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Mobility and lifetime fecundity in new versus old populations of the Glanville fritillary butterfly

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Abstract Life history theory often assumes a trade-off between dispersal and reproduction, and such a trade-off is commonly observed in wing-dimorphic insects. The results are less consistent for wing-monomorphic species, for which it is more difficult to assess dispersal capacity and rate. Three replicate experiments were carried out in consecutive years on the Glanville fritillary butterfly in a large outdoor population cage to study the relationship between lifetime egg production and mobility. The experimental material included females originating from newly-established and old populations, as previous studies have shown dispersal capacity to depend on population age. There was a consistent and significant interaction between mobility and population age, such that in newly-established populations mobile females had higher fecundity than less mobile females, while in old populations there was no such relationship. As selection favours individuals with the highest fecundity, selection pressure on mobility is likely to be different between the two population types, which may contribute to maintenance of variation in dispersal rate in the metapopulation as a whole. Several other female traits also affected lifetime fecundity, including lifespan, number of matings and date of eclosion, although these effects were not consistent across the years. These results highlight the importance of conducting experiments in more than one year before generalizing about patterns in life history variation.

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Introduction

A general assumption in life history theory is that the values of particular traits are often constrained by trade-offs among the traits (Roff 2002). A commonly assumed tradeoff in insects is the one between dispersal and reproduction, both of which are energetically demanding processes and could compete for the same resources (Baguette and Schtickzelle 2006; Roff 2002). Flight is, however, not an option but a fundamental prerequisite for successful life history in most insects, as flight is required for behaviours such as feeding, mating, and oviposition. In insects, support for a trade-off between reproduction and dispersal mainly comes from studies on wing-dimorphic species (Mole and Zera 1993, 1994; Zera and Denno 1997). In these species, the flightless morph can be easily distinguished from the dispersive morph as the former is either wingless or has highly reduced wings (Zera and Denno 1997). Several studies on wing-dimorphic insects have demonstrated that flight capacity is negatively correlated with reproductive performance (e.g. Mole and Zera 1993; see also Zera and Denno 1997 for a review). Apparently, the construction and maintenance of wings and flight muscles constrain reproduction.

Cost of increased dispersal ability in terms of reduced reproduction is less well documented for wing-monomorphic species, where dispersal is a continuously varying trait (but see Baguette and Schtickzelle 2006). Measuring dispersal capacity or rate is more difficult in wing-monomorphic than wing-dimorphic species, and therefore surrogates such as thorax weight, aspect ratio (wing span²/wing area), and wing loading (total dry mass/wing area) are often used

(Hill et al. 1999; Hughes et al. 2003). Hughes et al. (2003) demonstrated that in the speckled wood butterfly (*Pararge aegeria*) increased dispersal, as indicated by a relatively large and broad thorax, is associated with reduced investment in reproduction in expanding populations.

A shortcoming of many previous studies on wing-monomorphic species is that dispersal capacity was not measured directly. In one instance, where a more direct measurement of dispersal was available for the Glanville fritillary butterfly (Melitaea cinxia), the results challenged the generality of the dispersal-reproduction trade-off, and instead suggested that the population context may be important (Hanski et al. 2006). Both experimental (mark-releaserecapture) and theoretical studies on the Glanville fritillary have shown that females from newly-established isolated populations are more dispersive than females from old well-connected populations (Hanski et al. 2004). Furthermore, Hanski et al. (2006) found no overall trade-off between dispersal and reproduction, but instead there was an indication that cumulative number of clutches laid was greater in newly-established than in old populations. These results for the Glanville fritillary are consistent with previous findings showing that in migratory populations of the milkweed bug (Oncopeltus fasciatus), lines selected for long-duration flight showed higher early-life fecundity than non-fliers (Palmer and Dingle 1989), whereas no such correlation was found in a non-migratory population (Dingle et al. 1988).

Individual attributes other than mobility can affect lifetime fecundity in butterflies. For example, body weight (e.g. Calvo and Molina 2005), number of matings (Wiklund et al. 1993) and lifespan (Boggs and Freeman 2005) have been shown to affect female fecundity in many species. Furthermore, in ectothermic species such as butterflies, prevailing environmental conditions may have a great influence on reproduction, especially in areas where the species lives at its range boundary and where unfavourable weather conditions may be common. Finding out which traits interact and vary in natural populations and affect lifetime fecundity is important for assessing the likely course of life history evolution.

Here, I report on a 3-year study of lifetime egg production and mobility in the Glanville fritillary conducted under semi-natural conditions in a large population cage in the field. The aim was to find out to what extent lifetime fecundity varies with the individual trait of mobility as measured in the cage. Furthermore, as previous studies have shown that dispersal ability of the females depends on population age, comparisons were performed between females originating from newly-established and old populations. Finally, the effects of other life history traits on lifetime fecundity were analysed. Having conducted the studies in 3 consecutive years under common garden conditions allowed the assessment of the generality of the factors affecting lifetime fecundity.

Materials and methods

Study species and populations

The Glanville fritillary (M. cinxia) has a univoltine life cycle in the Åland Islands in Finland (Hanski 1999; Nieminen et al. 2004). The adult flight season lasts from early June to mid July. Females eclose with the full complement of oocytes in their ovarioles but egg maturation may be affected by availability of nectar (personal observation). Females lay eggs in clutches of 130-160 eggs on average (Saastamoinen 2007) and larval survival is positively correlated with group size (Kuussaari et al. 2004). In the Åland Islands, larvae have two host plant species, Plantago lanceolata and Veronica spicata (Kuussaari 1998). The Glanville fritillary has a classic metapopulation structure in the Åland Islands, with a high rate of population turnover (extinctions and recolonisations; Nieminen et al. 2004). Of the roughly 4,000 habitat patches in the entire study area about 500 are occupied at any given year (Hanski 1999).

Hanski et al. (2004) showed that females originating from newly-established isolated populations have higher dispersal rate than females originating from old populations. The new-population females have a higher flight metabolic rate than old-population females, which most likely is related to the difference in their dispersal rate (Haag et al. 2005). In the present study, individuals (larvae or adults) originated from tens of either newly-established or old (\geq 5 years) populations with varying connectivity (inverse of isolation) to other existing local populations (for measurement of connectivity see Hanski et al. 2004).

In the spring of both 2003 and 2005, fifth instar larvae were sampled from 40 to 60 local populations, respectively, located across the Åland Islands, and reared in the laboratory. Adult butterflies were released into the population cage (below) on the day of their eclosion (some butterflies eclosed in the evening and were released in the following morning). In 2004, adult butterflies instead of larvae were sampled between 2 and 12 June from 25 different populations across the Åland Islands. Only unworn and hence relatively young butterflies were sampled and released into the cage in the evening of the day on which they were collected. Prior to their release into the cage, butterflies were calmed by keeping them for $5-10 \text{ min at } +5^{\circ}\text{C}$, after which they were weighed (in 2004 and 2005) and individually numbered underneath the hind wing by a permanent marker. As butterflies were collected from the field in 2004 the life history data are not as complete for this year as for 2003 and 2005.

Lifetime egg production

The experiments were conducted in a large population cage $(32 \times 26 \times 3 \text{ m})$ constructed upon a natural habitat (dry meadow) in the field (Hanski et al. 2006; Saastamoinen 2007). The cage was covered with a mesh preventing the butterflies from escaping but allowing natural environmental conditions (rain, sunlight and wind) to enter the cage. Potted host plants were provided for oviposition in the central part of the cage, which was relatively bare of vegetation compared with the edges of the cage. In 2003 only P. lanceolata was used as an oviposition host plant. In 2004 both host plant species, P. lanceolata and V. spicata, were used but only one species was present in the cage on any given day. Both host plant species were present all the time in 2005. The edges of the cage had higher vegetation and greater abundance of flowering plants that provided nectar for adult butterflies. Numbers of females released into the cage were comparable in the 3 years and both the sex ratio and the ratio of butterflies originating from newly-established versus old populations were approximately equal (Table 1). In 2004 and 2005 a few females were omitted from the analyses as they were sampled for other purposes.

The cage was divided into 8×8 grid cells, which were surveyed systematically every second hour to obtain data about the location and mobility of the butterflies. As a measure of individual mobility in the cage I used the residual from the regression of the number of grid cells in which the butterfly had been observed against the number of observations during the surveys in the cage. Mobility was calculated for the first 3 days of life of each individual, as previous studies have shown that it is the early-life mobility that varies between females from newly-established versus old populations (Hanski et al. 2006). During the surveys 571

mating pairs were carefully recorded. Extra surveys were conducted during the warmer hours of the day to minimise the number of matings missed. Host plants were continuously monitored for ovipositing females (Hanski et al. 2006). The leaf on which the female laid the egg clutch was removed and the eggs were counted at the age of 3 days. Female lifetime fecundity was measured as the lifetime number of eggs laid. In 2005, one hundred and thirty-six egg clutches were weighed at the age of 5–6 days with a Scaltec SBC 33 electrobalance (accuracy 0.1 μ g). The mean weight of eggs was obtained by dividing the weight of the clutch by the number of eggs. To measure egg hatching rate the larvae in each clutch were counted at the age of 3 days.

Statistical analyses

To examine which factors affected whether a female laid any eggs at all during the experiment I used logistic regression (Proc Genmod, SAS version 8.02; SAS Institute 1999) with binomial error distribution. The data for the 3 study years were first analysed separately to find out which explanatory variables were significant. The final analysis was performed for the pooled data including all significant factors from the previous models as well as year and second-order interactions with year included. Year 2004 was omitted from this analysis as information for one of the factors (mated or not) was not available for this year.

The lifetime number of eggs laid correlated strongly with the number of larvae that hatched (e.g. in 2005: r = 0.912, P < 0.0001). As factors unrelated to the female such as rearing conditions may have affected egg-hatching rate, especially as small clutches desiccate easily under laboratory conditions, only the lifetime number of eggs laid

| 2003 | 2004 | 2005 |
|---------------------------|---|---|
| | | |
| 59 | 50 | 64 |
| 53 | 50 | 53 |
| 112 | 100 | 117 |
| | | |
| 38 | 36 | 68 |
| 45 | 40 | 57 |
| 83 | 76 | 125 |
| 78 | 54 | 50 |
| 133.0 (12.7) ^b | 130.4 (17.6) | 145.3 (22.6) |
| 6.0 (3.16) | 4.7 (4.08) ^c | 5.8 (2.0) |
| 3.01 (1.49) | 4.4 (2.36) | 2.04 (0.78) |
| 399 (228) | 494 (316) | 486 (310) |
| 53.5 (28) | 73 (18) | 54.3 (30.4) |
| | 59 53 112 38 45 83 78 133.0 (12.7) ^b 6.0 (3.16) 3.01 (1.49) 399 (228) 53.5 (28) | $\begin{array}{c ccccccccccccccccccccccccccccccccccc$ |

Table 1Summary of life history data for the Glanville fritillary in the experiments carriedout in 2003, 2004 and 2005.Average values and SD (*in parentheses*) are given

^a Females that did not lay eggs were omitted

^b Adult weight converted from pupal weight (linear regression; $r^2 = 0.512, P < 0.0001$)

^c Females were collected as adults and thus their real ages are not known, the "age" here is measured from the date of release into the cage was used as a measure of lifetime reproductive success. Females that did not lay eggs were omitted from this analysis. Data were normally distributed, and hence analysis of covariance (ANCOVA; Proc GLM, SAS version 8.02; SAS Institute 1999) was used to analyse which female traits affected lifetime egg production. Analyses were weighted by the number of observations for each female. This makes no essential difference in the results but increases the reliability of the measure of mobility. I did not analyse lifetime egg production in the pooled data, because there was a significant two-way interaction in the year-specific analyses.

Mixed ANOVA with female as a random factor (Proc Mixed, SAS version 8.02; SAS Institute 1999) was used to analyse factors affecting egg mass. Three clear outliers were omitted from this analysis as they were interpreted as typographical errors. Second-order interactions were included in the final model if they were significant or increased the model fit (Akaike's information criteria value).

Results

Description of the data

Table 1 summarizes the data for mating, oviposition and lifetime fecundity over the 3 years.

Matings

In 2003 and 2005, most females (86 and 71%, respectively) were observed to mate. In 2004 the proportion of females which mated was much lower, i.e. 35%; this was expected as butterflies were collected from the field as adults and many females had most likely mated prior to their capture (see Materials and methods). In 2004, forty-five percent of the females that laid eggs were not observed to mate in the cage, whereas in 2003 and 2005 the figure was much smaller (19 and 13%, respectively), indicating that most matings were observed (see also Hanski et al. 2006).

Most females were observed to mate only once in their lifetime: 66, 77, and 81% in 2003, 2004, and 2005, respectively. On average, females mated at the age of 1.5–2 days. Age at mating was lower, 1.2 days, in 2004, most likely because adult butterflies were sampled in the field and released into the cage. In 2003, the more mobile females mated sooner than the more sedentary females (linear regression, $F_{1,46} = 12.33$, P = 0.001), but there was no such effect in 2005 ($F_{1,86} = 0.8$, P = 0.373).

Ovipositions

Only half of the females released into the cage laid eggs in 2004 and 2005, while 78% of females laid eggs in 2003.

The average age at first oviposition was 6 days (Table 1). Some females laid eggs on the same day when they mated but the average number of days between the first mating and the first oviposition was 4 days. In 2004 and 2005 the more mobile females laid their first clutch sooner than the more sedentary females ($F_{1,35} = 4.01$, P = 0.053 and $F_{1,57} = 7.62$, P = 0.008, respectively). There was no significant effect in 2003 ($F_{1,64} = 2.37$, P = 0.128), though in this year mobility affected time to mating (above). The average number of days between consecutive ovipositions was between 2 and 3 days (Table 1).

Lifetime fecundity

The average lifetime number of eggs laid was between 400 and 500 eggs in all 3 years. Egg hatching rate was relatively high, 73%, in 2004, whereas in 2003 and 2005 it was much lower, 54% (Table 1).

Factors affecting lifetime fecundity

Probability of laying any eggs

Females that had a short lifespan, for whatever reason, were less likely to lay eggs than those that lived longer (Table 2). The effect of lifespan was especially strong in 2005, reflected in the significant interaction between lifespan and year. The average lifespan of females that laid eggs (12 days) and those that did not (6 days) differed significantly in 2005 (t = 9.62, P < 0.0001), whereas in 2003 there was no significant difference between the data (t = 0.9,P = 0.48). The average lifespan was significantly shorter in 2005 (9 days) than in 2003 (13 days; *t* = 5.86, *P* < 0.0001), though this difference was not apparent when only females that laid eggs were compared (12 and 13 days, respectively; t = 1.5, P = 0.13). Whether or not a female had been observed to mate affected the probability of egg laying (Table 2). A significant interaction between year and mating status indicated that this effect was stronger in 2003. In 2005, some females that had been observed to mate did not lay eggs. Females that eclosed later in the season were

 Table 2
 Effects of female traits and year on whether or not she laid eggs (logistic regression)

| Factor | df | χ^2 | P-value |
|------------------------|-------|----------|----------|
| Lifespan | 1,171 | 16.48 | < 0.0001 |
| Time of eclosion | 1,171 | 9.89 | < 0.0002 |
| Mated or not | 1,171 | 10.25 | < 0.0002 |
| Year | 1,171 | 13.26 | 0.0003 |
| Year \times Lifespan | 1,171 | 7.49 | 0.0062 |
| Year \times Mated | 1,171 | 4.77 | 0.0289 |
| | | | |

more likely to lay eggs than females that eclosed early (Table 2). Years differed significantly from each other, egg laying being significantly more common in 2003 than in the other years. In 2004, lifespan was the only significant factor that affected whether a female laid eggs or not.

Lifetime egg production

Lifespan had a significant positive effect on lifetime egg production in all years (Fig. 1a; Table 3). In 2005, females that eclosed earlier in June (release date) had lower lifetime egg production than females that eclosed later in June (Fig. 1b; Table 3). Release date did not affect lifetime egg production in 2003 or 2004.

The number of matings affected fecundity in 2005, with multiply mated females producing more eggs than singly mated females (Fig. 2a; Table 3). This effect was especially clear when data for females that lived less than 10 days were omitted (ANCOVA, $F_{1,30} = 9.32$, P < 0.004, Fig. 2b). Further analysis suggested that the second mating per se may have not increased lifetime egg production, as females that mated twice or more often had higher cumulative number of eggs laid already prior to their second mating

(Fig. 2c). Number of matings did not affect female fecundity in 2003 (not possible to analyse with the 2004 data).

Heavier females were more likely to mate twice than lighter females in both 2003 and 2005 (logistic regression, P = 0.033 and P = 0.061, respectively), but weight did not affect lifetime egg production (Table 3). Neither individual mobility nor the population age affected the likelihood of mating multiple times (logistic regression, mobility, P = 0.364, and P = 0.109; population type, P = 0.397 and P = 0.345, respectively, for 2003 and 2005).

The average egg weight was 0.082 mg (SD = 0.009), based on 136 egg clutches laid by 58 females. Heavier eggs had significantly higher hatching rate than lighter ones, indicating the importance of egg quality for female fitness (linear regression, $F_{1,145} = 4.01$, P < 0.05). There was no significant correlation between average egg weight and lifetime egg production (r = -0.016, P = 0.913) or between average egg weight and clutch size (r = 0.112, P = 0.172). One third (34%) of the variation in egg weight was due to variation among females, but no trait measured in this study was significantly related to egg mass (weight of the female, female age, mobility, population type, and oviposition temperature).



Fig. 1 Effect of female lifespan (a) and date of eclosion (b) on lifetime egg production in 2005

Table 3 Effects of female traits on lifetime egg production (analysis of covariance) in females that laid eggs^{a,b}

| Factor | 2003 | | 2004 | 2004 | | 2005 | |
|----------------------------|-----------------|---------|-----------------|-----------------|-----------------|-----------------|--|
| | <i>F</i> -value | P-value | <i>F</i> -value | <i>P</i> -value | <i>F</i> -value | <i>P</i> -value | |
| Mobility | 2.98 | 0.090 | 0.05 | 0.469 | 0.02 | 0.884 | |
| Weight | 2.29 | 0.136 | 3.70 | 0.064 | 0.73 | 0.398 | |
| Lifespan | 37.99 | < 0.001 | 10.35 | 0.003 | 52.52 | < 0.001 | |
| Release date | 2.91 | 0.094 | 2.47 | 0.126 | 8.01 | 0.007 | |
| Number of matings | 2.93 | 0.093 | n.a. | n.a. | 4.41 | 0.019 | |
| Population type | 0.75 | 0.390 | 3.07 | 0.089 | 0.36 | 0.549 | |
| Mobility × Population type | 1.88 | 0.176 | 5.6 | 0.024 | 14.41 | < 0.001 | |

^a Analysis weighted by the number of observations of each female to increase the accuracy of the measure of mobility (results were not essentially different without weighting)

^b df were 1,54, 1,31 and 1,39 for 2003, 2004, and 2005, respectively



Fig. 2 Lifetime egg production against lifespan in females that mated only once (*closed symbols*) and for females that mated more than once (*open symbols*); **a** for all females and **b** for females that lived longer than 10 days. **c** Cumulative number of eggs laid against age in females that mated only once (*circles*) and for females that mated twice (*squares*) prior (*open*) and subsequent (*closed*) to their second mating in 2005

There was a significant difference in mobility as measured in the cage between females from newly-established versus old populations only in 2003 (GLM, $F_{1,64} = 4.28$, P < 0.03; in 2004 and 2005, $F_{1,69} = 0.75$, P = 0.27 and $F_{1,113} = 1.65$, P = 0.21, respectively). Though neither

mobility nor population type (newly-established versus old) had a significant main effect on lifetime egg production, there was a consistent interaction between these two variables, which was also statistically significant in 2004 and 2005 (Fig. 3; Table 3). Thus in newly-established populations mobile females had higher lifetime egg production than less mobile females, whereas in old populations there was no such effect. When females in 2005 from old populations were analysed separately, a significant interaction suggested that highest egg production was obtained by long-lived sedentary females (lifespan, $F_{1,26} = 21.41$, P < 0.0001; mobility, $F_{1.26} = 2.91$, P = 0.099; lifespan \times mobility, $F_{1.26} = 4.31$, P < 0.05). The interaction between mobility and lifespan was not significant in newlyestablished populations ($F_{1,25} = 0.03$, P = 0.854), but both lifespan and mobility had significant main effects on lifetime egg production (lifespan, $F_{1,25} = 13.25$, P < 0.002; mobility, $F_{1,25} = 7.35$, P < 0.02).

Discussion

Studies on wing-dimorphic insects have routinely demonstrated negative phenotypic and genotypic correlations between dispersal and reproduction (Calow 1979; Mole and Zera 1993, 1994; Roff 2002; Roff and Fairbairn 2007; Zera and Harshman 2001). In contrast, the present results strongly suggest that there is no general trade-off between dispersal and reproduction in the Glanville fritillary. This conclusion is based on the following results. Firstly, lifetime egg production and individual mobility as measured in the cage were not negatively correlated. Admittedly, negative phenotypic correlation between dispersal and reproduction could be masked by favourable environmental conditions, as trade-offs are often more pronounced or appear only under unfavourable environmental conditions (Zera and Harshman 2001).

Secondly, more mobile females actually initiated reproduction earlier, not later, than the more sedentary females (in terms of mating in 2003 and oviposition in 2004 and 2005). Similarly, in a 2-year study conducted in the same population cage, a genetic correlation, even though not significant, between mobility and age at first reproduction indicated that more mobile females start reproducing at a younger age than more sedentary females (M. Saastamoinen, in preparation). Age at first reproduction is a key life history trait that often correlates with female lifetime fecundity (e.g. Roff and Fairbairn 1991).

Thirdly, previous studies have shown that females from newly-established populations are generally more dispersive in the field than old-population females (based on mark–release–recapture studies; Hanski et al. 2002, 2004) and the former have a higher flight metabolic rate (Haag



Fig. 3 Effect of mobility on lifetime egg production in females from newly-established (*open symbols*) and old populations (*closed symbols*) in 2003 (**a**), 2004 (**b**) and 2005 (**c**). See also Table 3

et al. 2005), which is correlated with dispersal rate (K. Niitepõld et al., in preparation). Yet in the present experiment there was no difference in the lifetime egg production between the two population types. However, there was a consistent and significant (in 2 out of 3 years) interaction between mobility and population age in affecting reproduction: in new populations, lifetime fecundity was positively correlated with mobility, while in old populations there was a significant interaction between lifespan and mobility, such that long-lived more sedentary females had the highest lifetime egg production.

Why should the more mobile females reproduce earlier and have higher lifetime fecundity in new populations? Increased mobility may allow increased food intake, not only to compensate for the energetic cost of extra mobility but also to increase the rate of egg maturation, allowing more mobile females to lay earlier and to lay larger clutches. Haag et al. (2005) showed that females from newly-established isolated populations, which are known to be particularly mobile (Hanski et al. 2004, 2006), have a higher flight metabolic rate than females from old populations. High metabolic rate could also contribute to high egg maturation rate and/or high oviposition rate. I hypothesize that the lower flight metabolic rate of females in old populations is somehow related to a lack of positive association between mobility and egg production in these females.

The observation of a dissimilar relationship between mobility and lifetime fecundity in females from newlyestablished versus old populations is reminiscent of some previous results comparing dispersive versus sedentary species/populations. There are intriguing interspecific differences in life history syndromes between two species of Tribolium, Tribolium castaneum and Tribolium confusum (Lavie and Ritte 1978). Selection experiments have shown that in T. castaneum, which is considered a "primary colonist", high dispersal rate is positively correlated with high fecundity, whereas in T. confusum, a "secondary colonist", there is no such correlation (Lavie and Ritte 1978; Ziegler 1976). Palmer and Dingle (1989) have demonstrated similar differences between a migratory (from Iowa) and nonmigratory (from Puerto Rico) strain of the milkweed bug O. fasciatus. In a selection experiment they found that the migratory population exhibited positive correlated responses in long-duration flight and early reproduction, while there was no similar correlation in the non-migratory population (Dingle et al. 1988; Palmer and Dingle 1989). In the present study, the difference appears between local populations of different ages in the same metapopulation.

The positive correlation between dispersal and reproduction in generally dispersive species or populations has been explained by the selective advantage of such correlation due to increased success while colonizing new habitats (Dingle et al. 1988; Lavie and Ritte 1978). In the present study, the most mobile individuals in the newly-established populations are likely to represent the most fit individuals, which are able to endure the energetic cost of high activity. While high dispersal rate is essential for populations and species with frequent colonisations, high dispersal rate is not essential for individuals living in more permanent populations. Instead, selection may favour individuals with other fecundity-related life history traits, for instance increased longevity, as indicated by the present results for females in old populations.

Even though no support for a general trade-off at the phenotypic level between mobility and reproduction was found in the present study, mobility or dispersal capacity is surely not a cost free behaviour in the Glanville fritillary butterfly. Correlation studies cannot unambiguously indicate whether or not traits interact functionally (Zera and Harshman 2001), and therefore internal (functional) trade-offs between dispersal and reproduction are still possible. As a matter of fact, a previous study on the Glanville fritillary demonstrated reduced potential fecundity (number of oocytes at eclosion) in females from newly-established populations compared with females from older populations (Hanski et al. 2004). The present results demonstrate that this apparent trade-off is not substantial enough to be expressed at the level of lifetime fecundity under natural environmental conditions, because females rarely live long enough to lay all the eggs they have at eclosion (see also Hanski et al. 2006).

Another evident cost of high mobility, though not a physiological one, is increased time spent in the matrix outside habitat patches by the more mobile females (Hanski et al. 2006). This is likely to decrease the lifetime fecundity of the more mobile females as it means less time for oviposition (Hanski et al. 2006) and may increase mortality. Hanski and Saccheri (2006) recently demonstrated that the allelic composition of the glycolytic enzyme phosphoglucose isomerase, which is known to affect flight metabolic rate and some life history traits in the Glanville fritillary (Haag et al. 2005), affects the growth of local populations. In small populations in small habitat patches the more dispersive females have higher lifetime egg production than the more sedentary females, whereas in large populations the more dispersive types performed worse, possibly due to their shorter lifespan and shorter residence time (Hanski and Saccheri 2006).

The new-population females were more mobile in the cage than the old-population females, as expected, in 2003 but not in 2004 and 2005. The non-significant difference between population types in 2004 and 2005 may be due to the butterfly material. In 2004, most mobile females from newly-established populations may have dispersed away from the natal patch before butterflies were sampled for the experiment (see Materials and methods). In 2005, the populations from which larvae were sampled had much higher connectivity (59 and 110 for new and old populations, respectively; for more details see Hanski et al. 2004) than in 2003 and 2004 (13 and 58 in 2003 and 12 and 26 in 2004), reflecting natural variation in the sizes and numbers of local populations. Previous studies on the Glanville fritillary have shown that the difference in dispersal rate (Hanski et al. 2004) and flight metabolic rate (Haag et al. 2005) is most evident between isolated newly-established and old populations. Furthermore, the mobility measure used in the cage is affected by environmental factors, and hence poor weather conditions may mask differences between population types that would be expressed under other conditions.

Other individual traits and lifetime fecundity

Several other traits apart from mobility affected lifetime fecundity. Consistent with other studies on insects (e.g. Boggs and Freeman 2005; Carroll and Quiring 1993), lifespan was the key determinant of both the likelihood of oviposition and the cumulative number of eggs laid. Time of eclosion affected lifetime fecundity with some variation among the years, most likely due to between-year variation in weather conditions.

A positive correlation between pupal and/or adult weight and fecundity is well documented in Lepidoptera (Tammaru et al. 1996, 2002), and is often explained by larger individuals having more space for eggs (Roff 2002). In the Glanville fritillary previous studies have demonstrated a positive correlation between body size and potential fecundity (number of oocytes at eclosion) but in the present study no relationship was observed between body size and lifetime egg production. Apparently, most females do not live long enough to run out of eggs (Hanski et al. 2006). Greater body size means more resources, in absolute terms, but females may be able to supplement their body reserves by food intake, in which case the importance of resources obtained during larval development (reflected in body weight) become less important (Boggs 1997).

In Lepidoptera, the relationship between fecundity and the number of matings varies between species (Bergström and Wiklund 2002; Jimenez-Perez et al. 2003; Karlsson 1998). In the present study around 20% of the females mated more than once. This figure is slightly higher than in a previous study (>10%) that was based on spermatophore counts in field-collected females (Kuussaari et al. 1998). In any case, is mating more than once beneficial for lifetime fecundity of female Glanville fritillary? The present results suggest no detectable benefit of multiple mating, as in 2003 no benefit was observed and it appears that females that mated multiply in 2005 would have obtained higher lifetime fecundity even without the second mating (Fig. 2c). The benefit of multiple mating can also be condition-dependent (Jimenez-Perez et al. 2003).

Another key life history trait apart from the number of eggs produced that is generally thought to be closely related to fitness is egg size (Fischer et al. 2002; Fox and Czesak 2000). Despite considerable variation in egg size among females, no apparent trade-off between egg size and any other life history trait measured here was observed. None-theless, fitness benefits due to larger eggs were indicated by clutches with larger eggs having higher hatching rate.

Conclusion

Several traits affect the lifetime number of eggs produced by female Glanville fritillary butterflies, with lifespan having the greatest effect. These results demonstrate that there is no general trade-off between reproduction and dispersal in the Glanville fritillary. To the contrary, more mobile females tend to start reproduction at younger age than more sedentary females. There is a significant interaction between mobility and population type, such that in newly-established populations the more mobile females have higher lifetime egg production whereas in old populations no such relationship is apparent. This result points to dissimilar selection on mobility between newlyestablished and old populations, which may maintain variation in dispersal rate in the metapopulation as a whole.

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