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Evolutionary trade-offs between reproduction and dispersal in populations at expanding range boundaries

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During recent climate warming, some species have expanded their ranges northwards to keep track of climate changes. Evolutionary changes in dispersal have been demonstrated in these expanding populations and here we show that increased dispersal is associated with reduced investment in reproduction in populations of the speckled wood butterfly, *Pararge aegeria*. Evolutionary changes in flight versus reproduction will affect the pattern and rate of expansion at range boundaries in the future, and understanding these responses will be crucial for predicting the distribution of species in the future as climates continue to warm.

Keywords: climate change; flight morphology; *Pararge aegeria*; trade-off; range expansion

1. INTRODUCTION

Global climates warmed by *ca.* 0.6 °C during the twentieth century and are predicted to continue warming by up to 5.8 °C this century (IPCC 2001). Some species have responded to this warming (see the review in Walther *et al.* 2002; Parmesan & Yohe 2003) and shifted their distributions to keep track of climate changes, but many have not. Recent studies show that availability of breeding habitat is crucial in determining whether or not species can track climate (Warren *et al.* 2001), and the rate at which they do so (Hill *et al.* 2001). These recent studies indicate that general patterns are emerging in terms of understanding ecological impacts of climate warming, but some less predictable responses to climate warming have been observed (Thomas *et al.* 2001). Theoretical (e.g. Travis & Dytham 2002) and empirical (Niemela & Spence 1991; Hill *et al.* 1999*a*; Thomas *et al.* 2001; Hanski *et al.* 2002) studies show that evolutionary increases in dispersal ability may occur in newly established populations as a consequence of altered costs and benefits of dispersal versus reproduction. Trade-offs between dispersal and reproduction have been shown in many insect species, particularly wing dimorphic species (review in Zera & Denno 1997); such evolutionary trade-offs might affect range expansion rates and thus affect predictions of species' ability to track future climate changes, but have rarely been considered (Hill *et al.* 1999*a*). Here, we investigate whether trade-offs between dispersal and reproduction are evident in populations that are expanding as a consequence of climate warming.

(a) *Study species*

The speckled wood butterfly, *Pararge aegeria*, is currently expanding its distribution in Britain (Hill *et al.* 1999*b*; Asher *et al.* 2001) and we investigated evolutionary changes in dispersal and reproduction across two expanding range margins: Scotland (Barbour 1986) and England (Hill *et al.* 2001) (figure 1). In butterflies, flight ability has been related to adult flight morphology: the thorax comprises predominantly flight muscle and individuals that fly faster have relatively larger, broader thoraxes (Dempster *et al.* 1976; Srygley & Chai 1990; Chai & Srygley 1990) and greater wing spans (Dudley 1990). Abdomen mass has been assumed to relate to investment in reproduction in butterflies (e.g. Hill *et al.* 1999*a*,*c*) but data are lacking, and relationships between fecundity and dispersal are poorly studied in butterflies. Here, we test the prediction that females from populations at range margins will have an increased investment in dispersal, and that females from the range core will invest more resources in reproduction.

2. MATERIAL AND METHODS

(a) *Material used*

Seventy-one females were collected from four woodland sites (two core and two range margin) in England and Scotland (England core: Ordnance Survey grid reference SP02, 18 females; England margin: grid reference SE53, 21 females; Scotland core: grid reference NH64, 15 females; Scotland margin: grid reference NJ46, 17 females) during August and September 2002 (figure 1). Core sites were chosen either if they apparently had been continuously occupied (England; according to Biological Records Centre (BRC) data at the Centre for Ecology and Hydrology, Monks Wood), or if they were within the same 10 km grid square as the first record for that region (Scotland; Barbour 1986). Range margin sites had been colonized in the 1990s (BRC data). F_1 female offspring from each female parent were mated with F_1 male offspring from a different mother, but the same site, to create seven to eight new F_2 families per site to provide material for the fecundity study. The remaining F_1 adults were frozen within 24 h of emergence to provide material for the measurement of adult flight morphology for the dispersal study. The F_2 generation was necessary to provide sufficient material to investigate investment in reproduction, and to ensure that the effects were owing to genetic variation. Care was taken to maintain similar levels of genetic variation among sites. F_1 material was reared under common environmental conditions in a greenhouse during August and September 2002, and F_2 material was reared in the laboratory under a constant temperature (20 °C) and photoperiod (16 L : 8 D). F_1 and F_2 larvae from different families were reared separately on potted *Poa pratensis* grass plants.

(b) *Fecundity study*

On emergence, adult F_2 females were paired with males and each pair was kept separately on potted *Poa pratensis* plants and allowed to lay eggs for 7 days. Males and females in the same pairing were the same age. After 7 days, both adults were killed and the number of eggs was counted. All matings were successful and produced eggs from the day after mating. Any females that died within the 7 day study period were excluded from the study. To determine fecundity schedules, 10 females from each site were allowed to lay continuously until they died naturally, and the number of eggs laid was counted every other day. This was to confirm that females from different sites did not differ in their pattern of egg laying and that females laid most of their eggs within the 7 day study period.

(c) *Dispersal study*

F_1 adults were thawed and measurements of thorax length and width were taken. Adults were dissected and dried to constant mass at 60 °C for 24 h and weighed (thorax, abdomen, total mass) on a Sartorius electrobalance (sensitivity of 0.1 μg). The thoraxes and abdomens from the English populations that were used in the study were approximately two months older than those from the Scottish populations owing to flight period and sampling regime.

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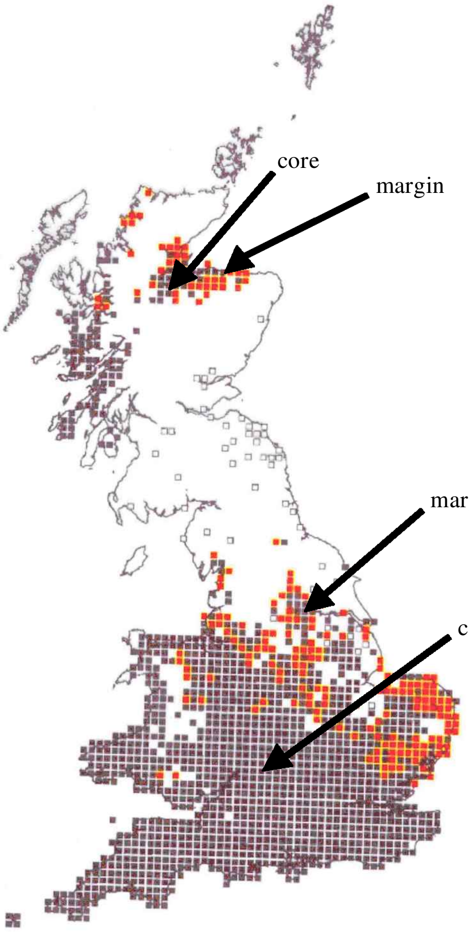

Figure 1. The current distribution of *Pararge aegeria* in Britain, and the location of the sampling sites in England and Scotland (indicated by arrows). Black squares, recorded (10 km grid resolution) distribution from 1940 to 1989; red squares, first recent recording during the 1990s; white squares, previously occupied (nineteenth century) sites that have not (yet) been recolonized.

(d) *Statistical analyses*

All data were tested for normality and log transformed for analysis where appropriate. Fecundity data were analysed by two-way ANOVA with country (England/Scotland) and site (core/margin) as factors, and family effects nested within location. To take account of the allometry, flight morphology data for thorax and abdomen mass were analysed by three-way ANCOVA with country and site as factors, total adult mass as a covariate, and family effects nested within site. Thorax shape (width/length) did not vary with total dry mass and was analysed by two-way ANOVA with country and site as factors, and family effects nested within location. Data from males and females differed in relationships between flight morphology measures and total dry mass and so males and females were analysed separately.

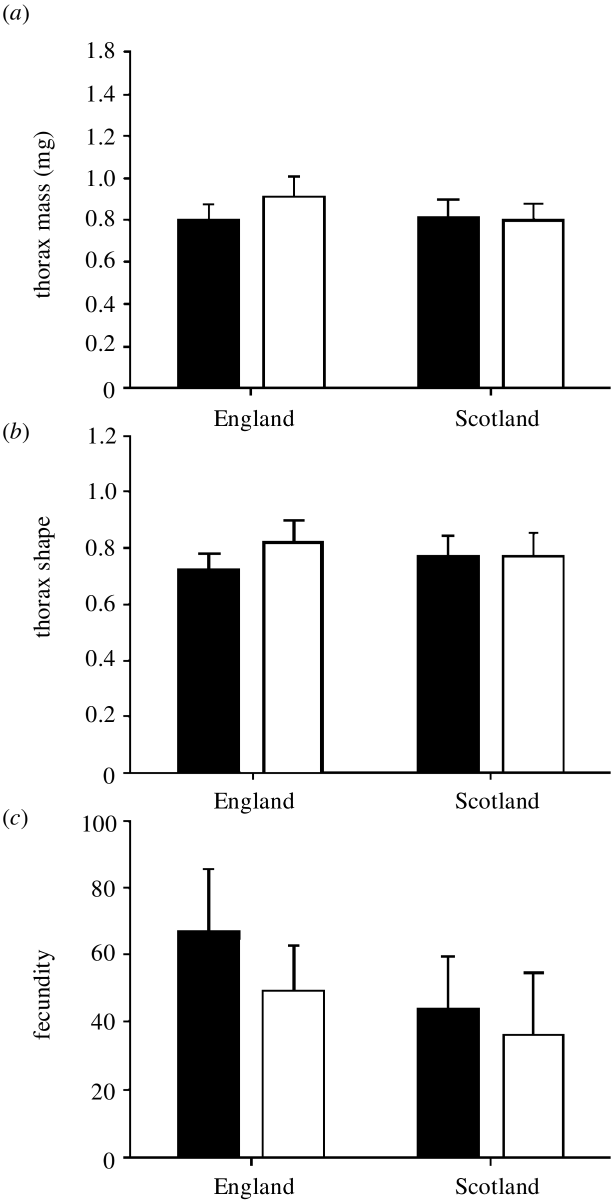

Figure 2. (*a*) Thorax mass, (*b*) thorax shape (width/length) and (*c*) fecundity (number of eggs laid in the first 7 days after mating) of females from populations at core (filled bars) and range margin (open bars) sites in England and Scotland. The means and standard deviations are shown.

3. RESULTS

A total of 71 females was collected from the field, which gave rise to 611 F_1 individuals (302 females, 309 males) from 13 to 17 families per site, and 324 F_2 females from seven to eight families per site. There were significant family effects in measures of total dry mass, thorax shape and mass, and number of eggs laid ($p < 0.03$ in all cases). Data on fecundity schedules ($n = 40$ females) showed that for all sites the number of eggs laid over time peaked at around 4 days after pairing and that females laid most of their eggs by day 7 (mean proportion of eggs laid: English core = 76.1%, English margin = 75.7%, Scottish core = 85.7%, Scottish margin = 75.3%). Thus, we are confident that the number of eggs laid over 7 days is a reliable measure of the reproductive potential of each female.

(a) *Investment in dispersal capability*

Females from range margin sites had relatively larger and broader thoraxes (thorax mass, two-way ANCOVA with total mass as a covariate, site effect, $F_{1,266} = 7.86$, $p = 0.006$, figure 2*a*; thorax shape, two-way ANOVA, site effect, $F_{1,267} = 25.64$, $p < 0.001$; figure 2*b*). For both thorax measures, significant country by site interactions indicated that the effect was greater in the English populations than in the Scottish ($p < 0.02$ in both cases). Similar results were obtained for males in measures of relative thorax mass (site effect, $F_{1,273} = 6.38$, $p = 0.013$). These results confirm that populations at range margins have greater investment in dispersal.

(**b**) *Investment in reproduction*

Overall, females from sites in England were more fecund than those from Scotland (two-way ANOVA, country effect, $F_{1,307} = 93.82$, $p < 0.001$). Females from core sites laid significantly more eggs than females from range margin sites (site effect, $F_{1,307} = 8.43$, $p = 0.012$; figure 2*c*) indicating reduced investment in reproduction at the range margin. This effect was greater in England than Scotland (country by site interaction, $F_{1,307} = 9.69$, $p = 0.002$). A one-way analysis and Tukey test showed that the egg output varied significantly between all four sites. None of these effects, however, was evident from the adult morphology data and there were no differences in the relative abdomen mass of females between sites (two-way ANCOVA, site effect, $F_{1,266} = 0.002$, $p = 0.96$) or countries ($F_{1,266} = 0.06$, $p = 0.81$).

4. DISCUSSION

The distribution of *P. aegeria* has fluctuated greatly in Britain over the past 150 years, probably in response to climate change (Asher *et al.* 2001). Towards the end of the nineteenth century its distribution contracted and by the early twentieth century it was essentially restricted to southwest England and Wales, with a small refuge population in west Scotland. Since the 1940s, the distribution has been expanding and populations were first recorded on the east coast of Scotland in the 1950s (Barbour 1986).

Range margin sites sampled in this study were colonized in the 1990s (figure 1) and results from this study showed evidence for an evolutionary trade-off between flight and reproduction in these populations. Females from populations near the range margins had larger, broader thoraxes indicating increased dispersal ability (see Dempster *et al.* 1976). Associated with this increased dispersal ability, females at range margins laid significantly fewer eggs than those from populations nearer the centre of the range, indicating a decreased investment in reproduction in newly colonized sites. However, the effect was greater in the English populations, therefore, the range margin effect may not apply to all margins.

Such trade-offs are expected (Zera & Denno 1997), but have not previously been demonstrated. However, observed differences in fecundity were not reflected in measures of abdomen mass of females. In species (such as *P. aegeria*) where females develop eggs throughout their adult lifetime, measures of abdomen mass at adult emergence may not reflect reproductive output, particularly where females feed as adults and can supplement larval resources. This may explain why studies measuring abdomen mass have failed to demonstrate a trade-off between flight and reproduction (e.g. Hill *et al.* 1999*a*).

Trade-offs were evident at expanding range margins in both England and Scotland but were more marked in English populations. Differences between the two countries could be caused by several factors. The Scottish 'core' site has only been established for *ca*. 50 years (Barbour 1986), and individuals from this site may still retain some characteristics of more recently established sites and thus be more similar to populations at the range margin than were the English core and margin sites. The two range margins also differ in their availability of breeding woodland habitat for *P. aegeria* and there is *ca*. 25% less woodland at the range margin in England than in Scotland (Hill *et al.* 2001). Fragmentation of breeding habitat has been related to evolutionary changes in dispersal ability in butterflies (Berwaerts *et al.* 1998; Thomas *et al.* 1998; Hill *et al.* 1999*c*) owing to altered costs or benefits of dispersal in such landscapes, and may also have contributed to the differences observed here. In addition, the shorter distance between study sites in Scotland may result in greater gene flow between study populations, and thus reduce any differences between populations.

The differences between the populations in England and Scotland in terms of fecundity may be explained by adaptation to local conditions and temperatures, with the Scottish populations being less well adapted to the conditions of the study. However, a previous study has shown that the speckled wood does not wholly perform better at a temperature most closely related to that experienced in the field (Sibly *et al.* 1997).

Global climates are predicted to continue warming by up to 5.8 °C by the end of this century (IPCC 2001), and predicting the ability of species to track climate and the rate and pattern of range expansion at cool, northern range margins will be crucial for predicting the distribution of biodiversity in the future. Previous studies have highlighted the overwhelming importance of habitat availability on patterns of range expansion in both specialist (Warren *et al.* 2001) and generalist species (Hill *et al.* 2001), but evolutionary changes occurring in expanding populations may also be important. Evolutionary increases in dispersal ability would also be expected to increase the potential colonization ability of species into areas beyond their current range margins and help species keep track of climate warming. Such changes might also help counteract impacts of habitat loss and fragmentation if they increase the probability that more isolated sites are colonized. Data from this study indicate, however, that any potential advantages arising from increased dispersal ability may be balanced by reduced reproductive output in populations at range margins; increased dispersal ability may result in more isolated sites being reached by migrants, but population growth rates in these sites may be reduced. Understanding the relative importance of changes in dispersal versus reproduction at range margins will be important for predicting patterns of range expansion in the future.

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