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Flight metabolic rate has contrasting effects on dispersal in the two sexes of the Glanville fritillary butterfly

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Abstract Evolution of dispersal is affected by context-specific costs and benefits. One example is sex-biased dispersal in mammals and birds. While many such patterns have been described, the underlying mechanisms are poorly understood. Here, we study genetic and phenotypic traits that affect butterfly flight capacity and examine how these traits are related to dispersal in male and female Glanville fritillary butterflies (*Melitaea cinxia*). We performed two mark–recapture experiments to examine the associations of individuals' peak flight metabolic rate (MR_{peak}) and *Pgi* genotype with their dispersal in the field. In a third experiment, we studied tethered flight in the laboratory. MR_{peak} was negatively correlated with dispersal distance in males but the trend was positive in females, and the interaction between MR_{peak} and sex was significant for long-distance dispersal. A similar but nonsignificant trend was found in relation to molecular variation at *Pgi*, which encodes a glycolytic enzyme: the genotype associated with high MR_{peak} tended to be less dispersive in males but more dispersive in females. The same pattern was repeated in the tethered flight experiment: the relationship between MR_{peak} and flight duration was positive in females but negative in males. These results suggest that females with high flight capacity are superior in among-population dispersal, which facilitates the spatial spreading of their reproductive effort. In contrast, males with high flight capacity may express territorial behaviour, and thereby increase the number of matings, whereas inferior males may be forced to disperse. Thus, flight capacity has opposite associations with dispersal rate in the two sexes.

Keywords Insect · Mate location · Sex-biased dispersal · Mobility · Phosphoglucose isomerase

Introduction

Dispersal is a highly variable life-history trait (Ronce 2007). One example of variability in dispersal is sex-biased dispersal, in which one sex tends to disperse more often or further than the other one (Perrin and Mazalov 2000). Males are typically the more dispersive sex in mammals, whereas females are more dispersive in birds (Greenwood 1980). Natal dispersal and philopatry have been linked to differences in mating systems, and it has been argued that monogamy would favour female-biased dispersal and polygamy male-biased dispersal (Greenwood 1980). This hypothesis may not fully explain the observed complexity of sex-biased dispersal (Lawson Handley and Perrin 2007), but in general sex-biased dispersal is expected to evolve when the costs and benefits of dispersal differ between the two sexes (Gros et al. 2008).

Variation in dispersal rate may occur between the sexes but also among individuals of the same sex. An extreme case is wing-dimorphism in insects, exemplified by short-winged or entirely wingless versus long-winged planthoppers and sand crickets (Roff and Fairbairn 2007; Zera and

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Denno 1997). Leg length in cane toads (Phillips et al. 2006) and shrews (Hanski et al. 1991) and relative flight muscle mass in butterflies (Hill et al. 1999a, b) represent more subtle morphological variation linked to dispersal. Variation in dispersal capacity may also be related to physiological traits, such as flight metabolic rate. In the Glanville fritillary butterfly (*Melitaea cinxia*), flight metabolic rate and dispersal distance were positively correlated in free-flying females tracked with harmonic radar in the field (Niitepõld et al. 2009), and other data support the hypothesis that high flight metabolic rate is associated with the tendency to disperse and establish new populations. Thus, in comparison with females originating from old local populations, females originating from newly-established populations have a higher flight metabolic rate (Haag et al. 2005) and a higher [ATP]/[ADP] ratio in their flight muscles after forced flight, suggesting high physiological flight capacity (Hanski et al. 2004). As mobility (in a large population cage) has been shown to have high heritability (Saastamoinen 2008), the above results can be best explained by new-population females having inherited their superior flight capacity from their mothers, who established the population following long-distance dispersal. There is thus both indirect and direct evidence for an association between flight metabolic rate and dispersal rate in female Glanville fritillary butterflies.

Here, we compare the effect of individual flight capacity on realised dispersal rate in the two sexes of the Glanville fritillary. In most insects, flight is used for practically all fitness-related processes, including foraging, escaping predators, mate location, searching for oviposition sites, and dispersal among populations. Mated females that disperse over a long distance may establish a new population, and by dispersing during the reproductive period they reduce competition among their offspring. In contrast, males spend most of their time in locating mates often within one population, either by perching and waiting or by patrolling the population in search of females (Davies 1978; Scott 1974; Wickman and Wiklund 1983). The question we ask here is whether the apparently different functions of flight in the two sexes affect the relationship between flight capacity and dispersal distance in the field. Flight capacity was measured as the peak flight metabolic rate (MR_{peak}) using flow-through respirometry. We also examined the association between dispersal distance and molecular variation in the gene phosphoglucose isomerase (*Pgi*), which has been found to be related to flight performance and related fitness traits in *Colias* butterflies (Watt 1983; Watt et al. 2003). In female Glanville fritillaries, *Pgi* genotype explains variation in flight metabolic rate and mobility (Haag et al. 2005; Niitepõld 2010; Niitepõld et al. 2009; Saastamoinen and Hanski 2008).

Materials and methods

Mark–recapture studies

A mark–release–recapture experiment was conducted on the small (1.6 km^2) island of Husö in the east Åland archipelago in southwest Finland. There is no native population of the Glanville fritillary on this isolated island though there are suitable habitat patches in the form of rocky outcrops and meadows maintained by sheep grazing. Altogether 77 habitat patches with the larval host plant *Plantago lanceolata* and nectar plants were identified in spring 2005.

The butterflies used in this study originated from the Åland Islands and from the island of Saaremaa in West Estonia and were reared in common garden conditions. Altogether 449 butterflies (234 males, 215 females) were individually marked on the underside of the hind wing after eclosion and released into 16 habitat patches between 6 and 20 June 2005. All habitat patches were searched for butterflies once a day until the end of the flight season with a search effort of 100 m^2 per min. The location and the identity of each encountered butterfly were recorded. A subset of 97 individuals was collected from the field for the measurement of flight metabolic rate (below). These latter butterflies were fed with 25% honey water ad libitum on the day of capture to reduce differences in their physiological condition. Individuals spent the night in a covered cage outdoors and were moved indoors 1 h before the measurement. After the measurement, butterflies were returned to the habitat patch in which they had been collected.

Two measures of dispersal were calculated from the mark–recapture results for each individual: the observed number of movements between habitat patches and the sum of the respective movement distances.

The second mark–recapture experiment was conducted in 2006 by capturing and marking butterflies in a natural metapopulation living in a network of 55 habitat patches in Saltvik in the north-eastern part of the main Åland island. The study area is 5 × 4 km in size and consists mainly of agricultural fields, but there are also small stands of forest and water bodies, roads and small villages. Every habitat patch was searched by two persons during the adult flight season using the effort of 270 m^2 per min. A small wing sample (2 × 1 mm) was taken from every individual for genotyping (below). Dispersal was characterised by the same measures as in the first experiment: the number of observed movements among populations and the sum of the respective movement distances.

Tethered flight

To examine the relationship between MR_{peak} and flight endurance, we performed a tethered flight experiment in

Fig. 1 A male Glanville fritillary (*Melitaea cinxia*) flying attached to a tether in the laboratory. Photograph by Rebecca Nesbit

the laboratory. Butterflies were the offspring of butterflies collected in the Åland Islands as larvae, reared in common garden conditions and mated in an experiment in an outdoor cage. The experimental butterflies were taken as pupae to Rothamsted Research, UK, where the experiment was performed. The butterflies were kept in flight cages for the first day after eclosion and allowed to use their flight muscles and pump out excess meconium. The flight metabolic rate was measured on the following day (below). Butterflies were not fed before the metabolic measurement but were fed immediately after it. The tethered flight experiment took place on the third day after eclosion.

In the experiment, the butterfly was fixed to a vertical rod with a horizontal loop at the tip using super glue (Fig. 1). The butterfly was hung inside a large white plastic cylinder with a light source above (one bulb emitting visible light, one emitting UV light). A laminar air flow was directed at the butterfly from below to stimulate flight. The ambient air temperature inside the cylinder was controlled using a heater which warmed the air blown at the butterfly. If an individual did not start flying spontaneously, we placed a finger under the butterfly and then removed it, after which the butterfly typically started to fly. The process was repeated when needed. The time at the start and at the end of each flight burst was recorded. In the analysis, we used the total amount of flight during a period of 5 min, starting from the first flight burst.

Flight metabolic rate

The flight metabolic rate was measured using flow-through respirometry (see Niitepõld et al. 2009 for details). CO_2 free dry air was pumped through a 1-L transparent jar at the rate of 1.0 L min^{-1}. Individuals were flown for 10 min by gently shaking or tapping the respirometry chamber whenever the butterfly landed on the walls of the jar. The jar was kept under a UV light source and the measurement temperature was kept constant using an electric heater. The jar was covered with a black cloth before and after the experiment to obtain a stable baseline of resting metabolic rate.

The average measurement temperature was 32.9°C (SD = 0.6) for the individuals in the first mark–recapture experiment and 32.2°C (SD = 0.7) in the tethered flight experiment. MR_{peak} was corrected for variation in body mass by regressing the peak flight metabolic rate against pupal mass and using the residuals in the analyses. Measurement temperature and the time of the day when the measurement was performed had no significant effect on peak flight metabolic rate. Individuals were measured in random order.

Genotyping

We genotyped two single nucleotide polymorphisms (SNPs) in the coding region of the *Pgi* gene. These SNPs, denoted as AA111 and AA361, have been described by Orsini et al. (2009), who demonstrated the relationship between the SNPs and allozyme alleles that have been used in previous studies on the Glanville fritillary (Haag et al. 2005; Hanski and Saccheri 2006). The combination of the two SNPs identifies the *f* allozyme allele, which has been shown to be associated with phenotypic variation in several life-history traits in the Glanville fritillary (Haag et al. 2005; Orsini et al. 2009; Saastamoinen 2007a). We define the *Pgi-f* genotype as the combination of the bases AC or CC in AA111 and CT or TT in AA361, while *Pgi*-non-*f* includes the remaining genotypes (Orsini et al. 2009). Genotyping was conducted as described by Orsini et al. (2009).

Statistical analyses

We used randomisation tests to examine the effects of MR_{peak} and *Pgi* genotype on dispersal using code written in R Version 2.8.1 (R Development Core Team, 2008). In the case of MR_{peak} in the first mark–recapture experiment, we analysed the slope of the linear regression of the number of between-patch movements made by the butterfly or the total distance moved against metabolic rate. Altogether 50,000 randomisations were performed separately for males and females. In the randomisations, we randomly shuffled the metabolic data with respect to the capture history data and then re-calculated the regression slope. This yielded a distribution of the regression slopes under the assumption that the metabolic rate and the two dispersal measures are not related, allowing the calculation of the probability of the observed slope. The significance of the

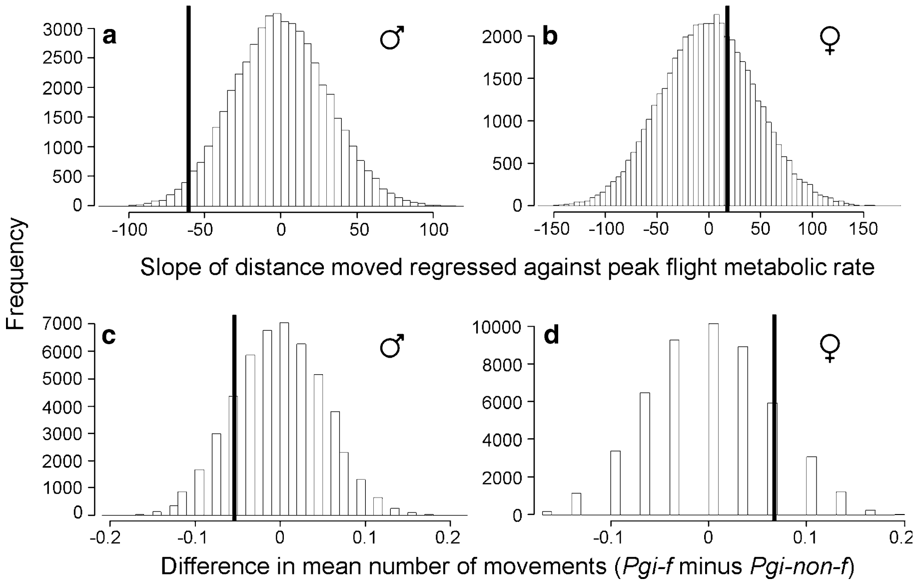

Fig. 2 Effects of peak flight metabolic rate ($\mathrm{MR}_{\mathrm{peak}}$) (*upper row*) and *Pgi* genotype (*lower row*) on dispersal. The *thick black lines* show the empirical values, the *histogram bars* give the distribution of randomised data. **a** $\mathrm{MR}_{\mathrm{peak}}$ correlated negatively with the distance moved ($P = 0.038$) in males, **b** whereas no significant relationship ($P = 0.68$) was found in females. **c** The number of movements observed tended to be lower in *Pgi-f* males than in *Pgi*-non-*f* males, **d** whereas in females the number of movements tended to be higher in *Pgi*-non-*f* individuals. The *Pgi* genotypic effects were not statistically significant

sex by metabolic rate interaction was calculated based on the difference in the respective slopes for males and females.

In the second mark–recapture experiment involving the determination of the *Pgi* genotype, we examined the null hypothesis that the means of the number of between-population movements and the total movement distance are the same for the *Pgi-f* and *Pgi*-non-*f* genotypes. The individual capture histories were randomly divided into two groups of the same size as the original genotype groups. For each of 50,000 randomisations, the difference in the mean number of movements and the mean total movement distance for the two groups were calculated. The probability of the observed value was calculated as above. To examine the genotype by sex interaction for the mean number of movements the following test statistic was used:

$$\left[\mathrm{Mov}(f)_{\mathrm{f}} - \mathrm{Mov}(\text{non-}f)_{\mathrm{f}}\right] - \left[\mathrm{Mov}(f)_{\mathrm{m}} - \mathrm{Mov}(\text{non-}f)_{\mathrm{m}}\right], \qquad (1)$$

where Mov (*f*) and Mov (non-*f*) give the mean number of movements in the randomised data for the *Pgi-f* and *Pgi*-non-*f* individuals, respectively, and the subscripts m and f indicate males and females.

Results

Flight metabolic rate and dispersal

Of the 449 butterflies released in the first experiment, 219 individuals (49%) were recaptured at least once during the study. Females had a slightly higher recapture rate (50%) than males (47%). Of the recaptured butterflies 89 were recorded in a different habitat patch than the release patch. These dispersers consisted of 41 females and 48 males, and thus, of the recaptured individuals, 19% of the females and 21% of the males dispersed. Among the dispersed individuals, the average sum of movement distances was 198 ± 152 m (SD) for males and 279 ± 203 m for females. The difference was significant ($F_{1,87} = 4.59$, $P = 0.03$).

The number of movements was positively related to $\mathrm{MR}_{\mathrm{peak}}$ in females and negatively in males, though these relationships were not significant ($P = 0.16$ and 0.60 for males and females, respectively, $P = 0.22$ for the interaction). The distance moved was negatively and significantly related to $\mathrm{MR}_{\mathrm{peak}}$ in males ($P = 0.038$; Fig. 2a) but not in females ($P = 0.68$). The sex by $\mathrm{MR}_{\mathrm{peak}}$ interaction was not statistically significant ($P = 0.15$).

The majority of the individuals were only observed in the release patch or moved a very short distance (Fig. 3a). To examine variation among individuals performing long-distance dispersal, we selected the individuals that moved a distance longer than the median (170 m). The distance moved was regressed against the age of the butterfly at the time of the last movement event and we used the residuals from this highly significant relationship ($t_{96} = 9.13$, $P < 0.0001$) as a measure of long-distance dispersal rate. Females had higher dispersal rate than males ($F_{1,27} = 4.25$, $P = 0.049$) and the main effect of $\mathrm{MR}_{\mathrm{peak}}$ was significant ($F_{1,27} = 4.42$, $P = 0.045$). The relationship between $\mathrm{MR}_{\mathrm{peak}}$ and dispersal rate was positive in females but negative in males, and the

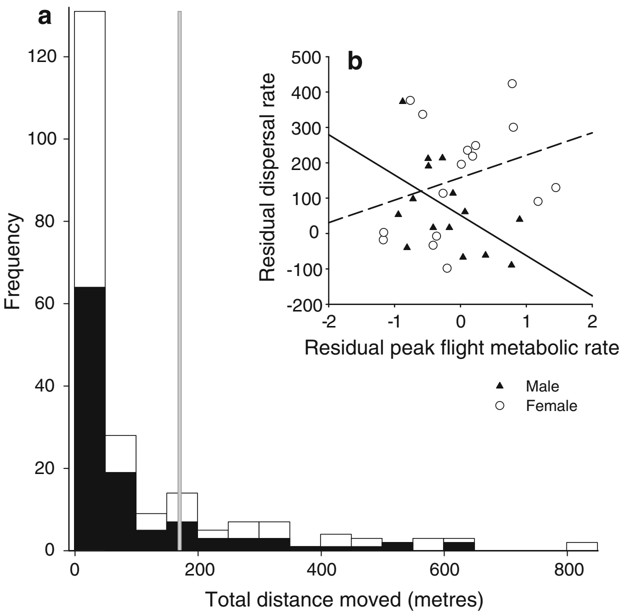

Fig. 3 **a** Frequency distribution of distances moved in the mark–recapture experiment involving the measurement of metabolic rate. *Black bars* represent the proportion of males, *white bars* the proportion of females. The effect of MR_{peak} on long-distance dispersal was examined among individuals that moved longer than the median of the distances moved (*grey line*). **b** Among these individuals, males showed a negative relationship between MR_{peak} (adjusted for pupal mass) and residual dispersal rate (distance adjusted with the age of the butterfly at the last movement event), whereas females showed a positive relationship. The interaction was significant ($F_{1,27} = 4.91$; $P = 0.035$)

interaction between MR_{peak} and sex was significant ($F_{1,27} = 4.91$, $P = 0.035$).

Pgi genotype and dispersal

In the second experiment, we captured and marked 334 individuals (122 females, 212 males), of which 45% of the females and 54% of the males were recaptured at least once. Ten (8.2%) females and 23 (10.8%) males were observed to have moved to another habitat patch during this experiment. There was no difference ($F_{1,31} = 0.368$; $P = 0.55$) between the sexes in the lifetime movement distance [544 ± 631 m (SD) in females and 675 ± 589 m in males].

Females with the *Pgi-f* genotype moved more frequently between the habitat patches than *Pgi*-non-*f* females, whereas in males the genotypic effect was the opposite (Fig. 2c–d), though the sex by genotype interaction was not statistically significant ($P = 0.15$). The results were qualitatively the same for the total movement distance ($P = 0.54$ for the interaction). The small numbers of among-population movements did not allow a separate analysis of long-distance dispersers in this experiment.

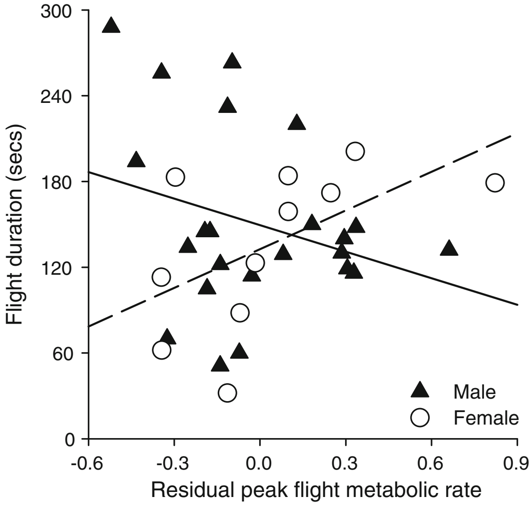

Fig. 4 Duration of the tethered flight versus MR_{peak} (adjusted for pupal weight) in males (*triangles*, *solid line*) and females (*circles*, *dashed line*). There was a significant interaction between sex and MR_{peak} ($F_{1,30} = 4.91$; $P = 0.035$)

Flight metabolic rate and the duration of tethered flight

There was a positive relationship between MR_{peak} and flight duration in females and a negative trend in males (Fig. 4). The interaction between sex and MR_{peak} was significant ($F_{1,30} = 4.91$; $P = 0.035$). The two sexes did not differ in their flight duration ($P = 0.44$) and the main effect of MR_{peak} on flight duration was not significant ($P = 0.68$).

Discussion

We examined the effects of flight metabolic rate and molecular variation in the *Pgi* gene on dispersal in the field and in tethered flight experiments in the laboratory. The results were systematically consistent across the three experiments though not all test results were statistically significant ($P < 0.05$): males with high MR_{peak} were less dispersive than males with low MR_{peak}, whereas in females, the pattern was reversed. A similar trend was seen with *Pgi* genotype: the *Pgi-f* genotype associated with high flight metabolic rate (Haag et al. 2005; Niitepõld 2009, 2010) was less dispersive in males but more dispersive in females. To assess the overall significance of the results, we summarised the probabilities of the three experiments using Fisher's sum of logs method (Becker 1994). The combined sex by flight capacity interaction was significant ($P = 0.03$) for the number of between-population movements in the two mark–recapture experiments and the duration of flight in the tethered flight experiment. Using the total distance moved as the measure of dispersal in the mark–recapture experiments yielded the summarised P value of 0.06. The analysis of long-distance dispersal rate was not included in the analysis of summarised probabilities as the data were not independent.

The positive trends between $\mathrm{MR}_{\mathrm{peak}}$ and dispersal in females are in accordance with previous studies on the Glanville fritillary. Haag et al. (2005) showed that females from isolated newly-established populations have a higher flight metabolic rate than females from old populations and that the frequency of the PGI allozyme allele *f* (corresponding to *Pgi-f* in SNPs, see "Materials and methods") that is associated with high flight metabolic rate was highest in the new populations. This result implies that females with high flight capacity are the ones that most frequently establish new populations in fragmented landscapes. Niitepõld et al. (2009) demonstrated more directly the relationship between flight metabolic rate, *Pgi* genotype and dispersal rate in females by following free-flying butterflies with a scanning harmonic radar. Flight metabolic rate showed a strong positive correlation with female mobility, and the differences in the mobility of the *Pgi* genotypes were clear in low to moderate ambient temperatures (Niitepõld et al. 2009).

A key function of flight in female butterflies in fragmented landscapes is dispersal among habitat patches and local populations, which reduces kin competition among the offspring and may lead to the establishment of new local populations with positive fitness consequences (Heino and Hanski 2001). Evolutionary models constructed for the Glanville fritillary suggest that selection favours high dispersal rate in habitat patch networks in which local populations have a high risk of extinction (Heino and Hanski 2001; Zheng et al. 2009).

The relationship between flight capacity and dispersal is different in males. Previous studies finding association between mobility and population age in females have failed to detect similar association in males (Hanski et al. 2004, 2006). Heritability of mobility in a population cage was strong from the mother to her female offspring but not to the male offspring (Saastamoinen 2008). Here, we found a contrasting pattern in the two sexes in the relationship between flight metabolic rate and mobility, as the most mobile males were the ones with low $\mathrm{MR}_{\mathrm{peak}}$.

The negative correlation between flight metabolic rate and realised dispersal in the field in males most likely reflects the different roles of flight in the two sexes. In males, the primary function of movements is to locate mates. Male butterflies have been classified as perchers employing a sit-and-wait strategy, and patrollers, which perform within-population searching flights (Scott 1974). The two mate location strategies require different types of flight. Perching males need to take off rapidly and either chase away intruding males or persuade females to mate. Patrollers spend significantly longer periods airborne and fly at low speeds. The different requirements for flight appear to be reflected in morphology. Interspecific comparisons indicate that males in perching species have higher thorax/body mass ratios, higher wing aspect ratios (more slender wings) and higher wing loadings than males in patrolling species (Wickman 1992). Similarly, within the speckled wood butterfly (*Pararge aegeria*), perching males have been shown to possess relatively heavier thoraces than patrolling males (Van Dyck et al. 1997). Flight metabolic rate is greatly affected by thorax mass, because the flight muscles are located in the thorax, but to date no other study has linked flight metabolic rate to the question about mate location strategies.

In the Glanville fritillary, both mate location strategies are used but the majority of males appear to be perchers in the well-studied Finnish population (Wahlberg 2000). Our findings suggest that males with high $\mathrm{MR}_{\mathrm{peak}}$ exhibit territorial behaviour successfully and therefore move little at the landscape level. In contrast, weaker males may be forced to disperse due to their low competitive ability. In *Pararge aegeria*, there is an indication that males that lose contests with other males end up being more mobile without following a true patrolling strategy (Bergman and Wiklund 2009). Success in male–male contests has been explained by a simple 'resident wins' rule (Bergman et al. 2007; Davies 1978; Kemp and Wiklund 2001), but in some butterflies morphological traits such as body mass (Martinez-Lendech et al. 2007; Peixoto and Benson 2008) have been shown to influence the outcome of aerial contests (though see Kemp et al. 2006). In some territorial insects, the outcome of contests and male mating success may correlate with energy reserves (Marden and Rollins 1994; Otronen 1995). In dragonflies, a male's ability to defend a territory and gain mates has been shown to be compromised when infected with parasites (Marden and Cobb 2004). Infected males adopt a satellite strategy and keep moving between occupied territories, and thus the inferior males end up moving longer distances than the superior males, a similar situation to that inferred from our results.

The results of the tethered flight experiment imply that males with low $\mathrm{MR}_{\mathrm{peak}}$ can nonetheless sustain flight for prolonged periods. Therefore, low $\mathrm{MR}_{\mathrm{peak}}$ of these individuals may not be a sign of poor performance but rather an adaptation for prolonged flight. Such an adaptation could be based on morphological traits such as a lighter body structure with low flight muscle mass, as described for patrolling butterflies by Wickman (1992). Behavioural adaptations such as flight at low speed could potentially reduce the cost of flight. Negative correlation between $\mathrm{MR}_{\mathrm{peak}}$ and flight endurance could also result from individuals with high $\mathrm{MR}_{\mathrm{peak}}$ running out of energy supplies, although there is no indication of this happening in females. In summary, perching males may be adapted to perform fast and agile but short flight bouts (Berwaerts et al. 2008, 2002).

Previous studies have found evidence for female-biased dispersal in the Glanville fritillary (Kuussaari et al. 1996) and related species (Singer and Hanski 2004). Our first mark–recapture study supported sex-biased dispersal, but in the second experiment there was no difference in the mobility of males and females. The two sexes did not differ in their average flight propensity as measured in the tethered flight experiment. Instead, our results support the notion that dissimilar functions are related to the process of dispersal. Previous studies have shown that female mobility is affected by population demography and landscape structure, as females from isolated newly-established populations are particularly mobile (Hanski et al. 2004; Ovaskainen et al. 2008; Saastamoinen 2007b). Our results suggest that the mobility of males is more related to the mating system, which in turn is affected by population density and sex ratio and can also vary between different landscape types (Merckx and Van Dyck 2005; Van Dyck and Matthysen 1999). Thermal conditions have been shown to affect male mate location behaviour at the population level (Ide 2002; Kemp and Rutowski 2001), but the effect is unclear at the individual level.

The finding that the *Pgi* genotype and flight capacity could affect male and female mobility in a dissimilar manner has interesting evolutionary consequences. For instance, it may help explain why the average mobility of female Glanville fritillaries decreases within a few years following the establishment of a new local population (Hanski et al. 2004; Ovaskainen et al. 2008). This has been previously explained by emigration of the most mobile females and higher reproductive fitness of sedentary females (Hanski and Saccheri 2006; Zheng et al. 2009). These factors probably play a role, but the present results suggest that the more mobile phenotype in males may be a genotype that is expressed as a sedentary phenotype in females. Therefore, immigration of males to a newly-established population may contribute to the decline in average female mobility. In addition, the most mobile *Pgi* genotype in females is heterozygous (Niitepõld et al. 2009; Orsini et al. 2009; Zheng et al. 2009), which necessarily introduces ‘sedentary alleles’ into new populations. Finally, the apparent interactions between *Pgi* genotype, sex and ambient temperature (Niitepõld et al. 2009) may constitute an important factor maintaining exceptionally high allelic variation in the coding region of the *Pgi* gene (Orsini et al. 2009).

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Conflict of interest The authors declare that they have no conflict of interest.

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