Journal of Animal Ecology 2006 **75**, 91–100

# Dispersal-related life-history trade-offs in a butterfly metapopulation

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### Summary

1. Recent studies on butterflies have documented apparent evolutionary changes in dispersal rate in response to climate change and habitat change. These studies often assume a trade-off between dispersal rate (or flight capacity) and reproduction, which is the rule in wing-dimorphic species but might not occur equally in wing-monomorphic species such as butterflies.

2. To investigate the relationship between dispersal rate and fecundity in the Glanville fritillary butterfly *Melitaea cinxia* we recorded lifetime individual movements, matings, ovipositions, and maximal life span in a large  $(32 \times 26 \text{ m})$  population cage in the field. Experimental material was obtained from 20 newly established and 20 old local populations within a large metapopulation in the Åland Islands in Finland.

**3.** Females of the Glanville fritillary from newly established populations are known to be more dispersive in the field, and in the cage they showed significantly greater mobility, mated earlier, and laid more egg clutches than females from old populations. The dispersive females from new populations exhibited no reduced lifetime fecundity in the cage, but they had a shorter maximal life span than old-population females.

**4.** These results challenge the dispersal–fecundity trade-off for nonmigratory butterflies but instead suggest a physiological trade-off between high metabolic performance and reduced maximal life span. High metabolic performance may explain high rates of dispersal and oviposition in early life.

5. In fragmented landscapes, an ecological trade-off exists between being more dispersive and hence spending more time in the landscape matrix vs. having more time for reproduction in the habitat. We estimate with a dispersal model parameterized for the Glanville fritillary that the lifetime egg production is 4% smaller on average in the more dispersive butterflies in a representative landscape, with much variation depending on landscape structure in the neighbourhood of the natal patch, from -26 to 45% in the landscape analysed in this paper.

*Key-words*: dispersal, fecundity, life history, *Melitaea cinxia*, metabolic performance, metapopulation, trade-off.

*Journal of Animal Ecology* (2006) **75**, 91–100 doi: 10.1111/j.1365-2656.2005.01024.x

### Introduction

Most organisms have the capacity to disperse from one place to another, but high dispersal rate is especially characteristic of species living in rapidly changing environments. Anthropogenic habitat loss and fragmentation and climate change pose novel challenges for many

Correspondence: Ilkka Hanski, Department of Biological and Environmental Sciences, PO Box 65, Viikinkaari 1, FI-00014 University of Helsinki, Finland. E-mail: ilkka.hanski@helsinki.fi species and are often assumed to select for increased mobility. Hill, Thomas & Blakeley (1999a), Thomas *et al.* (2001), Hill *et al.* (2002) and Hughes, Hill & Dytham (2003) have reported putative examples on butterflies. Dispersal capacity is unlikely to evolve independently, however, and correlated changes in other life-history traits may either bolster or hinder the performance of more (or less) dispersive individuals in changing environments (Roff & Fairbairn 2001; Ronce *et al.* 2001; Ronce & Olivieri 2004). In general, knowledge of possible life-history trade-offs is necessary for a satisfactory

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understanding of life-history evolution (Stearns 1992; Roff 1992).

Most of the research on dispersal in insects has been conducted on wing-dimorphic species (Dingle 1996). These species possess the advantage of clearly distinct dispersive (long-winged) and sedentary (short-winged) phenotypes, which are easy to record in the field and in the laboratory. In contrast, in wing-monomorphic species, which comprise the vast majority of insect species, just measuring the individual rate of dispersal and flight capacity poses a challenge, and researchers have been tempted to generalize the results for wing-dimorphic species also for wing-monomorphic species. In particular, a trade-off between flight capacity and fecundity, which is strongly supported for wing-dimorphic species (Roff 1977; Roff & Fairbairn 1991; Rankin & Burchsted 1992; Zera & Denno 1997), is routinely assumed also for wing-monomorphic species, although it might not apply widely to the latter (Roff & Fairbairn 2001; Min et al. 2004). For instance, researchers working on butterflies have assumed that large ratio of thorax weight to abdomen weight characterizes highly dispersive individuals (Dempster, King & Lakhani 1976; Thomas, Hill & Lewis 1998; Hill, Thomas & Lewis 1999b). The usual justifications for this assumption are that thorax weight is correlated with the mass of flight muscles, that abdomen weight is correlated with the level of reproductive investment, and that the ratio of the two is a proper measure because of dispersal-fecundity tradeoff. However, these studies have not been backed up by direct measurements of dispersal rate, flight capacity, and fecundity, and it remains a largely open question whether a similar dispersal-fecundity trade-off characterizes both wing-dimorphic and wing-monomorphic insect species. Though this trade-off could be expected on the grounds of a general argument about resource allocation, the biology of wing-dimorphic and wingmonomorphic insects is so different that different physiological mechanisms might well underpin variation in dispersal rate in the two types of insects.

Previous studies on the Glanville fritillary butterfly Melitaea cinxia (L.) have revealed a systematic difference in the rate of dispersal of females (though not of males) in newly established vs. old populations (Hanski et al. 2002) and a significant interaction in the effects of population age and spatial connectivity on dispersal (Hanski et al. 2004). Briefly, females from new isolated populations are most dispersive, and females from old isolated populations are least dispersive, apparently because the more dispersive females are over-represented among the colonizers and are most likely to leave from existing populations (Hanski et al. 2004). The large metapopulation of the Glanville fritillary in the Åland Islands in Finland with about 100 new local populations being established in each year (Hanski et al. 1995) and a documented history for hundreds of older populations (Nieminen, Siljander & Hanski 2004) provides a unique model system to study dispersal and evolution of dispersal in a wing-monomorphic insect. Here we

© 2006 British Ecological Society, *Journal of Animal Ecology*, **75**, 91–100 employ a large population cage erected above the natural habitat in the field to investigate mobility, matings, ovipositions, and life span of individual butterflies under seminatural conditions. We combine this technique to study individuals with an opportunity to sample butterflies for experiments from local populations with dissimilar histories and hence, based on our previous results (Hanski *et al.* 2002, 2004), with significant differences in dispersal rate.

The purpose of this study was to investigate whether there exist differences in lifetime fecundity and survival between dispersive butterflies originating from newly established populations and the more sedentary butterflies originating from old populations. We also examined whether individuals in the two types of populations would differ in their mobility in the cage. Another tradeoff operating in natural metapopulations in fragmented landscapes is the increased amount of time spent in nonhabitat by more dispersive individuals. This trade-off cannot be studied directly, but we used for this purpose a model of dispersal that has been parameterized with empirical data (Hanski *et al.* 2004) and was here run for the real fragmented landscape of the Glanville fritillary.

### Materials and methods

#### ORIGIN AND MAINTENANCE OF BUTTERFLIES

Post-diapause larvae were collected in the spring 2003 from 20 new (established in 2002) and 20 old local populations (mostly  $\geq$  5 years old) located across the Åland Islands. Spatial connectivity of population *i* was measured by

$$S_i = \sum_{i \neq i} \exp(-\alpha d_{ii}) N_i,$$

where  $N_j$  is the observed number of larval groups in population *j*, *d<sub>ij</sub>* is the distance between populations *i* and *j*, and 1/ $\alpha$  is the average migration distance, set to 1 (km) based on previous studies (Hanski, Alho & Moilanen 2000; Ovaskainen 2004). The 20 new populations tended to be small, with an average of 2·2 (SD 1·9) larval groups in autumn 2002, and they were all relatively isolated from other local populations (by design of sampling; *S* < 20). In contrast, the old populations were larger, with 11·9 (SD 6·4) larval groups on average, and they were well connected (*S* > 40). We are hence comparing individuals originating from new, small and isolated populations (called new populations for short) with individuals originating from old, large and wellconnected populations (called old populations).

The larvae were reared on the natural host plant *Plantago lanceolata* L. under common garden conditions in the laboratory, with 25 °C at day and 15 °C at night. Pupal weight was used as a measure of body size. Newly eclosed butterflies were sexed, marked individually by writing a number on the underside of the hind wing, and released in the population cage during the day of eclosion. The cage is  $32 \times 26 \times 3$  m in size and covered

with mesh (similar to that in the study of Norberg, Enfjall & Leimar 2002). It has been erected in the field to enclose an entire small dry meadow, the usual habitat of the butterfly. Altogether 95 and 99 individuals from new and old populations with approximately equal sex ratio were released in the cage within a period of 11 days starting on 7 June 2003. The density of butterflies in the cage was relatively high but not higher than the maximum densities observed in the field (IH, own observations). Naturally occurring flowers provided nectar to adult butterflies, and we placed around 200 potted larval host plants (P. lanceolata) into the cage for ovipositing females (naturally occurring host plants were removed). The densities of nectar plants and larval host plants were comparable with their densities on meadows with natural populations of the Glanville fritillary.

# OBSERVATIONS ON MOBILITY, MATINGS AND OVIPOSITIONS

We marked an  $8 \times 8$  grid in the cage. We recorded the position of individual butterflies in systematic censuses of the entire grid conducted at 2-h intervals weather permitting (butterflies were not recorded during completely cloudy periods with low temperature, when none were active). One census lasted up to 2 h when the density of butterflies was maximal. Individual detectability was calculated as the proportion of censuses in which the butterfly was recorded following its first and preceding its last sighting ( $30 \pm 14$  SD sightings per butterfly). Detectability was equally high in both males (0.48, SD 0.16) and females (0.52, 0.16), and there was no difference between butterflies from new (0.48) and old populations (0.50).

To obtain a measure of mobility in the cage that is independent of the number of observations, we regressed the number of grid cells in which a butterfly was recorded against the number of observations, separately for three periods in the life of each butterfly, from 0 to 3 days, from 4 to 8 days, and 9 days and more (79% of butterflies survived for 9 days or longer). The residual from the regression was used as a measure of mobility.

We spent extra time in locating as many mating pairs as possible. Mating pairs typically rest on a plant for about 60 min and are relatively easy to detect. The 200 potted host plants were arranged in a loose cluster in the centre of the cage and were constantly monitored for ovipositing females. Having the potted plants in a cluster facilitated observations, but this is also how the plants occur naturally on rocky meadows. All plants were carefully inspected every evening for possible egg clutches laid by females that had not been detected ovipositing. All egg clutches were collected soon after oviposition and the eggs were counted. It was not practical to measure the weight of eggs, hence we do not know about possible egg number vs. egg size trade-off. However, we know that in the field larval survival systematically increases with larval group size (Kuussaari et al. 2004), implying that females would not benefit of laying fewer but larger eggs.

© 2006 British Ecological Society, Journal of Animal Ecology, **75**, 91–100 We used mixed linear models to analyse the data with source population included as a random factor. In those analyses in which it was necessary to weight the regression with sample size, ordinary linear regression was used. This makes no essential difference, because the individuals originated from a large number (40) of populations.

### MODELLING THE TRADE-OFF BETWEEN DISPERSAL RATE AND TIME SPENT IN HABITAT

To assess the cost of dispersal among habitat patches in terms of reduced time spent in habitat and hence reduced time for oviposition, we employed an individualbased model that has been previously parameterized for the Glanville fritillary (Hanski *et al.* 2004). The model incorporates the main benefits of dispersal in a metapopulation, reduced sib-competition and the opportunity to establish new populations (Heino & Hanski 2001). The movement model is based on a diffusion approximation of correlated random walk with biased behaviour at patch boundaries (Ovaskainen & Cornell 2003). The dispersal phenotype of each individual is characterized by  $r = (\pi/2)\sqrt{(D/\mu)}$ , the mean lifetime dispersal distance (Turchin 1998), where *D* is the diffusion coefficient and  $\mu$  is the daily mortality rate.

The model was run in a network of 197 habitat patches in the Åland Islands (shown in fig. 1 in Hanski et al. 2004) until an evolutionary equilibrium. To obtain a rough estimate of r for butterflies in new and old populations, the two kinds of butterflies used in the cage experiment, we sampled butterfly phenotypes in the model from a small isolated population in the year following its establishment, and from a large well-connected population when the population had persisted  $\geq$  5 years. The cost of dispersal was calculated by dividing the difference in expected lifetime number of egg clutches laid by the two types of butterflies by the lifetime number of egg clutches laid by the less dispersive phenotype. This calculation assumes no difference in the rate of oviposition while the butterflies are in habitat patches (we document such a difference in the first part of the results, but this effect was not included in the model because the effect is slight and because it is possible that what we have measured in the cage does not apply as such to butterflies moving at the landscape level). The model assumes a constant size of egg clutches.

### Results

#### MOBILITY

Only a small proportion of females (7.5%) laid the first clutch of eggs before day 4 of life. As it is possible that pre-reproductive females exhibit dissimilar mobility to ovipositing females, we examined individual mobility for three periods in the life of each butterfly. Among young females, from 0 to 3 days of age, mobility decreased

94 I. Hanski, M. Saastamoinen & O. Ovaskainen



**Fig. 1.** Mobility of young ( $\leq$  3 days old) females (a) and males (b) originating from new (open symbol, dashed line) and old populations (solid symbol, continuous line) in relation to body size (pupal weight). Individuals with less than seven observations are excluded from these graphs, but they were included in a linear model, which was weighted by the number of observations. In females, the effects of population age ( $F_{1,77} = 7.38$ , P = 0.008) and body size ( $F_{1,77} = 6.01$ , P = 0.02) were significant (type III SS). In males, the interaction between population age and body size was significant ( $F_{1,106} = 8.61$ , P = 0.004), as was the main effect of population age ( $F_{1,106} = 7.94$ , P = 0.006; main effect of body size,  $F_{1,106} = 3.50$ , P = 0.06).

with increasing body size and females from new populations were highly significantly more mobile than females from old populations (Fig. 1a). In older butterflies, neither population-type nor body size had a significant effect on mobility in the cage. Comparing the level of mobility across age classes, mobility of preovipositing females originating from old populations was exceptionally low, while new-population females were mobile already before they started to search for host plants for oviposition.

The result was distinctly different for males. Mobility of young males (0-3 days) decreased with increasing body size in old-population males, but mobility increased with body size in new-population males (Fig. 1b). Among older males, there were no significant differences in mobility.

### REPRODUCTION

In females, time from eclosion until mating decreased significantly with increasing early life mobility (0–3 days of age; mixed linear model with the source population as a random factor, population type  $F_{1,16} = 0.01$ , P = 0.91, mobility  $F_{1,9} = 15.6$ , P = 0.003). Time from mating until first oviposition varied from 1 to 15 days (median 5 days) and was not significantly affected by mobility, body size, or population type. Prevailing weather conditions have an influence on oviposition, as females lay only during sunny weather. During our experiment, there was a 3-day rainy period in mid-June when not a single oviposition was recorded.

Though we made our best to observe all matings, several matings were none the less missed, as 13 of the 67 females that were subsequently observed to oviposit fertile eggs had not been observed to mate. Relatively fewer ovipositions were missed, as a careful examination of the host plants for eggs every evening yielded only 32 previously unnoticed egg clutches, compared with 225 clutches that were laid by females under direct observation. The 13 females that were not observed to oviposit at all survived for a much shorter time (average  $6 \cdot 6$  days) than the remaining females (13.8 days; n = 67).

The average clutch size was 120 eggs. In old-population females, clutch size remained constant throughout the life, but in new-population females and in the pooled material clutch size declined with female age (Fig. 2a). The cumulative number of clutches laid by individual females increased faster with age in new-population than in old-population females, and the difference was significant at 5% level in females older than 13 days (Fig. 2b). Cumulative egg production was also higher in females from new than old populations, but the difference was not statistically significant (Fig. 2c). The effect of pupal weight on the cumulative number of eggs and egg clutches was positive but clearly nonsignificant.

Lifetime egg production increased significantly with early life mobility in new-population females (P = 0.01) but not in old-population females (Fig. 2d). The most significant determinant of lifetime egg production was life span, which explained 35% of variation.

### SURVIVAL

Butterflies survived a relatively long time during this experiment because weather was mostly cloudy and temperatures were relatively low. The average lifetime was 12·2 and 13·0 days in new-population and old-population females, respectively. There was no difference in survival during the first 2 weeks, but among the butterflies that survived for at least 14 days the old-population females had a significantly longer life span than new-population females (Fig. 3a). There was no such difference in survival between new- and old-population males (Fig. 3b).

# COST OF DISPERSAL IN A FRAGMENTED LANDSCAPE

The cost of dispersal in terms of reduced lifetime egg production was assessed with the individual-based model described in *Material and methods*. Figure 4(a–d) shows the distribution of dispersal phenotypes in four contrasting habitat patches. In model predictions, isolated patches tend to have more dispersive phenotypes



**Fig. 2.** (a) Clutch size against age in females originating from new (open symbol, dashed line) and old populations (solid symbol, continuous line). The main effect of individual age was significant ( $F_{1,149} = 7.94$ , P = 0.004) in a linear model including repeated measures of clutch size for individual females (interaction between individual age and population age,  $F_{1,149} = 2.11$ , P = 0.15). (b,c) Give the cumulative number of egg clutches and eggs laid by females that were alive by the age given on the horizontal axis. The vertical lines give the standard error of the mean. (d) Lifetime egg production of females from new and old populations in relation to observed mobility in the cage during the first 3 days of life. The interaction between mobility and population age was significant ( $F_{1,61} = 3.93$ , P = 0.05; the main effect of mobility,  $F_{1,61} = 3.33$ , P = 0.07; the main effect of population age  $F_{1,61} = 0.21$ , P = 0.65).



**Fig. 3.** Maximal life span against body size in females (a) and males (b). The vertical axis gives the residual from a model explaining life span by the date of eclosion in butterflies that lived for 14 days or longer. In females, the effect of population type on life span was significant ( $F_{1,15} = 13.97$ , P = 0.002; the effect of eclosion date  $F_{1,15} = 25.33$ , P = 0.0001, body size not included in the model). Butterflies from new and old populations are indicated by open (dashed line) and solid symbols (continuous line), respectively. In males, population type had no effect on life span.

at equilibrium than well-connected patches. The actual butterflies in the present experiment originated from newly established, small and isolated populations vs. old, large and well-connected populations. Based on the results in Fig. 4, we estimate that the butterflies in our experiment originating from new populations had r = 1650 m on average and the ones originating from old populations had r = 860 m on average. Entirely independent estimates of r for new and old populations based on mark–release–recapture data gave similar values, r = 1350 and 840 m, respectively (estimation described in Appendix I).



**Fig. 4.** (a–d) Show the distribution of dispersal phenotypes in four habitat patches, a small isolated (a; 0.09 ha, average population age 4·1 years) and a small well-connected patch (b; 0.09 ha, 7·7 years), and a large isolated (c; 1·0 ha, 18·0 years) and a large well-connected patch (d; 1·0 ha, 31·5 years). The blue lines give the distribution of phenotypes in the metapopulation as a whole. The red lines in (a) and (d) show the distribution for newly established (a) and old ( $\geq$  5 years; d) populations in the respective patches separately. (e) Lifetime number of egg clutches as a function of *r* (mean lifetime dispersal distance) for the four populations in (a–d) (blue lines for well-connected populations, red lines for isolated populations, continuous lines for large and dashed lines indicate the position of model-predicted new, small and isolated vs. old, large, and well-connected populations (the red distributions in a and d). (f) The cost of being a dispersive butterfly (*r* = 1650 m as opposed to *r* = 860 m) born to a particular habitat patch in the network of 197 patches in relation to patch area and spatial connectivity. The size of the symbol is proportional to the magnitude of the cost. Red colour indicates negative cost (the more dispersive phenotype lays more egg clutches). The five patches indicated by circles are the ones for which further results are given in panels (a–e). The results in (e,f) were calculated analytically with the expression given in Ovaskainen & Cornell (2003), the other results are based on simulation.

In model predictions for the real landscape, lifetime egg production generally decreases with increasing dispersal rate (Fig. 4e), as the more dispersive individuals end up spending more time in the landscape matrix where oviposition is not possible. Comparing phenotypes with r = 1650 and 860 m shows that the cost of elevated dispersal rate is 2-25% in the four representative patches in Fig. 4(a-d), the largest cost being paid by dispersive individuals born to the small and isolated habitat patch. Among all the 197 patches in the network, lifetime egg production is predicted to be 4% (SD 7.5%) smaller on average in the more dispersive butterflies. However, the magnitude of the cost depends greatly on the size and spatial connectivity of the natal patch, and varies from -26 to 45% (Fig. 4f). The cost is small in well-connected patches, and the cost may even

© 2006 British Ecological Society, *Journal of Animal Ecology*, **75**, 91–100 be negative in small patches with intermediate connectivity (the patch shown with black line in Fig. 4e).

### Discussion

### LIFE-HISTORY TRADE-OFFS

Our direct measurements of fecundity made under seminatural conditions in a large population cage in the field lend no support to the dispersal–fecundity trade-off in the Glanville fritillary: the lifetime egg production was higher, not lower, in the more dispersive females from new populations than in the less dispersive females from old populations. Furthermore, the females that were more mobile in the cage tended to have higher lifetime egg production than the less mobile females.

These results, which represent perhaps the most inclusive test so far of the dispersal-fecundity trade-off in butterflies, challenge the notion that wing-dimorphic and wing-monomorphic insects would exhibit similar dispersal-related life-history trade-offs.

Rankin and coworkers have previously reported other insect examples of positive correlation between dispersal (long-duration flight) and reproduction, which they expected to be common in species frequently colonizing ephemeral habitats (Rankin & Burchsted 1992). In the migratory but wing-monomorphic grasshopper *Melanoplus sanguinipes* long-duration flight to exhaustion accelerated the onset of first reproduction and enhanced reproductive success during the entire lifetime. Min *et al.* (2004) attributed this result to an increased level of juvenile hormone induced by long flight, which is known to be involved in the control of reproduction in most insects.

If high dispersal rate does not lead to reduced fecundity, what might be the physiological and ecological costs? Considering the energetic cost, one possibility is that the more mobile individuals can increase their food intake sufficiently to compensate for the energetic cost of extra mobility. For instance, in the wing-polymorphic hemipteran Sigara, a strong dispersal-fecundity tradeoff is apparent under restricted food availability but not under unlimited food availability (Zera & Denno 1997). In our experiment, butterflies fed on the nectar of naturally occurring flowers in the cage, but unfortunately we could not quantify their food intake. It is, however, doubtful whether the less mobile females would have been any more limited by nectar in the cage than the more mobile females. It should also be noted that our comparison between new- and old-population females relates to the known difference in their dispersal rate in the field (Hanski et al. 2002, 2004) rather than to any difference in their mobility in the cage, though there is such a difference in young females (Fig. 1a). Our interpretation of these results is that they reflect general lifehistory differences between butterflies in new and old populations rather than differential mobility in the cage. On the other hand, we cannot infer from these results what would be the rate of oviposition in the natural landscape, where some females move long distances while others remain in the natal habitat patch. Quantifying the effects of actual long-distance flight on oviposition remains a challenge for the future.

Intriguingly, the present results on oviposition in newand old-population females are in apparent conflict with our own previous finding on the same species. Hanski *et al.* (2004) reported a dissimilar scaling of potential fecundity (essentially the number of oocytes at eclosion) with body size in new- and old-population females, yielding greater potential fecundity of large females originating from old than new populations (fig. 4 in Hanski *et al.* 2004). In the previous study, we recorded 100 oocytes on average per ovariole (SD = 21, n = 91), with a maximum of 164 oocytes (I. Hanski, unpublished). Given the eight ovarioles, these figures give 800 and 1312 as the expected and maximal potential lifetime egg production, assuming that all oocytes are visible at eclosion. These numbers may be compared with those in Fig. 2(d), showing that the top five females managed to lay 800–900 eggs (maximum 916) during their lifetime. Therefore, a small minority of females may have run out of eggs during their lifetime, but the vast majority did not. Given the previous and present results, it is possible that there is some reduction in the number of oocytes at eclosion in the more dispersive females, though there is no difference in the realized lifetime egg production (because females do not generally have a chance to lay all eggs), or the difference is in the opposite direction (implying a difference in the rate of oviposition, as in Fig. 2b,c).

Instead of the expected negative association between dispersal rate and lifetime fecundity, we found a negative association between dispersal rate and maximal life span. We hypothesize that this relationship may reflect variation in the metabolic performance of individuals. Hanski et al. (2004) found that the [ATP]: [ADP] ratio in the flight muscles of female Glanville fritillary following a controlled period of flight was related to population age and spatial connectivity in the same manner as field-measured dispersal rate. Thus the [ATP] : [ADP] ratio was highest in females from new isolated populations and lowest in females from old isolated populations. Hanski et al. (2004) suggested that variation in the [ATP] : [ADP] ratio reflects variation in cellular capacity to renew ATP during flight, and the result would hence imply that a part of the observed variation in dispersal rate is due to variation in the flight metabolic performance of individuals. Recalling that a wide range of studies on various taxa have reported a negative relationship between metabolic rate and life span (for a review see van Voorhies 2001), the reduced life span of the more dispersive butterflies may represent a cost of high metabolic performance. These results suggest that there is a contrast between 'fast' females that are dispersive and mature eggs fast, and 'slow' females that avoid paying a large cost of dispersal and are superior in surviving a longer time.

### DIFFERENCES BETWEEN THE SEXES

Variation in dispersal rate and other life-history traits in relation to population age and connectivity is strikingly different in the two sexes in the Glanville fritillary. In contrast to females, new-population males are not more dispersive than old-population males (Hanski *et al.* 2002, 2004; the present study), nor does the [ATP] : [ADP] ratio (Hanski *et al.* 2004) or life span in males (Fig. 3b) relate to population age or connectivity. Why should the results be so different for males and females?

One obvious difference between the two sexes lies in the benefit of dispersal to previously empty habitat patches. Females tend to become mated soon after eclosion, and they usually mate only once in their lifetime (Boggs & Nieminen 2004). We found that females

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### 97

that were more mobile in the cage became mated faster than the less mobile females, most likely because males find the more mobile females faster. In any case, most females immigrating to previously empty patches are already mated, and hence males arriving at such patches would have only limited mating opportunities. Males dispersing to existing populations would have better chances of mating, though once again they would mostly encounter mated females. Males born to small populations might do better by dispersing, as there would be limited mating opportunities in small populations and mating with close relatives would lead to inbreeding depression (Saccheri et al. 1998; Haikola et al. 2001). However, whatever the benefits of dispersal in males, the situation is clearly different in female Glanville fritillary in highly fragmented landscapes, where the opportunity to establish new local populations is a major factor selecting for dispersal (Heino & Hanski 2001).

## COSTS AND BENEFITS OF DISPERSAL AND LANDSCAPE STRUCTURE

An often-assumed cost of dispersal is high risk of mortality in the landscape matrix (Clobert, Ims & Rousset 2004). In insects that oviposit repeatedly, time and potential opportunities for oviposition are lost during dispersal, even if the rate of mortality would be the same in the matrix and in the habitat. Assuming correlated random walk as the mode of dispersal, the cost of dispersal may be viewed as a trade-off between emigration and immigration: high immigration rate in the more mobile individuals is necessarily associated with high emigration rate, also from a habitat patch at which an individual has just arrived.

Ovaskainen (2004) modelled mark-release-recapture data for Melitaea diamina, a close relative of the Glanville fritillary. He inferred that females spend roughly half of their lifetime in the matrix in a landscape in which the empirical study had been conducted. In this paper, we compared the time spent in the matrix by individuals corresponding to the dispersive butterflies from new populations and to the less dispersive butterflies from old populations in the cage experiment. We found that the direct cost (time spent in the matrix) that the more dispersive butterflies paid in comparison with the more sedentary ones was 4% on average in a representative landscape for the Glanville fritillary. This is not a large cost, but it is important to note that the cost varies greatly depending on local landscape structure, and hence the fitness of butterflies with a particular dispersal phenotype varies from one part of the landscape to another. Spatial variation in landscape structure is thereby a powerful mechanism to maintain variability in dispersal rate and associated life-history traits in real landscapes (Hanski et al. 2004).

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Given the assumptions of the movement model, the cost of dispersal may unexpectedly be negative in some parts of a heterogeneous landscape. In our example, the cost was negative in small patches with an intermediate connectivity to other patches. In such situations, butterflies with low r do poorly, because all butterflies regardless of their r are likely to leave a small patch soon, and individuals with low r end up spending much time in the matrix because the natal patch was relatively isolated. Note, however, that if the natal patch is very isolated, the cost is again positive, as now all individuals regardless of their r will be able to reproduce only in the natal patch before dispersal, and individuals with low r would spend more time on average in the natal patch before dispersal.

High or relatively high dispersal rate is expected in species that occur in highly fragmented landscapes consisting of small habitat patches with ephemeral local populations. The Glanville fritillary in the Åland Islands is a prime example (Hanski 1999). None the less, at the individual level high dispersal rate imposes a cost in terms of high emigration rate from suitable habitat, which is reflected in the high frequency of less dispersive phenotypes in old isolated populations (Hanski et al. 2002, 2004). Secondly, the shorter maximal life span of more dispersive females might also select, indirectly, against dispersal especially in more continuous habitats. Weather conditions are commonly unfavourable for mating and oviposition during the adult flight season, making it possibly important to stay alive for a long time. There may be yet other costs and benefits of dispersal that will be detected in closer examination, but the present results conclusively refute the classic dispersal-fecundity trade-off for the Glanville fritillary. We suggest that this trade-off should not be assumed as the default in studies of dispersal and evolution of dispersal in nonmigratory wing-monomorphic insects.

### Acknowledgements

We thank Steve Cornell, Niclas Fritzén, Anne Holma and Kata Valosaari for help in running the cage experiment, and C. Boggs, C. Thomas, S. van Nouhuys and two anonymous referees for comments on the manuscript. Funding was provided by the Academy of Finland (Finnish Centre of Excellence Programme 2000–05, grant number 44887).

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Received 12 April 2005; accepted 22 July 2005

### Appendix I

### DERIVATION OF AVERAGE LIFETIME DISPERSAL DISTANCE BASED ON MARK-RELEASE-RECAPTURE DATA

The dispersal phenotype of individual butterflies is characterized by  $r = (\pi/2)\sqrt{(D/\mu)}$ , the mean lifetime dispersal distance, where *D* is the diffusion coefficient and  $\mu$  is the daily mortality rate. In the main text, the value of *r* for new- and old-population butterflies was estimated by sampling butterfly phenotypes in the model from a small isolated population in the year following its establishment, and from a large well-connected population when the population had persisted  $\geq$  5 years. This corresponds to the types of local populations sampled for the cage experiment.

Another set of estimates of *r* was derived from the daily emigration rate estimates reported by Hanski *et al.* (2002), who conducted a mark–release–recapture experiment in a system consisting of two habitat patches and roadside habitats. The butterflies in that experiment originated from 20 newly established (in the previous generation) and 36 old ( $\geq$  5 years) populations in the Åland Islands. Post-diapause larvae were sampled

from the field and reared in common garden as in the present experiment. Hanski et al. (2002) pooled the recaptures for the release patch vs. the other patch and roadside habitats, and they thereby estimated that the daily emigration probability was  $E_D = 0.109$  for females originating from new populations and  $E_D = 0.051$  for females originating from old populations (the 95% confidence intervals were 0.043 - 0.176 and 0.024 - 0.077, respectively). The estimated daily survival rate in the habitat patch was equal in the two groups of butterflies, about 0.8, giving  $\mu = 0.2$  (day<sup>-1</sup>) [new populations: 0.814] (0.744-0.885), old populations: 0.791 (0.749-0.833); mortality rate was relatively high during the experiment due to dry and warm weather]. The strength of edgemediated behaviour h (Ovaskainen & Cornell 2003) was set at h = 1000, which is the value used in the cal-

culations of the cost of dispersal in this paper and yields realistic dynamics for local populations and for the metapopulation as a whole (Hanski et al. 2004). We employed a formula for the lifetime emigration probability (eqn 4.2 in Ovaskainen & Cornell 2003)  $E_{L(r)}$ , defined here as the probability that an individual with phenotype r reaches the distance of 150 m (the distance between the two patches in the experiment) from a patch of 0.35 ha in size (the size of the larger patch, which produced most of the observations) before it dies. As the mean lifetime of individuals was estimated to be 5 days, we mapped the daily emigration probability  $E_D$ to the lifetime emigration probability  $E_{L(r)}$  by the formula  $E_{L(r)} = 1 - (1 - E_D)^5$ . These estimates are somewhat biased, because we cannot take into account variation in the spatial connectivity of the source populations.