing individuals also had relatively larger thoraxes and lower wing aspect ratios indicating that evolutionary changes in flight morphology may be related to colonization. However, sex by site interactions in analyses of thorax mass and abdomen mass suggest different selection pressures on flight morphology between the sexes in relation to colonization. Overall, the subspecies *aegeria*

was smaller (adult live mass) and had a relatively larger thorax and wings, and smaller abdomen than subspecies *tircis*. Evolutionary changes in flight morphology and dispersal rate may be important determinants of range expansion, and may affect responses to future climate change.

Key words Dispersal · Range expansion · Distribution · *Pararge aegeria*

Introduction

Extinction and colonization dynamics of populations in recently fragmented landscapes, and shifts in species' ranges in response to climate change may select for important changes in dispersal capacity (Olivieri and Gouyon 1997). Individuals colonizing unoccupied habitats are rarely a random selection of the source population, and typically share a suite of distinct life history characteristics, particularly traits directly associated with dispersal (Simberloff 1981; Dingle 1986; Leslie 1990). In insects, colonization success and flight ability are related to adult morphology. For example, the propensity and duration of flight is related to wing length (Palmer and Dingle 1989; Fairbairn and Roff 1990), and an increased incidence of macropterous (long-winged) individuals in newly established populations indicates that colonization ability is related to wing size in dimorphic species (Den Boer 1970; Niemela and Spence 1991). Many studies have demonstrated a trade-off between flight and reproduction, and non-dispersive morphs typically have higher fecundities and/or reproduce earlier (reviewed by Zera and Denno 1997).

In butterflies, there is some evidence that colonization ability may be related to adult morphology. Flight speed is positively related to wing span (Dudley 1990), thorax mass (principally flight muscle; Srygley and Chai 1990) and thorax width (Dempster et al. 1976; Chai and Srygley 1990), and it is negatively related to abdomen mass (Srygley and Chai 1990), while flight manoeuvra-

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bility is related to thorax mass (Srygley and Kingsolver 1998). In addition, expanding populations of the large blue butterfly *Maculinea arion* were associated with an increasing ratio of thorax width to length (i.e. broader thoraxes, Dempster 1991), and evolutionary changes in flight morphology in several butterfly species have been related to habitat fragmentation (Berwaerts et al. 1998; Thomas et al. 1998; Hill et al. 1999b). Taken together, these results suggest that morphology, flight ability and colonization success are related, although direct comparisons of colonizing and source populations are lacking.

Study species

The speckled wood butterfly *Pararge aegeria* (L.) occurs throughout the western Palaearctic (Tolman 1997), reaching a northern limit in the United Kingdom and central Scandinavia (subspecies *tircis*). During the 19th century, *P. aegeria tircis* was widely distributed throughout the United Kingdom, as far north as central Scotland [Emmet and Heath 1990; Biological Records Centre (BRC), Institute of Terrestrial Ecology, Monks Wood], but during the 1920s and 1930s it disappeared from northern and eastern areas and essentially became restricted to Wales, southwest England and around Oban in Scotland (Emmet and Heath 1990; BRC). Over the past 60 years, the United Kingdom distribution has expanded and many formerly occupied areas have been re-colonized.

P. aegeria reaches a southern limit in North Africa (subspecies *aegeria*), and was first recorded on the island of Madeira in 1976 (33°N, 17°W; Higgins 1977), although the exact date of arrival is uncertain (Owen and Smith 1994). Madeira lies approximately 850 km southwest of Portugal and 540 km west of Morocco. Over the past 20 years, the distribution of subspecies *aegeria* on Madeira has continued to expand (Owen et al. 1986; Jones and Lace 1992). In western Europe, the ranges of the two subspecies meet in central France and southern Switzerland (Tolman 1997).

In this paper, we study relative investment in flight (wing area and shape, and thorax mass) and reproduction (abdomen mass) in the two subspecies, and compare populations from areas that have been continuously occupied in recent history with areas that have been colonized over the past 20 years. We test the prediction that individuals from colonized sites have increased investment in flight, whereas individuals from continuously occupied sites have increased investment in reproduction.

Materials and methods

Material was obtained from four sites which were chosen in pairs to include a continuously occupied resident site (R) and a recently colonized site (C) for each subspecies. Eggs were obtained during

summer 1996 and spring 1997 from 11 females of subspecies *tircis* collected from two locations within the United Kingdom [resident site: north Wales, 53°15'N, 3°50'W (Smith 1948), $N = 3$ females]; colonized site: west Yorkshire, 53°50' N, 1°21' W (Jackson 1983), $n = 8$ females] and from four females of subspecies *aegeria* from one location in northern Spain (resident site: 43°30'N, 5°45'W). Eggs of subspecies *aegeria* were also obtained from four females from a laboratory culture derived from >40 eggs collected on Madeira (colonized site: 33°N, 17°W; Higgins 1977) in summer 1995, and which had subsequently been reared in the laboratory for four generations prior to the experiment. All larvae and pupae were reared at 20°C and a 18L:6D photoperiod on potted *Poa pratensis* plants grown from seed. Adults were weighed on emergence once their wings had fully expanded, killed by freezing, and subsequently thawed, dissected under a microscope, and dried to constant mass at 60°C. Body parts (thorax, abdomen, wings, head and legs) were weighed on a Cahn electrobalance (sensitivity 0.1 µg). Wings were mounted on glass microscope slides and their areas and lengths measured using an image analysis system (TAS software, University of Leeds).

To take account of effects of allometry, relative investment in flight (wing area and thorax mass) and reproduction (abdomen mass) were analysed by ANCOVA, with sex, subspecies and R/C site as factors, and total dry mass as a covariate. Family origins of all *tircis* individuals were known, and thus when *tircis* data were analysed separately, family effects were nested within sites. For subspecies *aegeria*, however, offspring from different females were not separated in the material we received and thus it was not possible to take account of family effects. To avoid problems of pseudoreplication in analyses of the complete data set, values for each offspring were included in ANOVAs and ANCOVAs, but error sums of squares (SS) and mean square (MS) values were calculated for total degrees of freedom of 19 (total number of females producing eggs) rather than 147 (total number of individuals measured, see below). Values of F were subsequently calculated for each factor in the analyses using adjusted error SS and MS values, and tested for significance using degrees of freedom appropriate for a total sample size of 19 (for example, this resulted in error df of 11 and 10 in analyses of the complete data set by ANOVA and ANCOVA, respectively). When *aegeria* data were analysed separately, error SS and MS values and subsequent F -values were calculated using degrees of freedom appropriate for a total sample size of 8 (number of females producing eggs). All variables were \log_{10} transformed for analysis and did not differ significantly from normal ($P > 0.2$ in all cases). The wings of eight individuals did not expand fully on emergence and were not measured, and live masses of five individuals were not measured, and so the sample sizes for these measurements are smaller than for other measurements. All reported results are from analyses that include all interaction effects between the main factors. Only significant results ($P < 0.05$) are quoted.

Results

Size, wing shape and wing loading

A total of 147 individuals was measured (56 *tircis* and 91 *aegeria*; 19 families). In terms of adult live mass, individuals from colonized sites were heavier than those from continuously occupied sites (three-way ANOVA with sex, subspecies and R/C site as factors; $F_{1,11} = 7.19$, $P < 0.025$), and *tircis* was heavier than *aegeria* ($F_{1,11} = 7.52$, $P < 0.025$), although there was a site by subspecies interaction ($F_{1,11} = 8.82$, $P < 0.025$). Separate analyses of the two subspecies showed that *aegeria* from the colonized site were heavier than those from the permanently occupied site ($F_{1,4} = 60.44$, $P < 0.0025$), but there was no difference between sites for *tircis*. There were no differ-

ences in total dry mass, aspect ratio (wing span²/wing area) or wing loading (total dry mass/wing area) among individuals from colonized or continuously occupied sites, or between subspecies, although differences in total dry mass were close to significance (Fig. 1a; between sites $F_{1,11} = 4.23$, $P < 0.07$; between subspecies $F_{1,11} = 4.69$, $P < 0.06$; all other variables $P > 0.1$). Overall, males were lighter than females in both total dry mass ($F_{1,11} = 51.53$, $P < 0.001$) and live mass ($F_{1,11} = 9.28$, $P < 0.025$), and had lower wing loadings ($F_{1,11} = 85.81$, $P < 0.001$).

Separate analysis of *tircis* data, with families nested within sites, showed that individuals from colonized sites had lower aspect ratios than individuals from continuously occupied sites ($F_{1,37} = 6.12$, $P = 0.018$). There was also evidence that colonizing *tircis* individuals were heavier than those from continuously occupied sites (total dry mass; $F_{1,41} = 4.04$, $P = 0.051$; Fig. 1a).

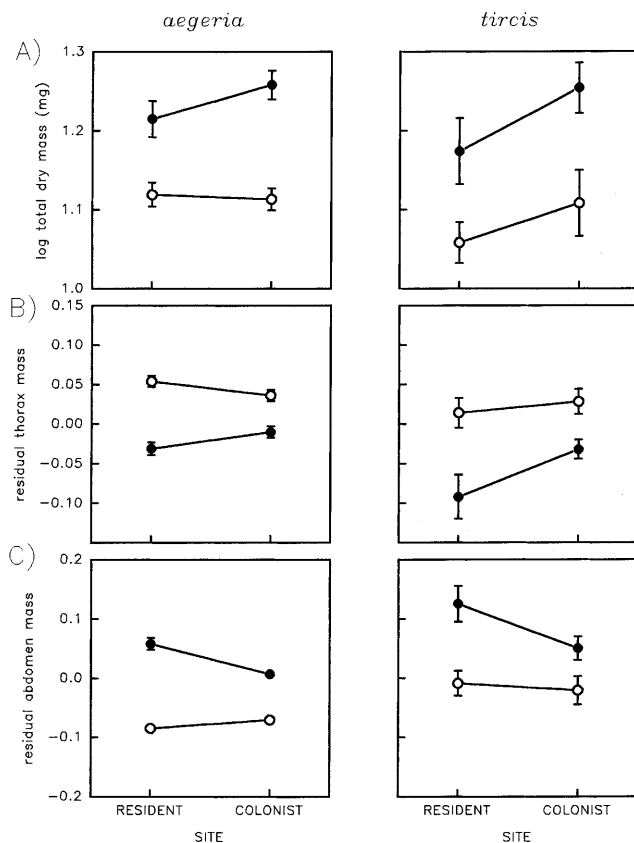


Fig. 1 Log total dry mass (A), residual thorax mass (B) and abdomen mass (C) of *Pararge aegeria aegeria* and *P. aegeria tircis* from colonized and continuously occupied, resident sites. Means and standard errors are shown (open circles males, solid circles females). Residual values are calculated from regression of log thorax mass or log abdomen mass on log total dry mass (combining data for both subspecies). Data for *tircis* are based on family means ($n = 11$ families). Subspecies *tircis* from the recently colonized site was larger and had a relatively larger thorax than *tircis* from the resident site. Subspecies *aegeria* had a relatively larger thorax and smaller abdomen than *tircis* (see Results)

Relative investment in wings and thorax

The slope of the relationship between wing area and total dry mass did not differ significantly between sexes, sites or subspecies (ANCOVA on 147 offspring with sex, R/C site and subspecies as factors and total dry mass as a covariate). Subspecies *aegeria* had relatively larger wings than *tircis* (three-way ANOVA with sex, R/C site and subspecies as factors; $F_{1,10} = 15.25$, $P < 0.005$), and males had relatively larger wings than females ($F_{1,10} = 21.97$, $P < 0.001$) but there was no difference between sites ($P > 0.25$).

A second index of flight investment was produced from measures of thorax mass. Subspecies *aegeria* individuals had relatively larger thoraxes than *tircis* (three-way ANCOVA with sex, R/C site and subspecies as factors, and total dry mass as a covariate; $F_{1,10} = 17.63$, $P < 0.0025$) and males had relatively larger thoraxes than females ($F_{1,10} = 170.90$, $P < 0.005$). There was no difference in thorax mass between individuals from colonized sites and permanently occupied sites ($P > 0.25$), although there was a marginal sex by site interaction ($F_{1,10} = 4.72$, $P < 0.06$). However, in this analysis, the slope of the relationship between thorax mass and total mass differed significantly between subspecies ($F_{1,139} = 6.28$, $P = 0.013$). To check that the above results were not due to differences in this relationship, separate analyses were carried out for the two subspecies. Subspecies *tircis* individuals from the colonized site had relatively larger thoraxes than those from the permanently occupied site (two-way ANCOVA with sex and R/C site as factors, total mass as a covariate and family nested within site; $F_{1,40} = 7.32$, $P = 0.01$) but there was no difference between *aegeria* individuals from Spain and Madeira ($F_{1,3} = 0.06$, $P > 0.25$). Figure 1 shows differences in relative thorax mass and abdomen mass for *aegeria* and *tircis* from permanently occupied and recently colonized sites. Residual values from regressions of thorax mass on total dry mass (Fig. 1b) and abdomen mass on total dry mass (Fig. 1c) are plotted to illustrate differences in allocation to different body parts after accounting for allometry effects.

Relative investment in the abdomen

Subspecies *aegeria* individuals had relatively smaller abdomens than *tircis* individuals (three-way ANCOVA with sex, subspecies and R/C site as factors, and total dry mass as a covariate; $F_{1,10} = 44.04$, $P < 0.001$), and males had relatively smaller abdomens than females ($F_{1,10} = 242.80$, $P < 0.001$). There was no difference in abdomen mass between individuals from colonized and permanently occupied sites ($F_{1,10} = 3.12$, $P > 0.10$), although there was a significant sex by site interaction ($F_{1,10} = 6.93$, $P = 0.025$). However, as with the thorax data, the slope of the relationship between abdomen mass and total mass differed significantly between subspecies ($F_{1,139} = 23.54$, $P < 0.001$), and so data for

tircis and *aegeria* were analysed separately. These results showed no significant differences between individuals from colonized and continuously occupied sites for either subspecies (*tircis* $F_{1,40} = 0.04$, $P > 0.8$; *aegeria* $F_{1,4} = 1.75$, $P \geq 0.2$).

Family effects

Family origins of all *tircis* offspring were known and there were significant family effects in adult size (total dry mass and live mass), relative thorax mass, and wing loading ($P < 0.02$ in all cases), and marginal effects of aspect ratio ($F_{9,37} = 2.05$, $P = 0.061$) and relative wing size ($F_{9,36} = 1.95$, $P = 0.076$). Non-genetic maternal effects could also contribute to these results but, nonetheless, these results are consistent with the hypothesis that genetic variation is present for these traits. Twenty-five percent of the variation in relative thorax mass was explained by family effects (method in Sokal and Rohlf 1995).

Discussion

Changes in distribution

The distribution of *P. aegeria* has fluctuated markedly over the past 150 years, possibly in response to changing climate (Dennis 1993; Pollard et al. 1995; Hill et al. 1999a). Major expansions have occurred in the UK over the past 60 years, and *P. aegeria* has re-colonized many former areas and its distribution is still expanding (e.g. Barnham et al. 1993). The collecting site in west Yorkshire was probably re-colonized during a period of major regional expansion in the 1970s (Jackson 1983), and Madeira specimens were derived from material collected from sites that were probably colonized between 1976 and 1985 (Owen et al. 1986). *P. aegeria* is not a particularly mobile species, but it is possible that it colonized Madeira naturally from North Africa or Iberia, the nearest continental land masses (Owen et al. 1986), or it may have been introduced accidentally by human activities. Two endemic *Pararge* species already occur on the Madeira and Canary archipelagos (*Pararge xiphia* and *Pararge xiphioides*), demonstrating that *P. aegeria*, or a *P. aegeria*-like form, colonized in the past, before speciating in isolation (Owen et al. 1986). Additional evidence comes from the fact that other butterfly species have colonized Madeira in recent times (Higgins 1977), and although many species on the Madeira and Canary archipelagos are well-known migrants (e.g. Jones et al. 1987), others are not, showing that it is not only species with well-known dispersal abilities that make good colonists (Simberloff 1981). Even if *P. aegeria* was accidentally introduced to Madeira, it can still legitimately be regarded as a colonizing population, because the butterfly has since expanded its distribution and colonized most of the island (Jones and Lacey 1992).

Morphology in colonized and resident sites

Family effects were found in most of the measured traits implying a probable genetic basis for variation in traits between sites (Thomas et al. 1998; Van Dyck et al. 1998). Individuals from colonized sites were larger than those from continuously occupied sites in terms of adult live mass, and *tircis* individuals from the colonized site were also larger than those from the permanently occupied site in terms of adult dry mass. There is some evidence that larger *tircis* individuals are more likely to fly further (Van Dyck et al. 1997b), as shown for other butterfly species (Kuussaari et al. 1996), and migrants are larger than non-migrants in several other insect species (McLachlan 1983; Davis 1984). Thus, larger individuals from colonized sites in this study might be expected to fly further. Subspecies *tircis* individuals from the recently colonized site also had larger thoraxes than residents, but examination of Fig. 1 and the significant sex effects showed that these effects of colonization were stronger in females than males. In butterflies, thorax mass is principally flight muscle mass, and females with large flight muscles from the colonized site would be expected to be faster fliers (Dempster et al. 1976; Srygley and Chai 1990) and might therefore have greater dispersal potential (e.g. ability to fly further).

In subspecies *tircis*, colonizing individuals also had lower aspect ratios (= broad wings). The relationship between wing shape and flight performance is poorly understood in butterflies, but there is some evidence that low aspect ratios favour slow, agile flight (Betts and Wootton 1988). There is no relationship between aspect ratio and flight speed (Dudley 1990), although relatively low aspect ratios have been reported in patrolling species, in which males spend sustained periods flying in search of females (see below; Wickman 1992).

Effects of colonization were stronger in the northern subspecies *tircis* than in the southern subspecies *aegeria*. The Madeira material was derived from laboratory stock, and although the material had only been in culture for four generations prior to sampling, morphological changes may have occurred during this time. In addition, the structure of the data were not ideal for *aegeria* (material had not been separated by family), which may have reduced the statistical power in our analyses. There is also a difference in effective time since colonization between sites. Although the two sites were probably colonized around the same time, the number of generations since colonization differs because *P. aegeria* develops continuously on Madeira (four to five generations per year) but only develops through 1.5 generations per year in Yorkshire (Blakeley 1996). This would result in approximately 100 generations since colonization for subspecies *aegeria* (and possibly more if *P. aegeria* arrived on Madeira before 1976), but only 30 generations for *tircis*. It is possible, therefore, that differences in flight morphology in Madeira *aegeria* at colonization have subsequently been lost. Oceanic island populations typically show evolutionary changes in

investment in flight and reproduction as a consequence of isolation (e.g. Williamson 1981), and it is possible that further evolutionary changes in flight morphology of *P. aegeria* on Madeira may occur as a consequence of isolation (Cody and Overton 1996). In addition, the climate in colonizing sites may differ between subspecies. If certain flight morphologies differ in their fitness consequences in different climates (Van Dyck and Matthyssen 1998), differences in effects of colonization between subspecies may also result from selection on different flight morphologies under different climatic conditions.

Flight morphology and mate location strategy

We have assumed that differences in flight morphology are related to dispersal potential. However, flight has many functions in addition to long-distance dispersal (e.g. foraging, finding oviposition sites, predator avoidance, mate location), with certain morphological characteristics almost certainly being more advantageous for different types of flight (Betts and Wootton 1988; Chai and Srygley 1990; Srygley and Chai 1990). For example, male *P. aegeria* display two mate location strategies: males can hold territories and sit and wait for females, flying out to investigate passing individuals ('perching'), or they can fly in search of females ('patrolling') (Shreeve 1987). These different behaviours require different types of flight: perchers require short, fast, powerful flight, and have relatively larger thoraxes than patrollers (Wickman 1992; Van Dyck et al. 1997a).

Differences between the sexes in flight morphology in this study may result from selection on these different behaviours and their different morphologies. For example, unoccupied habitats will most probably be colonized by females that have already mated in their natal patch (females mate shortly after emergence and will therefore undertake most dispersal after mating). Our results show that for *tircis*, females from the recently colonized site show the predicted investment in flight, typical of colonists (Den Boer 1970; Niemela and Spence 1991). By contrast, in males, selection on flight morphology may be related to mate location strategy rather than long-distance dispersal, and may explain why effects of colonization in males in this study were absent, or less marked than in females.

Flight morphology in subspecies *aegeria* and *tircis*

Subspecies *aegeria* was smaller than *tircis* in terms of live mass, in agreement with other studies (Nylin et al. 1993). Subspecies *aegeria* also had a relatively larger thorax than *tircis*, indicating that *aegeria* was a faster flier (Srygley and Chai 1990), and also had relatively larger wings than *tircis*, although the consequences of large wings on flight performance are less clear. Data are lacking as to whether these results reflect differences in mate location strategies between subspecies (for exam-

ple, *aegeria* having a thorax morphology better suited to perching, and *tircis* to patrolling), or differences in other flight-related behaviours: other differences in life history traits between these subspecies have also been demonstrated (Nylin et al. 1993, 1995; Gotthard et al. 1994).

Climate change and range expansions

Over the past 60 years, the distributions of several UK butterflies have expanded, probably in response to climate change (Pollard et al. 1995; Hill et al. 1999a). The results presented here suggest the possibility that evolutionary changes in flight ability in populations at range margins may affect rates of range expansion. Responses of species to predicted future anthropogenic climate change are likely to involve migration and shifts in species' distributions (Parmesan 1996; Parmesan et al. 1999); results from this study indicate that evolutionary changes during range expansions may need to be considered as seriously as ecological factors.

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