

Can brief marking campaigns provide reliable dispersal estimates? A Nickerl's Fritillary (*Melitaea aurelia*, Lepidoptera: Nymphalidae) case study

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Functions expressing dispersal probability decays with increasing distance are widely used in studies of animal movements. The inverse power function (IPF) exhibits the property of self-similarity, and hence should perform robustly against variation in marking efforts, allowing comparisons across studies. We investigated this function property using dispersal data of Nickerl's fritillary (*Melitaea aurelia*), a little studied checkerspot butterfly which is currently expanding in Central Europe. During mark-recapture in South Moravia, Czech Republic, a single researcher worked for the entire flight period in 2005, while in 2006 five researchers worked for just 5 days. Slopes of the fitted functions did not differ between the two seasons, illustrating the robustness of the function and suggesting the possibility to obtain reliable dispersal estimates even from brief marking campaigns. For both years, it was predicted that approximately one individual per one thousand would cross 10 km distance, the maximum distance separating the most isolated colonies in the region.

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1. Introduction

The awareness of insect losses from habitat fragments surrounded by human dominated landscapes, such as the intensive farmlands of Western and Central Europe, has raised interest in insect dispersal, or mobility related to gene flow (Habel *et al.* 2009, Hanski & Mononen 2011). Losses from habitat fragments are explicable by the metapopulation theory, which predicts that small local populations are prone to eventual extinctions due to deterministic or stochastic pro-

cesses, unless saved by occasional colonisation (Hanski 1999). Studies on model groups such as butterflies have provided ample evidence that in such isolated populations losses indeed occur (Wenzel *et al.* 2006, Leidner & Haddad 2011). The data amassed in empirical butterfly dispersal studies, using a variety of approaches from classical mark-recapture to molecular and electronic tools, are now allowing broad generalisations which link dispersal to species' life histories and aim to assist practical conservation (Hovestadt & Nieminen 2009, Stevens *et al.* 2010, Sekar 2012).

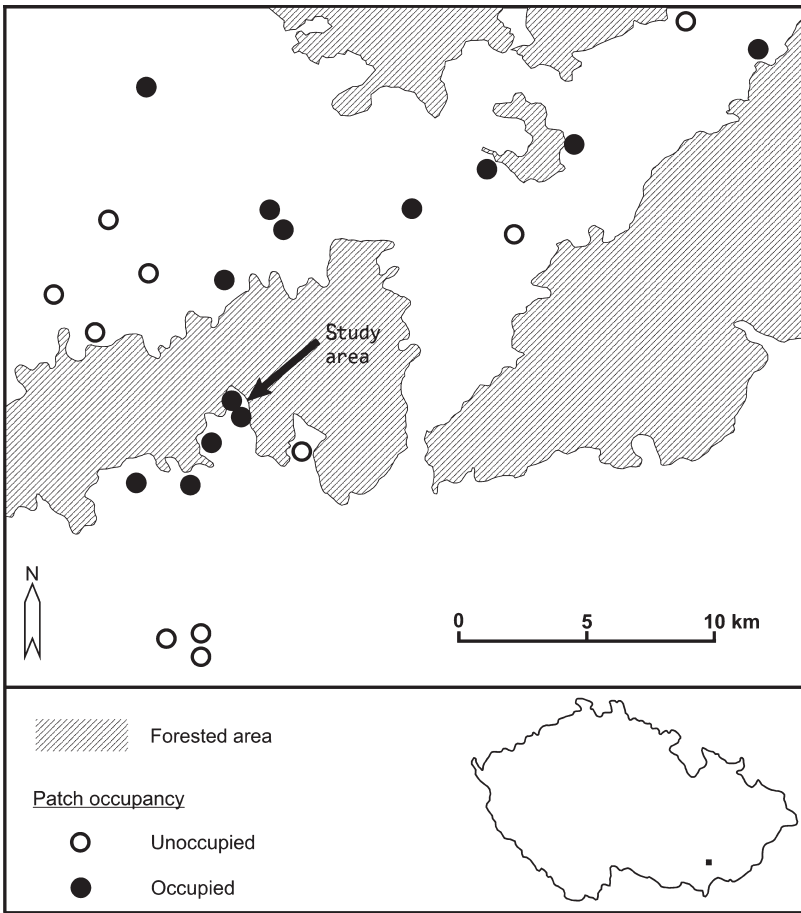


Fig. 1. Schematic representation of Ždánický les hills, Czech Republic, showing the study site, the distribution of xeric grasslands, and their occupancy by *Melitaea aurelia* within the mostly intensively farmed, or forested, area.

Checkerspot butterflies (Nymphalidae: Meliteaeinae) represent a popular model in population ecology (e.g., McLaughlin *et al.* 2002, Hellmann *et al.* 2003, Ehrlich & Hanski 2004, Bulman *et al.* 2007, Zimmermann *et al.* 2011). They often form spatially distinct colonies, are easily detectable both as larvae and adults, are rather poor fliers and occur in high densities. At the same time, they display a remarkable diversity of life history traits (Ehrlich & Hanski 2004), which transfers into varying levels of threat from intensive land use. Some European species are among the most endangered butterflies on the continent (e.g., *Euphydryas maturna*, cf. Freese *et al.* 2007), while others vary in status regionally (e.g. *Melitaea athalia*, cf. Hodgson *et al.* 2009). An interesting case in Central Europe is *Melitaea aurelia* Nickerl, 1850. This xeric grasslands specialist has declined severely during the 20th century (e.g., Van Swaay & Warren 1999, Beneš *et al.*

2002), but is currently re-expanding to historically occupied regions (Germany: Eichel & Fartmann 2008, the Czech Republic: Spitzer & Beneš 2010). It hence offers an excellent comparison with much more studied, but recently declining, checkerspots.

Mobility studies based on capture-mark-recapture often miss rare long-range movements (Baguette & Schtickzelle 2003, Zimmermann *et al.* 2011), instrumental in the recolonisation/expansion processes. Franzen and Nilsson (2007) recommended that a sampling area as large as 100 km² is necessary to estimate lepidopteran (re)colonisation ability. A way to overcome this logistic limitation is to use dispersal kernel functions, predicting long-range movements from short-range ones. This does not fully eliminate the problem with undetected long-range dispersal, but at least allows comparisons among species, sexes, regions and seasons (Fric *et al.*

2010). Contributing to the debate (e.g., Baguette *et al.* 2000, Kuras *et al.* 2003) on the appropriate shape of dispersal kernel functions, Fric and Konvička (2007) showed that a particular function form, the inverse power function (IPF), is particularly robust to variation in the marking effort, owing to the scale invariance of the function slope; i.e., the parameter expressing decay of dispersal with distance.

The scale invariance of IPF offers an attractive possibility to collect reliable dispersal data with reduced marking effort and to compare dispersal data collected under varying study circumstances. We examined this by performing a two-seasons mark-recapture study targeting movement patterns in a strong *M. aurelia* population inhabiting xeric grasslands in the Czech Republic. In the first season, we followed a traditional approach, marking the population during the entire flight period. In the second season, we substantially increased the study area, restricted marking to peak adult flight, and increased per-day marking intensity. Here, we (1) describe the basic demography and movement patterns in the population of *M. aurelia*, and (2) assess the robustness of the movement estimates obtained while following different marking protocols.

2. Material and methods

2.1. Study system

The study was carried out in a system of valleys at the southern slopes of the Zdanický les hills (49°05'N, 17°02'E, altitude 245–330 m), Southern Moravia, SE Czech Republic. While most of Southern Moravia consists of intensively farmed lowlands, Zdanický les is a ridge (maximum altitude 437 m), formed by base-rich Carpathian flysch and covered by oak-hornbeam and beech forests. Its south-facing valleys, historically covered by a patchwork of gardens, hay meadows, orchards and pastures, were largely abandoned several decades ago, and now are in varying stages of succession. The prevailing vegetation is classified as *Bromion erecti* dry grasslands, *Geranium sanguinei* forb-rich mantles, and *Berberidion xeric scrub* (Chytrý *et al.* 2001). Despite high biotic diversity (e.g., 74 butterfly species re-

corded to date, including 17 nationally threatened ones, according to unpublished Czech Butterfly and Moths Recording data), complex land-holding patterns have so far prevented legal protection. A part of the dry grassland area is actively managed by conservation volunteers.

2.2. Study species

Melitaea aurelia is a univoltine butterfly, displaying colonial distribution at short-bladed xeric grasslands with a high cover of its host plant, *Plantago media* L. (Eichel & Fartmann 2008). Females lay small egg batches on the underside of host plant leaves, larvae are gregarious until autumn. Its total distribution stretches from France through Central and Eastern Europe, Transcaucasia, the Southern Urals and Siberia up to the Tian Shan region (Tolman & Lewington 2008). In the Czech Republic, a decline during the 20th century has restricted its distribution to the warmest regions of the country, but recent records document a return of the species to parts of its former range.

2.3. Mark-recapture data

We worked in four adjoining valleys with a total dry grasslands area of 51 ha, divided into eleven subsites for the purpose of dispersal analysis (Fig. 1). Two adjoining valleys (32 ha) were covered by marking in 2005, and two others (19 ha) were added in 2006.

In 2005, the marking covered the entire adult flight period (25. VI–28. VII), every day with favourable weather, from 10:00 to 17:00 (CEST). Each netted butterfly was assigned a numeric code and released at its point of capture. A single person carried out the marking, working for 32 person-days in total.

In 2006, the marking was limited to the peak of adult flight season (5.–9.VII), but covered an expanded area. Five persons did the marking each day, resulting in the total marking effort of 25 person-days. Daily marking intensity, i.e. the number of marking persons per day and unit area, was 3.6 times higher in 2006 than in 2005 (5-fold increase in persons marking, but covering an area 1.37 times larger).

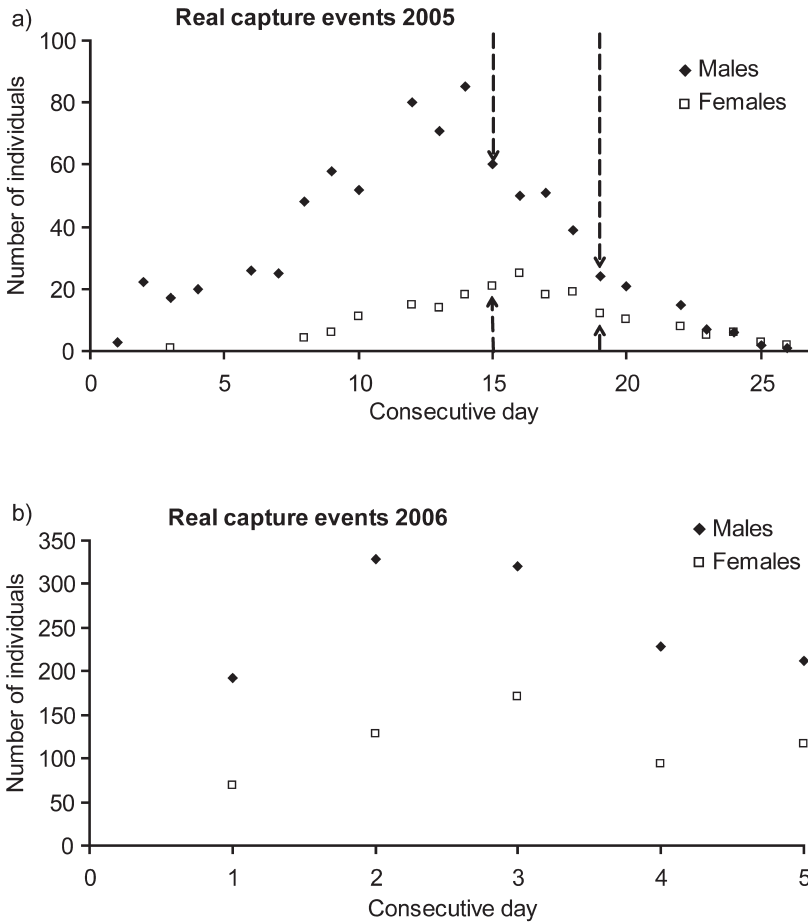


Fig. 2. Daily numbers of captures of *Melitaea aurelia* males and females. – a. In 2005. – b. In 2006. The arrows in panel (a) show the 2005 days phenologically corresponding to the five marking days in 2005.

2.4. Demography estimates and dispersal analysis

Population size in 2005 was estimated using the Jolly-Seber method, POPAN parametrisation suitable for open populations with births, deaths, and migration, as implemented in the program MARK v. 4.3. The residence rate (*Phi*) combining deaths and emigration, capture probability (*p*) and proportional recruitment (*pent*) are POPAN primary parameters, which may be constant for sexes and time (·) sex-dependent (*g*); or factorially (*t*), linearly (*T*) or polynomially (*Tx*) time-dependent; additive (*g + t*) or interactive (*g × t*). POPAN derived parameters are daily recruitment (*Bi*), daily population size (*Ni*), and total population size (*Ng*) (Schtickzelle *et al.* 2002, Vlasanek *et al.* 2009).

To compare mobility between years and sexes, we used data on patch-to-patch move-

ments, lumped them into 50-m distance classes (e.g., Drag *et al.* 2011), and fitted the inverse power function, expressing the probability density (*I*) of movements as

$$I = C \cdot D^{-n} \tag{1a}$$

or, in logarithmic form,

$$\ln I = \ln C - n(\ln D) \tag{1b}$$

To compare the 2006 (shorter term, expanded area) data with the 2005 data, we used two 2005 datasets. One consisted of all available data. For the second, we selected movements on five consecutive days with a sex ratio corresponding to 2006 data (see Fig. 2a).

We fitted IPFs on these three datasets and compared obtained slopes and intercepts using the Tukey HSD test (Zar 1996).

Table 1. Overview of mark-recapture data collected during the study for *Melitaea aurelia* males (M) and females (F).

| | Marking days M/F | Individuals captured M/F | Individuals recaptured M/F | Capture events M/F | Movements M/F |
|--------------|------------------|--------------------------|----------------------------|--------------------|---------------|
| 2005 | 32 / 29 | 304 / 108 | 318 / 98 | 649 / 230 | 146 / 20 |
| 2005 reduced | 5 / 5 | 113 / 55 | 62 / 11 | 191 / 67 | 29 / 8 |
| 2006 | 5 / 5 | 827 / 468 | 455 / 110 | 1375 / 598 | 274 / 151 |

3. Results

For the 2005 marking (Table 1), the best demography model was $\Phi(t)p(g+t)pent(g*T2)N(g)$, containing 50 parameters (AICc = 2162.58). The second-ranking candidate model differed by $\Delta AICc > 3.0$. *Melitaea aurelia* residence Φ thus responded factorially to the day of marking, independently of sexes; capture probability p varied among marking days and was always higher in males; and recruitment $pent$ was approximated by domed quadratic polynomials, differing in shape between sexes and revealing protandrous recruitment (Fig. 3). The total estimated population size was 490 (± 35 SE) males and 270 (± 36 SE) females.

In the 2006 marking, we marked 3.1 times more individuals than in 2005. Based on sex ratio on capture, the marking period in 2006 (5.–9. VII) corresponded to 10.–14. VII in 2005. The males had already passed their annual peak, whereas females were just peaking (Fig. 2). The number of butterflies marked in those phenologically corresponding 2005 days was 168 (Table

1). The total population size for 2006 was not realistically identifiable from the data, due to too low number of marking days, but probably reached a few thousand individuals.

The mean / median flight distances in 2005 were 307 ± 36 SE m / 200 m for males and 203 ± 6 m / 100 m for females; in 2006, 377 ± 23 m / 200 m for males and 398 ± 8 m / 250 m for females. Based on the reduced 5-day data, the mean / median distances were 256 ± 10 m / 200 m for males and 132 ± 4 m / 100 m for females. In both years, the longest detected movements were those of males (Table 2).

All fitted IPFs approximated the dispersal data significantly (Table 2), with all $R^2 > 0.7$ (Fig. 4). Comparing the functions across years and sexes did not reveal any overall difference in intercepts ($F = 0.25, df = 1, 5, p = 0.618$) or slopes ($F = 0.08, df = 1, 5, p = 0.775$). In other words, the short-term marking in 2006 detected identical dispersal parameters as the entire flight period marking in 2005. Post-hoc comparison of all possible combinations, however, suggested a difference in slopes between the total data of females in

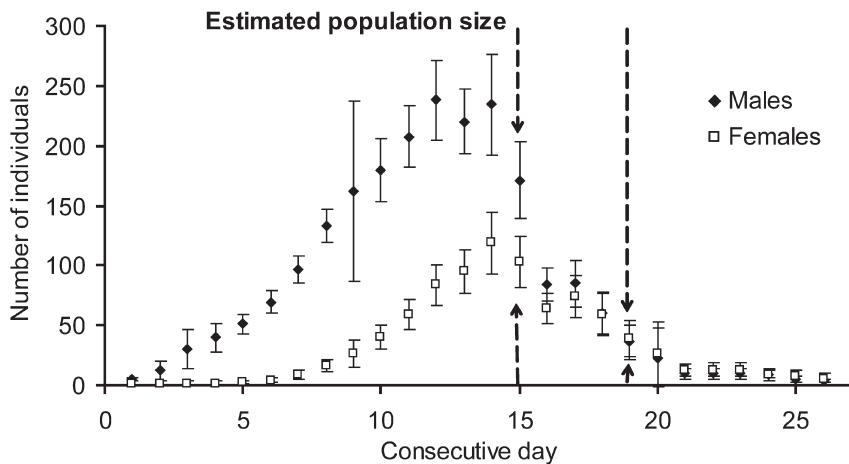


Fig. 3. Estimated daily population sizes (\pm standard errors of the estimates) for *Melitaea aurelia* males and females according to best-fitting model for 2005. Black arrows show the phenological phase corresponding to the five marking days in 2006.

Table 2. Test statistics for the inverse power functions linear regressions and derived estimates of *Melitaea aurelia* movement probabilities to distances longer than those covered by the marking.

| | | d.f.; F; p | Predicted movements (%) | | | | Max. distance |
|--------------|---------|--------------------|-------------------------|------|------|-------|---------------|
| | | | 1 km | 2 km | 5 km | 10 km | |
| 2005 | | | | | | | |
| | males | 1,15; 66.4; <0.001 | 2.94 | 1.03 | 0.25 | 0.09 | 1,250 m |
| | females | 1,7; 38.7; 0.004 | 3.12 | 1.36 | 0.46 | 0.20 | 600 m |
| 2005 reduced | | | | | | | |
| | males | 1,11; 20.8; <0.001 | 2.49 | 1.14 | 0.41 | 0.18 | 750 m |
| | females | 1,3; 47.8; 0.002 | 1.06 | 0.52 | 0.2 | 0.01 | 450 m |
| 2006 | | | | | | | |
| | males | 1,13; 51.4; <0.001 | 1.79 | 0.73 | 0.22 | 0.09 | 2,000 m |
| | females | 1,14; 38.2; <0.001 | 4.18 | 2.26 | 0.99 | 0.54 | 1,050 m |

2005 and males in 2006 (at $p = 0.05$), but this single difference was likely influenced by the different sample sizes in the two regressions.

The IPF-derived predictions of movements to 5 (10) km distances suggest that a population containing 1,000 (10,000) individuals will likely contain a few individuals moving to such distances. The occupancy pattern in a wider region (Fig. 1) shows that patch-to-patch distances among occupied xeric grassland patches are within this distance range.

4. Discussion

Estimation of the parameters of the inverse power function dispersal kernel using the *M. aurelia* mobility data obtained in two consecutive years resulted in very close function parameters, and hence predicted identical migration rates. The functions were identical despite major differences in data collection in the two years: while in 2005 we covered the entire flight period, in 2006 we marked the butterflies only during the peak flight, albeit with higher marking intensity.

The unchanged function performance supports the conjecture by Fric and Konvička (2007) that given the scale invariance of IPF, it should predict identical dispersal rates under a great variety of marking protocols. The authors showed this by subsampling data for two species, *Euphydryas aurinia* (Rottenburg, 1775) and *Parnassius mnemosyne* (Linnaeus, 1758). Here, we in fact subsampled the 32-day 2005 data to 5-day 2005

data. On the other hand, the increased marking intensity in 2006 expanded the data set, but none of the two procedures changed the original (i.e., total data 2005) IPF kernel.

Melitaea aurelia adult demography patterns do not deviate from those found in other checkerspots (Ehrlich & Hanski 2004, Konvička *et al.* 2005, Schtickzelle *et al.* 2005, Hodgson *et al.* 2009), or other single-brood nymphalids (e.g., *Proclossiana eunomia*: Schtickzelle *et al.* 2002; *Boloria aquilonaris*: Baguette & Schtickzelle 2003). Neither does the increase in numbers between 2005 and 2006 appear unusual, as abundance fluctuations by an order of magnitude occur frequently in butterfly populations (Hellmann *et al.* 2003, Schtickzelle *et al.* 2005, Čížek & Konvička 2009). In species with communal larval nests, such changes may be particularly prominent as entire broods are easily destroyed by catastrophes, parasitoids or pathogens (Ehrlich & Hanski 2004, Schtickzelle *et al.* 2005), which might be responsible for the rapid patch occupancy turnover in checkerspot metapopulations (Hanski 1999).

Mean and median movements also fell within the ranges reported in previous checkerspot studies i.e. a few hundred meters for mean distances and 1–2 kilometres for maxima (e.g., Wahlberg *et al.* 2002, Baguette 2003, Hovestadt & Nieminen 2009, Zimmermann *et al.* 2011). The 2006 marking returned longer mean distances, which could have been caused by either the increase of marking area (e.g., Schneider 2003, Zimmermann *et al.* 2011), or by density-dependent emigration

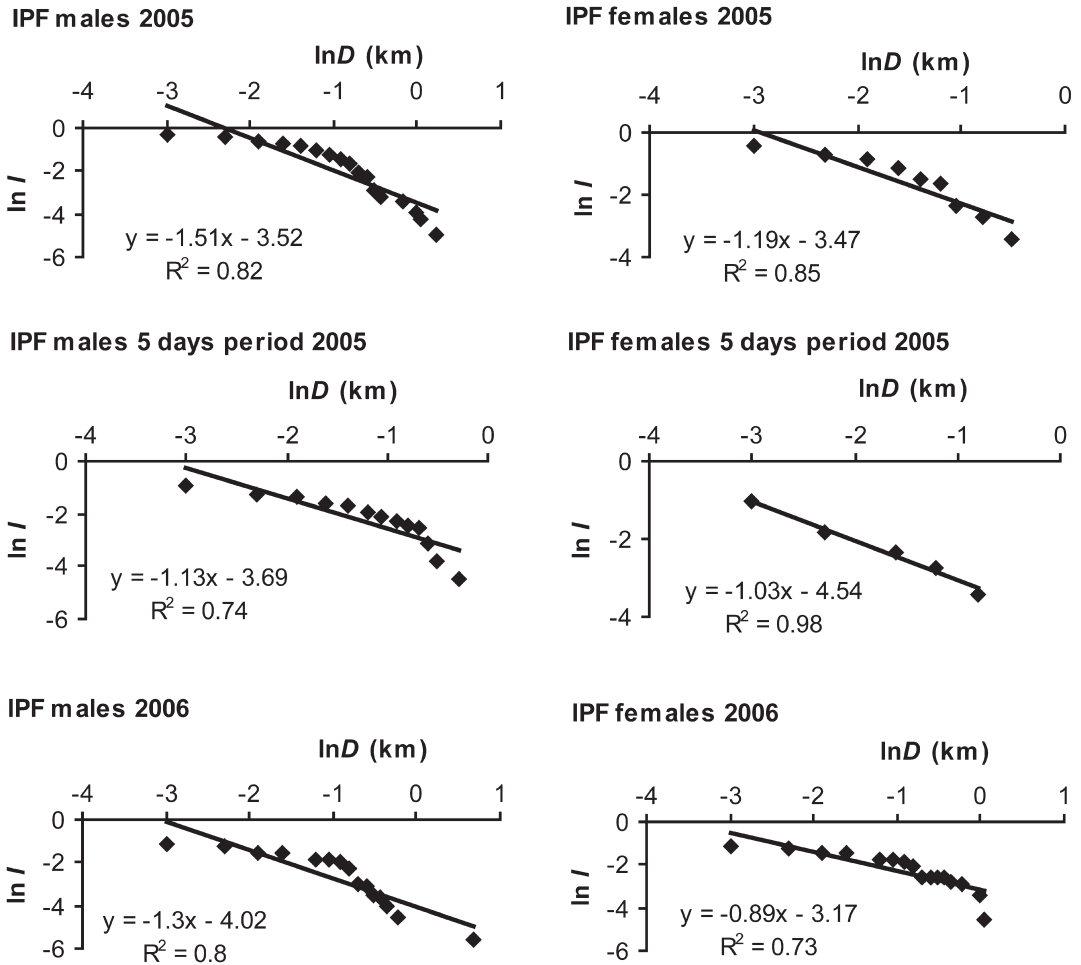


Fig. 4. Fitting of inverse power functions (IPF) expressing the probability density of *Melitaea aurelia* movements to certain or longer distances against the distances (\ln - \ln scale). Short-term intensive marking in 2006 returned identical dispersal kernels (i.e., slopes and intercepts of the function) as did the marking in the whole flight period in 2005.

(Nowicki & Vrabec 2011); the data do not allow distinguishing between the two alternatives. The mean flight distances obtained with the reduced 2005 data were by one-third (males) or even by one-half (females) shorter compared to the total 2005 data, which is attributable to a lower chance of detecting long individual displacement during the shorter marking time. It is hence more encouraging that IPF did not differ among the three data sets.

The ranges of fitted IPF slopes (–1.1 to –1.5 for males, –0.9 to –1.2 for females) were also similar to other checkerspot studies (e.g., Fric *et al.* 2010, Zimmermann *et al.* 2011). The overlap of

the values with other checkersspots suggests a taxonomic conservatism in mobility. This justifies using data from closely related species, such as various checkersspots, for such purposes as modelling or reserve design (cf. Wahlberg *et al.* 1996, Fric *et al.* 2010), however, the further verification on other taxonomic groups is needed. Differences between sexes were not statistically significant, although male slopes tended to be steeper, indicating fewer long-distance movements compared to females. This pattern, explicable by different fitness consequences of dispersal for sexes (Zonneveld & Metz 1991), is frequent in butterflies (Scott 1975, Baguette & Nève 1994, Hanski

& Thomas 1994, Gutiérrez *et al.* 1999). Female dispersal results in establishment of new colonies, and ultimately, in range expansions. Identical movements in butterfly sexes, however, were also reported for some checkerspots (Wahlberg *et al.* 2002, Wang *et al.* 2004).

In Germany, *M. aurelia* often forms small colonies at calcareous grassland islets (Eichel & Fartmann 2008). Habel *et al.* (2009) showed that despite living in small colonies, it maintains high levels of genetic polymorphism by occasional long-distance dispersal. Our IPF-derived movement probabilities (Table 2) predict that one individual per thousand reaches a 10 km distance. Given the xeric grasslands distribution in the region (Fig. 1), this should maintain a mutual interconnection of the system. Recent capture-mark-recapture studies at scales of hundreds of square kilometers (Franzen & Nilsson 2007, Zimmermann *et al.* 2011) revealed that occasional long-distance dispersal movements occur even in apparently sedentary species. Such movements are obviously rare, but critical for species survival in increasingly fragmented landscapes.

In summary, this study supports the earlier observation by Fric and Konvička (2007) that dispersal probabilities obtained with the inverse power function should be robust with respect to variation in marking protocols. While the earlier study re-sampled single-year data, this study analysed data sets generated under different marking protocols. Despite unavoidable year-to-year variation in such factors as weather (effects on butterfly mobility: e.g., Cormont *et al.* 2011) or population density (e.g., Nowicki & Vrabec 2011, Konvička *et al.* 2012), the dispersal probability decays did not change. This opens the exciting possibility of obtaining reliable dispersal estimates even from brief marking campaigns. Although we understand that a comparison based on just two seasons should not allow too much optimism, the possibility still deserves investigation. We also understand that too brief marking campaigns cannot provide information on such population traits as longevity, or temporal development of sex ratio. Regarding dispersal, however, it is increasingly apparent that to predict species' fates in fragmented landscapes, the knowledge of habitat patch distribution and occupancy patterns may be more critical than movement data (cf. Fric

et al. 2010). Dispersal is a probabilistic process and the chance to reach more distant sites increases with abundance at the source colonies, highlighting the need for appropriate conservation management of as large as possible stretches of suitable habitats (Eichel & Fartmann 2008).

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