



Dispersal kernels of butterflies: Power-law functions are invariant to marking frequency

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Summary

Despite recent developments of sophisticated dispersal modelling, simple regression-based models remain useful for estimating frequencies of long-distance movements of animals. Since the inverse power function, IPF ($\ln l = \ln C - m \ln D$), but not the negative exponential function, NEF ($\ln l = \ln a - kD$), exhibits the property of self-similarity, it should be robust against variation in effort invested into mark-recapture studies. We illustrate this using three data sets on movements of butterflies (Lepidoptera): *Euphydryas aurinia*, year 2002 (better fitted by IPF), *E. aurinia*, year 2003 (better fitted by NEF) and *Parnassius mnemosyne* (better fitted by NEF). By simulated reductions of numbers of animals, numbers of marking days, and marking effort, we show that IPF withstands severe decline in marking frequency without a change of parameters of regressions based on reduced data. In contrast, parameters of NEFs fitted to the reduced data widely varied and differed from functions based on unreduced data. Owing to the robust performance of IPF, reliable dispersal estimates may be obtained at relatively small field effort, which may facilitate quick and efficient comparisons of movement patterns among species, locations and populations.

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Zusammenfassung

Trotz der derzeitigen Entwicklung von hochentwickelten Ausbreitungsmodellen, bleiben einfache regressionsbasierte Modelle nützlich, um die Häufigkeit der Bewegung von Tieren über weite Distanzen abzuschätzen. Da die inverse Potenzfunktion, IPF ($\ln l = \ln C - m \ln D$) im Gegensatz zur negativen Exponential-

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funktion NEF ($\ln l = \ln a - kD$) die Eigenschaft der Selbstähnlichkeit zeigt, sollte sie robust gegen die Variation des investierten Aufwands bei Fang-Wiederfang-Methoden sein. Wir illustrieren dies an drei Datensätzen über die Bewegung von Schmetterlingen (Lepidoptera): *Euphydryas aurinia* im Jahr 2002 (besser durch IPF angepasst), *E. aurinia* im Jahr 2003 (besser durch NEF angepasst) und *Parnassius mnemosyne* (besser durch NEF angepasst). Wir zeigen durch die simulierte Reduktion der Anzahl der Tiere, der Anzahl der Markierungstage und des Markierungsaufwandes, dass die IPF eine ernsthafte Verringerung der Markierungshäufigkeit übersteht, ohne dass sich die Parameter der Regressionen verändern, die auf den reduzierten Daten basieren. Im Gegensatz dazu variierten die Parameter der NEFs, die an die reduzierten Daten angepasst wurden, in einem weiten Bereich und unterschieden sich von den Funktionen, die auf den nicht-reduzierten Daten basieren. Infolge der robusten Leistung der IPF können verlässliche Ausbreitungsabschätzungen mit einem relativ geringen Freilandaufwand gewonnen werden. Dies kann schnelle und effiziente Vergleiche von Ausbreitungsmustern zwischen Arten, Orten und Populationen ermöglichen.

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Introduction

Dispersal is a crucial biological trait that allows living organisms to colonise unoccupied areas, locate vital resources including mates, and avoid unfavourable conditions (Bowler & Benton 2005; Clobert, Danchin, Dhondt, & Nichols 2001; Trakhtenbrot, Nathan, Perry, & Richardson 2005). With enhanced interest in species persistence in fragmented landscapes, increasingly sophisticated modelling tools allow studying dispersal with respect to varying animal conditions (Johnson & Horvitz 2005; Petit, Moilanen, Hanski, & Baguette 2001) or landscape properties (Grosbois & Tavecchia 2003; Hanski, Alho, & Moilanen 2000; Lebreton, Hines, Pradel, Nichols, & Spendelov 2003; Ovaskainen 2004). Despite these advances, the questions most frequently asked by conservationists remain simple: what is the probability for an average individual to cover a certain distance, and which maximum distances are realistically reached by dispersers. The answers are critical for reserve design, delimitation of areas for population-level management, or for choosing between re-introductions and relying on spontaneous colonisation in recovery programmes (e.g. Leon-Cortes, Lennon, & Thomas 2003; Maes, Vanreusel, Talloen, & Van Dyck 2004; Schultz 1998). Without downgrading the sophisticated modelling, time and resources will always be scarce in conservation, and practitioners will always embrace simple tools allowing for quick and efficient dispersal estimates.

Among such tools are regression-based models that use mark-release-recapture (MRR) data collected within a bounded range to predict movements beyond the range (Hill, Thomas, & Lewis 1996; Konvicka et al. 2005; Okubo & Levin 1989;

Vandewoestijne & Baguette 2004). Two commonly used models, both fitting probability densities of movements to given distances against the distances, are the negative exponential function (NEF) and the inverse power function (IPF), the latter having a fatter tail over long-distances. Fitting the functions may answer the two questions outlined above and facilitates comparisons among species and locations (e.g. Baguette, Petit, & Quéva 2000; Kuras, Benes, Fric, & Konvicka 2003; Ricketts 2001). Performances of the functions are also considered in more sophisticated modelling (Cizek & Konvicka 2005; Hanski et al. 2000).

Several studies working with butterflies (Table 1) and other insects (Elliott 2003; Roslin 2000; Zolubas & Byers 1995) compared fits of NEF and IPF to empirical mobility data. They often found that IPF attained the better fit, and even in cases where NEF was superior, IPF attained sufficiently high coefficients of determination to be used for inference (Table 1).

Better fit of the IPF carries two important connotations. First, if dispersal of natural populations indeed follows power functions, species would have much higher chances to colonise distant habitats than previously thought (Hovestadt, Messner, & Poethke 2001; Smith & Green 2005).

Second, IPF, as a power-law function, exhibits the property of self-similarity, or scale-invariance, manifested as a linear relationship on log-log scale. The self-similarity over wide range of scales is a characteristic of fractals, that is, geometric objects whose topological distances (between two measured points) are lower than real distances (Mandelbrot 1967, 1986). Because patterns fitted by IPF exhibit identical behaviour over a range of scales, a knowledge of behaviour of the function

Table 1. Overview of selected mark–recapture studies of butterfly movements that compared the fits of negative exponential function (NEF) and inverse power function (IPF) to dispersal data

Species	Sex	Days	IPF- R^2	NEF- R^2	Better fitting	Source
<i>Aporia crataegi</i>	B	NA	0.72	0.89	NEF	Baguette et al. (2000)
<i>Boloria aquilonaris</i> (1995)	B	28	0.60	0.96	NEF	Baguette (2003)
<i>B. aquilonaris</i> (1996)	B	39	0.63	0.99	NEF	
<i>B. aquilonaris</i> (1997)	B	27	0.57	0.93	NEF	
<i>B. aquilonaris</i> (1995+1997)	B	28+27	0.54	0.96	NEF	
<i>Brenthis ino</i>	M	40	0.91	0.97	NEF	Zimmermann, Fric, Filipova, and Konvicka (2005)
	F	31	0.92	0.88	IPF	
<i>Erebia epiphron</i>	M	20	0.58	0.92	NEF	Kuras et al. (2003)
<i>E. sudetica</i> (within biotope)	M	29	0.62	0.99	NEF	Kuras et al. (2003)
<i>E. sudetica</i> (total movements)	M	29	0.62	0.88	NEF	Kuras et al. (2003)
	F	29	0.73	0.82	NEF	
<i>Euphydryas aurinia</i> (2004)	M	37	0.89	0.97	NEF	Fric, Hula, Klimova, Zimmerman, and Konvicka (unpublished)
	F	32	0.96	0.89	IPF	
<i>E. maturna</i>	M	16	0.94	0.96	NEF	Konvicka et al. (2005)
	F	14	0.95	0.87	IPF	
<i>Hesperia comma</i>	B	11	0.98	0.76	IPF	Hill et al. (1996)
<i>Melanargia galathea</i>	B	NA	0.83	0.70	IPF	Baguette et al. (2000)
<i>Melitaea athalia</i>	M	49	0.86	0.97	NEF	Fric et al. (unpublished)
	F	49	0.97	0.88	IPF	
<i>M. diamina</i>	M	44	0.79	0.98	NEF	Fric et al. (unpublished)
	F	42	0.96	0.80	IPF	

NA: not available.

B: both sexes combined.

over some part of the range should suffice to predict the patterns over other parts of the range. This property of power law functions has been much explored in various subfields of ecology, including population size fluctuations, species-area relationships, extinction risks, or community distributions of body sizes (Brown et al. 2002). Researchers of dispersal seem to neglect this phenomenon, an exception being studies of shapes of movement trajectories (Benhamou 2004; Cole 1995; Johnson, Milne, & Wiens 1992; With 1994).

In the context of fitting frequencies of movement distances, the self-similarity implies scale invariance in distribution of long and short movements. Therefore, knowledge of a subset of movement frequencies should allow to estimate remaining movement frequencies in a population. This could have tremendous implications for mobility studies. Namely, it could allow for obtaining reliable estimates of movement frequencies with much lower effort invested into field work than is routinely invested at present, and, hence, exploring movements of more species and/or populations with a given money and time budget.

We explored the self-similarity property of IPF dispersal kernels using simulated reductions of three sets of empirical data on movements of butterflies. We illustrate the robustness of movement parameters obtained by fitting the power law function, as opposed to its alternative, the negative exponential function, which does not exhibit scale invariance. We begin with a data set that was originally fitted better by the power law function, and proceed to two sets for which the alternative originally performed better. We argue that the robustness of power-law function is a logical consequence of the nature of mark-recapture data at animal movements.

Material and methods

Dispersal kernels and self-similarity of power function

In studies of butterfly dispersal, dispersal kernels refer to the cumulative distributions of dispersal

distances. Fitting dispersal kernel functions proceeds as follows. Individual-based MRR data with information on spatial locations of captures are collected and distances between consecutive capture points per individual are summed to obtain individual movement distances.

Under the negative exponential function (NEF), the probability density I of animals moving to distances D is

$$I_{NEF} = ae^{-kD} \text{ or } \ln I = \ln a - kD, \quad (1)$$

where a and k are parameters, estimated by fitting the logarithms of cumulative fractions of individuals moving to certain distances against the distances.

The inverse power function (IPF) expresses the probability density I as

$$I_{IPF} = CD^{-m} \text{ or } \ln I = \ln C - m \ln D. \quad (2)$$

The parameters C and m are estimated by fitting the logarithms of cumulative fractions of individuals moving to certain distances against logarithms of the distances.

It is easy to show that IPF, but not NEF, exhibits self-similarity. A pattern is self-similar if it obeys the generalised relation

$$\text{Constant} = px^m \quad (3)$$

and there is a similarity between x at different scales. By substituting D and I from (2) for x and p , we obtain

$$C = ID^m \text{ or } I = CD^{-m}.$$

This phenomenon is well known from fractal geometry. A classical example is measuring length of complex objects with rulers of varying lengths and obtaining different, but self-similar, distances (e.g. Turchin 1996). Note that recorded movement distances in MRR studies are topological distances between consecutive capture points, representing snapshots of real trajectories crossed by individuals. Decreasing frequency of marking is equivalent to using coarser ruler for measuring movement distances. However, had movement patterns exhibited self-similarity, the resulting frequency distribution of movements should be independent of marking frequency under the power-law IPF.

Data and species studied

We use three sets on butterfly mobility data, collected via mark-recapture method (Table 2).

- (i) *Euphydryas aurinia* (2002): The movements were originally better fitted by IPF and we analyse them in detail.

Table 2. Mark-recapture data used for modelling effects of truncating dispersal data on resulting movement parameters in the Marsh Fritillary *Euphydryas aurinia*

	Marking days	Individuals marked	Individuals recaptured	Recapture events	Population size ^a	Movements	Number of sites ^b	Max. possible distance ^c	Mean distance ± SD (m)	Max. total distance (m)
<i>E. aurinia</i> (2002)										
♂	25	643	289	544	1900	129	18	3.9	180 ± 359	1520
♀	25	203	60	109	2000	15	18	3.9	240 ± 532	2360
<i>E. aurinia</i> (2003)										
♂	21	412	240	787	900	342	14	1.6	260 ± 390	2950
♀	21	170	81	225	800	48	14	1.6	102 ± 228	1400
<i>P. mnemosyne</i>										
♂	31	1320	638	1248	3500	360	22	2.2	144 ± 206	1280
♀	30	553	199	261	2100	104	22	2.2	154 ± 260	1560
<i>E. maturna</i>										
♂	16	57	22	32	80	16	27	1.3	183 ± 248	950
♀	16	79	33	89	120	26	27	1.3	171 ± 252	1050

^aPopulation sizes were estimated using the Jolly-Seber model, details of the estimates will be published elsewhere.

^bSeparate sites delimited in field in order to record dispersal distances. If weather permitted, all sites were visited at each marking day, and the sequences of the visits were randomised among days.

^cThe distance between two outermost sites covered by the MRR study.

- (ii) *E. aurinia* (2003): Originally better fitted by NEF, although IPF still retained good fit.
- (iii) *Parnassius mnemosyne* (2005): Again originally better fitted by NEF.

E. aurinia (Rottemburg, 1775) (Nymphalidae) is a univoltine butterfly of unimproved damp meadows, endangered throughout Europe due to intensification of agriculture and abandonment of traditional land use (Hula, Konvicka, Pavlicko, & Fric 2004; Warren 1994). The MRR data were collected in 2002 (29 May–25 June) and 2003 (28 May–17 June), in a hilly region of Western Bohemia, Czech Republic. The study site (50°09'N, 13°03'E; 650 m a.s.l.) consists of 21 ha of unimproved meadows within a 1.5 km² of a mosaic-like landscape. One to three persons visited the study area on a daily basis, capturing as many as possible butterflies, marking them with alcohol-based felt-tip pens and recording their positions of capture.

P. mnemosyne (Linnaeus, 1758) is an univoltine species of open woodlands and woodland clearings, endangered due to changes in woodland management (Konvička & Kuras 1999). The MRR data, collected in 2005 (11 May–10 June), originated from a large population inhabiting clearings and glades in the Milovický wood, Czech Republic (48°45'N, 16°49'E, 220 m a.s.l.). The marking again proceeded on everyday basis, with recording positions of capture.

We also refer below to MRR data from a population of *Euphydryas maturna* (Linnaeus, 1758), a close relative of *E. aurinia*. Movements of this critically endangered species of sparse deciduous forests were studied within its last population in the Czech Republic in 2–25 June 2002; the butterfly is used here as an example of an extremely small population (see Konvicka et al. 2005).

Simulations of truncated capture histories

Each set of dispersal data consisted of a capture history matrix with individual butterflies in rows, marking days in columns, and capture sites indicated by different symbols in matrix cells.

For the detailed analysis of *E. aurinia* in 2002, we simulated three data reduction scenarios: (i) random deletions of individuals (rows), corresponding to smaller population sizes; (ii) random deletions of days (columns), as if fewer days were spent marking; and (iii) random deletions of individual \times days, or matrix cells, corresponding to lower marking effort. Each of the scenarios had three levels. (a) Reduction to one half of the dataset,

i.e., half number of days for (i), half number of individuals for (ii), and half number of cells for (iii); (b) Reduction to one quarter of the *E. aurinia* dataset; and (c) reduction to the size of the *E. maturna* dataset, i.e. 16 days for (i), 136 individuals for (ii) and 258 capture events for (iii) (Table 2).

For each of the scenario/level combinations, we simulated fifty replicates of reduced capture histories. Following each simulation, we separated data for males and females, and further worked with sexes separately. We then fitted NEF and IPF to each replicate, and compared slopes of thus obtained regressions with the original dispersal kernel using paired *t*-tests (Zar 1996).

Each comparison could have resulted in three situations: (i) a significantly steeper slope of the regression based on reduced data indicating a faster decrease of movements with distance; (ii) no difference; or (iii) a significantly gentler slope indicating a slower decrease of movements with distance. (A fourth possibility was that the reduction diluted the data to such an extent that linear regression was not applicable.) We then compared, for each scenario and level, the frequencies of steeper versus shallower slopes using binomial tests.

Only random deletions of individuals (i) to one quarter of the original data (b) were simulated for *E. aurinia* (2003) and *P. mnemosyne*.

Results

Table 3 presents results of fitting NEF and IPF to the original data. Comparison of R^2 suggests that IPF was considerably better than NEF for *E. aurinia* in 2002, but NEF performed better for *E. aurinia* in 2003 and *P. mnemosyne*. The fatter tails of IPF kernels is apparent from the predictions of long-range movements.

For *E. aurinia* (2002) the reductions of data resulted in NEF regressions significantly differing from the original model, whereas for IPF, the regressions fitted to reduced data did not differ from those based on the complete data (Table 4 and Fig. 1). This applied to deletion of days, individuals and cells, and to both sexes. In the case of NEFs, the reduced regressions tended to be biased towards steeper slopes, underestimating migrations to long distances.

IPF thus sustained severe reduction of data without a change in its parameters. In the case of females, reduction to *E. maturna* data did not allow performing linear regressions in 41 out of 50

Table 3. Results of fitting the negative exponential (NEF) and inverse power (IPF) functions to unreduced mark-recapture data on movements of three butterfly systems, with predicted relative frequencies of movements to 1 and 5 km

Model	Sex	Fitted function	R^2	1 km	5 km
<i>Euphydryas aurinia</i> (2002)					
NEF	♂♂	$\ln l = -1.27 (\pm 0.16) - 1.38 (\pm 0.14) \cdot D$	0.82	0.070	10^{-4}
	♀♀	$\ln l = -1.33 (\pm 0.24) - 0.76 (\pm 0.18) \cdot D$	0.66	0.124	0.006
IPF	♂♂	$\ln l = -3.14 (\pm 0.08) - 1.22 (\pm 0.07) \cdot \ln D$	0.93	0.043	0.006
	♀♀	$\ln l = -2.51 (\pm 0.09) - 0.72 (\pm 0.06) \cdot \ln D$	0.94	0.081	0.026
<i>Euphydryas aurinia</i> (2003)					
NEF	♂♂	$\ln l = -0.54 (\pm 0.07) - 2.09 (\pm 0.05) \cdot D$	0.98	0.072	10^{-5}
	♀♀	$\ln l = -0.72 (\pm 0.15) - 3.29 (\pm 0.21) \cdot D$	0.95	0.018	10^{-8}
IPF	♂♂	$\ln l = -3.14 (\pm 0.10) - 1.48 (\pm 0.10) \cdot \ln D$	0.88	0.043	0.004
	♀♀	$\ln l = -3.78 (\pm 0.17) - 1.33 (\pm 0.13) \cdot \ln D$	0.88	0.023	0.003
<i>Parnassius mnemosyne</i>					
NEF	♂♂	$\ln l = -0.34 (\pm 0.07) - 3.41 (\pm 0.08) \cdot D$	0.99	0.023	10^{-8}
	♀♀	$\ln l = -0.18 (\pm 0.17) - 4.45 (\pm 0.28) \cdot D$	0.95	0.012	10^{-10}
IPF	♂♂	$\ln l = -3.97 (\pm 0.11) - 2.03 (\pm 0.14) \cdot \ln D$	0.90	0.019	0.001
	♀♀	$\ln l = -4.20 (\pm 0.16) - 2.03 (\pm 0.15) \cdot \ln D$	0.93	0.015	0.001

Both functions express probability densities if movements to certain distances (l) as functions of the distances (D). Better-fitting functions are shown in bold.

Table 4. Results of fitting the negative exponential (NEF) and inverse power (IPF) functions to reduced mark-recapture data on movements of *Euphydryas aurinia* in 2002

Kernel	Scenario	Deletion	Males					Females				
			Identical	Steeper	Gentler	Diluted	P	Identical	Steeper	Gentler	Diluted	P
NEF	Reduction of days	Half	13	35	2	0	***	37	9	0	4	***
		Quarter	11	35	0	4	***	11	35	0	4	***
		<i>E. matura</i>	39	10	1	0	***	14	36	0	0	***
	Reduction of individuals	Half	31	11	8	0	NS	20	30	0	0	***
		Quarter	26	21	3	0	***	28	22	0	0	***
		<i>E. matura</i>	12	24	14	0	NS	21	29	0	0	***
Reduction of cells	Half	19	31	0	0	***	37	12	0	1	***	
	Quarter	15	33	2	0	***	5	45	0	0	***	
	<i>E. matura</i>	28	21	1	0	***	9	0	0	41	n.a.	
IPF	Reduction of days	Half	49	1	0	0	NS	46	0	0	4	n.a.
		Quarter	46	0	0	4	n.a.	46	0	0	4	n.a.
		<i>E. matura</i>	50	0	0	0	n.a.	50	0	0	0	n.a.
	Reduction of individuals	Half	50	0	0	0	n.a.	50	0	0	0	n.a.
		Quarter	50	0	0	0	n.a.	50	0	0	0	n.a.
		<i>E. matura</i>	50	0	0	0	n.a.	50	0	0	0	n.a.
	Reduction of cells	Half	50	0	0	0	n.a.	49	0	0	1	n.a.
		Quarter	50	0	0	0	n.a.	50	0	0	0	n.a.
		<i>E. matura</i>	50	0	0	0	n.a.	9	0	0	41	n.a.

Fifty replicates were simulated for each scenario and deletion combination, and slopes of dispersal kernel functions were compared with slopes of the regression fitted to the complete data via paired t -tests. Numbers of replicates yielding identical, steeper and gentler slopes are shown; "diluted" refer to number of simulations that yielded data too sparse for linear regressions.

P : binomial tests comparing occurrence of significantly gentler or steeper slopes relative to slopes of original regression.

n.a.: test not applicable; NS: binomial test not significant; ***: $P < 0.001$.

replicates. The reduced data then consisted, on average, of just 50 capture events, and the nine cases where linear regression was possible still gave predictions identical to the complete data set.

IPF was originally the better fitting function for *E. aurinia* (2002). Therefore, it was possible

that its better performance in reduced data sets was just a consequence of its original better fit. However, IPF was robust against reductions even in case of *E. aurinia* (2003), and *P. mnemosyne*, while NEF again gave widely varying results (Table 5).

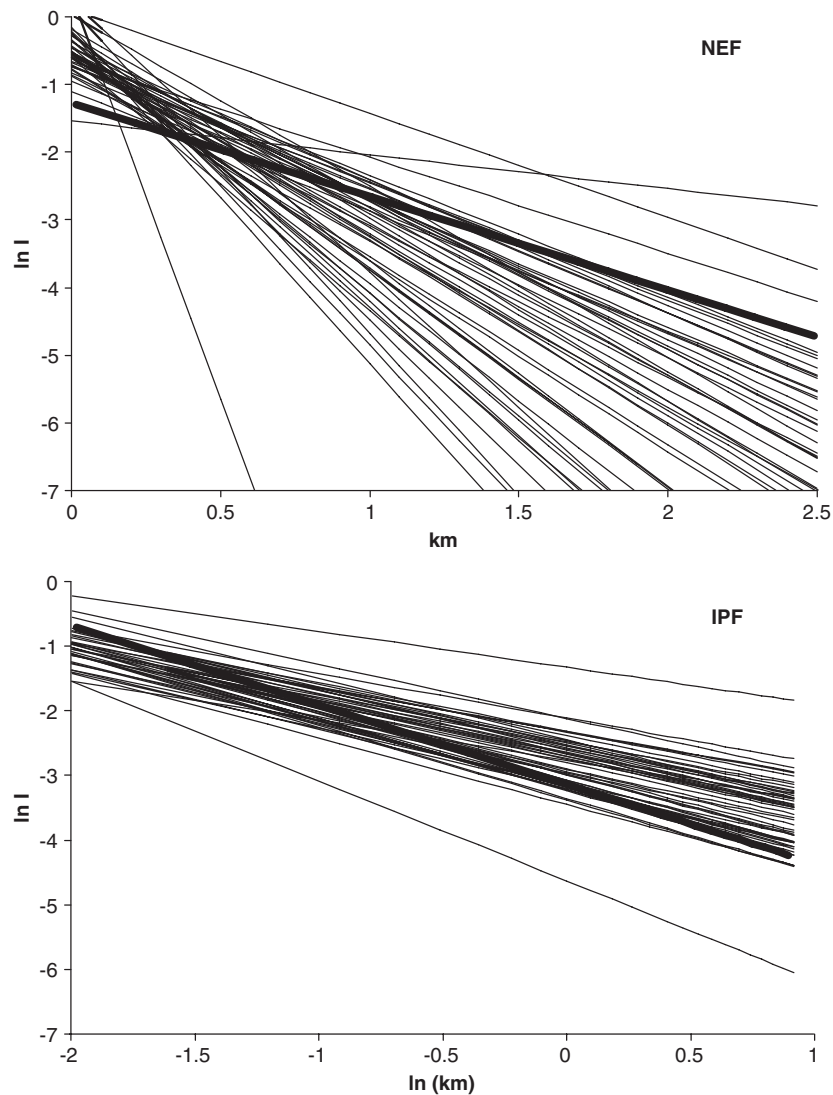


Figure 1. Example of the performance of the negative exponential (NEF) and inverse power (IPF) functions following reduction of original movement data. Males of *Euphydryas aurinia* (2002), reduction of days \times individuals (corresponding to decreased marking effort) to the much smaller data set collected for *Euphydryas maturna*. The thin lines represent functions fitted to fifty simulated replicates, the thick lines are the functions fitted to the original *E. aurinia* data.

Discussion

Reduction of marking effort in three butterfly mark–recapture studies did not change parameters of the resulting power function (IPF) for fitting frequency distribution of dispersal distances: the frequency distribution of movements was self similar over a relatively wide range of marking intensity. In contrast, NEF responded sensitively to simulated reduction of marking intensity and returned widely varying responses.

To interpret the self similarity, note that all mark–recapture studies record movements as straight distances between pre-selected dispersal coordinates (analogous to topological distances),

whereas animals follow complex trajectories (real movement distances). The same applies at the temporal scale. All MRR schemes record animal movements in discrete time units (such as days), intervals between them being analogous to topological distances, whereas the animals are present continuously.

However, the self-similarity documented here applies to movement frequencies and should not be used for interpolation to longer spatial scales. For real fractals, spatial invariance over two orders of magnitude was suggested as a minimum condition for fractality (Halley et al. 2004). Invariance over shorter ranges represent ‘apparent fractality’ (Halley et al. 2004), in which slopes of power

Table 5. Results of fitting the negative exponential (NEF) and inverse power (IPF) functions to reduced mark-recapture data on movements of *Euphydryas aurinia* in 2003, and *Parnassius mnemosyne*

Kernel	Males				Females			
	Identical	Steeper	Gentler	P	Identical	Steeper	Gentler	P
<i>Euphydryas aurinia</i> , year 2003								
NEF	18	19	13	NS	30	12	8	NS
IPF	50	0	0	NS	50	0	0	NS
<i>Parnassius mnemosyne</i>								
NEF	18	20	12	**	25	13	12	NS
IPF	50	0	0	NS	50	0	0	NS

In both cases, the data were reduced by deleting marking days to one quarter of the original data. Fifty replicates were simulated for each reduction, and slopes of dispersal kernel functions were compared with slopes of regression fitted to complete data via paired *t*-tests. Numbers of replicates yielding identical, steeper and gentle slopes are shown.

n.a.: linear regression was not applicable for truncated data set.

P: binomial tests comparing occurrence of significantly gentler or steeper slopes relative to slopes of original regression. NS: binomial test not significant; **: $P < 0.01$.

functions change with changing spatial scale (Turchin 1996; Westcott & Graham 2000). In spatial terms, this phenomenon was present in the data for *E. aurinia* (2002), in which the cumulative proportion of movements bent downward over distances close to 1 km (Fig. 2). Such inflexion might represent a change in dispersal behaviour at these distances (cf. Van Dyck & Baguette 2005). Our data do not allow for estimating the magnitudes of invariance in temporal terms, but they are certainly bounded as well, the upper bound being the lifespan of individual butterflies.

Still, the invariance with respect to marking frequency applies to ranges typically covered by MRR studies. The finding that IPF is robust over these scales carries two important practical implications. First, since NEF but not IPF is sensitive to variation in marking effort, and MRR data always cover just subsets of true movements, NEF-derived assessments of long range movements are intrinsically unreliable. As exemplified by the *E. aurinia* (2002) and *P. mnemosyne* data, this applies even to situations in which IPF attains poorer fit than NEF over the original data (Table 1 lists further examples). Therefore, researchers should prefer the more robust IPF, even for situations when its original fit is poorer, unless there are very strong reasons for rejecting it (such as a very low coefficient of determination).

Baguette (2003) presented a strong case for the butterfly *Boloria aquilonaris* (Stichel, 1908), in which NEF performed better than IPF if only short (within-habitat) movements were analysed. Despite this, the frequencies of rare long-distance (>0.5 km) movements agreed with predictions derived from fitting IPF. It is obvious that the probability of recording long movements increases with effort, and there are

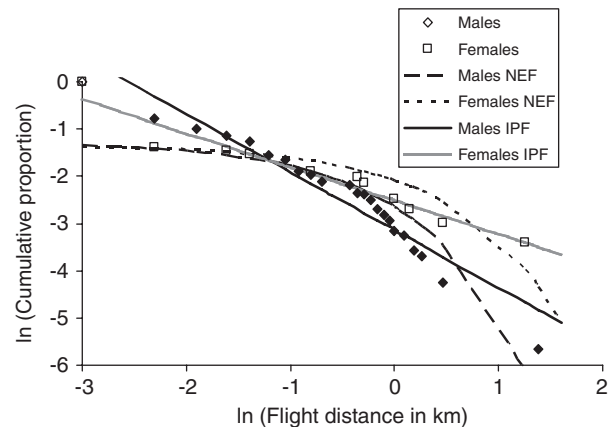


Figure 2. Fitting the inverse power function (IPF) and the negative exponential (NEF) function to complete data on movements of *Euphydryas aurinia* (2002). The same (ln–ln) scale is used for both functions. IPF attain a better fit than NEF, but in IPF, the cumulative proportions of males bends downward at distances close to 1 km.

indications that such movements do occur, but escaped detection. Some such indices were obtained using genetic markers (e.g. Keyghobadi, Roland, & Strobeck 1999; Vandewoestijne & Baguette 2004). Auckland, Debinski, and Clark (2004) obtained longer movement estimates after adjusting observed distances covered by the butterfly *Parnassius clodius* (Menétriés, 1855) to butterfly longevity. A study of landscape occupancy by lycaenid the *Cupido minimus* (Fuessly, 1775) revealed a minimum effect of isolation on site occupancy (Krauss, Steffan-Dewenter, & Tschamtkke 2004). Regarding *Euphydryas aurinia*, Warren (1994) reported rare instances of moving over 10 km in Britain.

However, there can be situations when long distance dispersal does not occur. The mountain

satyrid *Erebia epiphron* (Knoch, 1783) is confined to alpine meadows. Its adults hesitate to enter forests and both distribution patterns (Cizek, Bakesova, Kuras, Benes, & Konvicka 2003) and genetic markers (Schmitt, Cizek, & Konvicka 2005) confirm that they do not disperse across them. Alternatively, dispersal may be hindered by physical barriers, such as forested areas in the case of satyrid *Erebia medusa* (Denis, & Schiffermüller, 1775) (Schmitt, Varga, & Seitz 2000). These examples warn us that decisions to use IPF for dispersal estimates should not be automatic, should always consider the biology of the studied species and spatial distribution of their habitats.

The second implication is that the robust performance of IPF opens new opportunities for mobility studies. Flight periods of a typical univoltine butterfly last four to six weeks in Europe. Since IPF withstood truncation of data to one fifth of the original number, a field team may obtain reliable movement estimates for five species, or five sites, instead of one species or site, per given effort. Sparse or "incomplete" MRR data, which likely fill the drawers of many insect ecologists, deserve to be reanalysed, as the resulting movement predictions can essentially be trusted. Much lower effort than usually thought will be necessary to address important questions that have remained unanswered because of supposedly high demands for time and personnel. They include comparisons of dispersal for large sets of co-occurring species, of dispersal propensities in differently structured landscapes and long-term dispersal variation in response to weather or landscape changes, and many others.

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