

Restricted within-habitat movement and time-constrained egg laying of female *Maculinea rebeli* butterflies

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Abstract The movement of butterflies within habitat patches is usually assumed to be random, although few studies have shown this unambiguously. In the case of the highly specialized genus *Maculinea*, two contradictory hypotheses exist to explain the movement and distribution of imagos within patches: (1) due to the high spatial variance of survival rates among caterpillars, the “risk-spreading” hypothesis predicts that females will tend to make linear flight paths in order to maximize their net displacement and scatter the eggs as widely as possible; and (2) recent mark–release–recapture (MRR) data suggest that within-habitat displacement of some *Maculinea* species is constrained and that adults may establish home ranges. We tested both hypothesis by analysing the movement pattern of individuals. We also investigated whether egg laying is time constrained, which would enhance the trade-off between flying and egg laying. Thirty females of *Maculinea rebeli* (Lepidoptera: Lycaenidae) were tracked within a single population in Central Hungary. Their egg-laying behaviour and individual patterns of movement were recorded, and the latter were compared

with random walk model predictions. The population was also sampled by MRR to estimate survival rates, and four non-mated, freshly eclosed females were dissected to assess their potential egg load. Net squared displacement of females was significantly lower than predicted by the random walk model and declined continuously after the 15th move. The ratio of net displacement and cumulative move length decreased with the number of moves, supporting the hypothesis that *Maculinea* butterflies establish home ranges. We found that low survival and a low rate of egg laying prevented females from laying their potential number of eggs within their lifespan. Time limitation increased the cost of movement, providing another possible explanation for the restricted movement of females.

Keywords Home range · Myrmecophily · Oviposition · Random walk model · Risk spreading

Introduction

The specialized interactions between *Maculinea* (Lycaenidae: Lepidoptera) butterflies and other species have been under studied at length [for a review see Thomas et al. (1998a, b)]. Less attention has been paid to the behaviour of the imagos, even though an understanding of a threatened species’ mechanisms and patterns of behaviour may greatly assist in the development of conservation strategies for it (Sutherland 1998; Caro 1999).

Uniquely among European butterflies, *Maculinea* species are obligate social parasites of *Myrmica* ant colonies. All *Maculinea* species are also endangered at national or continental scales in Europe, and are consequently regarded as “flagship” species of nature conservation (Thomas and Settele 2004; Settele et al. 2005). The life cycle of

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Maculinea rebeli and its interactions with associated species have been thoroughly studied both empirically (Elmes et al. 1991a, b, 1996; Thomas et al. 1991, 1993, 1997) and in theory (Hochberg et al. 1992, 1994; Clarke et al. 1997, 1998). *M. rebeli* females lay eggs on specific host plants (typically *Gentiana cruciata*), where its caterpillars briefly feed on flowers and seed. Fourth instar caterpillars descend to the ground and await discovery by foraging *Myrmica* workers, which adopt them into their nests (Elmes et al. 1991a, b). Caterpillars do not seek host ant nests actively, and die if they hatch on a plant that is beyond the foraging range of a host ant colony (Thomas 1995; Thomas et al. 1997). Lack of adoption or adoption by non-host ants is a major cause of mortality (Elmes et al. 1991a, b). So far, studies based on counting the eggs on host plants have shown that oviposition is independent of the presence of host ants (Thomas et al. 1989; Elmes et al. 1996; Thomas and Elmes 2001; Thomas 2002; Musche et al. 2006), although Van Dyck et al. (2000) found some association between the density of *Maculinea alcon* eggs on *Gentiana pneumonanthe* and the presence of its presumed host ant species.

Due partly to apparent competition between its sequential hosts (Thomas et al. 1997), *M. rebeli* usually occupies sites where only a small proportion (<30%) of *G. cruciata* plants coincide with host *Myrmica* colonies (Elmes et al. 1996). Assuming that *Maculinea* butterflies are unable to detect the presence of host ants beneath the host plants (Thomas and Elmes 2001), and that the distribution of *Myrmica* colonies is primarily affected by microclimatic conditions, the spatial variance of larval survival is inevitably high (Thomas et al. 1998a, b). Root and Kareiva (1984) suggested that in such cases “risk spreading” is a reasonable oviposition strategy. It assumes that females scatter their eggs over a wide area in order to minimize the generation-to-generation variance in reproduction rates. This hypothesis predicts that females follow linear flight paths during egg laying, eggs are usually laid singly on plants, and females pass over many suitable hosts. However, recent analyses of mark–release–recapture (MRR) data suggest that *Maculinea teleius* and *Maculinea nausithous* may establish home ranges, since their within-habitat displacement appears to be limited (Hovestadt 2005; Hovestadt and Nowicki 2005).

Animal movement can be classified by its behavioural background into routine and special movements (Van Dyck and Baguette 2005). Routine movements are associated with daily activities, while special movements involve large net displacement. In fragmented landscapes, dispersal is a by-product of special movements that are directed and cover large distances in a given unit of time (Van Dyck and Baguette 2005). Since dispersal is a key process in spatially structured populations (Hanski 1999), several studies have

investigated the behavioural aspects of dispersal in butterflies by tracking individuals (e.g. movement at habitat boundaries, Schultz 1998; Ries and Debinski 2001; Schultz and Crone 2001; Conradt and Roper 2006; foraging in the matrix, Conradt et al. 2000, 2001; or changes in movement behaviour within and outside habitat, Schtickzelle et al. 2007). Alternatively, explorative routine movements are performed within habitat patches with high levels of return and rarely contribute to dispersal in fragmented landscapes (Van Dyck and Baguette 2005). However, movement data collected within habitat patches may uncover important information about the animals’ behaviour (Mallet 1986) and studies of individual movement patterns play a significant role in the conservation of species (Caro 1999). Recently Lindenmayer et al. (2003) have stressed the importance of accurate knowledge of movement rules for the validity of population viability analyses. Metapopulation models usually assume that movement within habitat patches follows a random walk (Ovaskainen 2004; Ovaskainen and Hanski 2004), an assumption also underlying other studies (Odendaal et al. 1989; Turchin 1991; Schultz and Crone 2001). Nevertheless, the appropriateness of a random walk model for within-habitat movement of butterflies has been established in only a few cases (Kareiva and Shigesada 1983; Root and Kareiva 1984; Schtickzelle et al. 2007), while Fownes and Roland (2002) demonstrated its inadequacy.

We aimed to test the appropriateness of the random walk model for the movement of egg-laying *M. rebeli* females by analysing the flight paths of individuals. Movement patterns may differ from a random walk in two ways. The “risk-spreading” hypothesis predicts that egg-laying females follow linear flight paths, resulting in larger net displacement than predicted by random walks. Alternatively, if butterflies establish home ranges and restrict their movements to subsets of the habitat patch, net displacement will be shorter than predicted by the random walk.

We attempted to ascertain whether egg laying is time constrained or egg constrained in *M. rebeli* by estimating the egg-laying rate of females, their individual survival rates, and the potential number of eggs that an average female could produce.

Materials and methods

Study species

The taxonomic status of *Maculinea rebeli* (Hirschke 1904) is unclear, because recent cladistic studies based on either genetic (Als et al. 2004; Berezcki et al. 2005) or morphometric (Pech et al. 2004) data showed that it may only be a

distinct ecological form of *Maculineaalcon* (Denis et Schiffermüller, 1775). However, *M. rebeli* has previously been treated as a distinct species in many papers (see Elmes et al. 1991a, b; Thomas et al. 1991, 1993), so we use the term *M. rebeli* to denote the ecotype of *M.alcon*, which occupies dry calcareous grasslands in Hungary, flies from mid June to mid July and uses the cross-leaved gentian *Gentiana cruciata* (L.) as the main larval food-plant. Larvae in the population under examination feed exclusively on *G. cruciata* and are hosted by both *Myrmica sabuleti* (Mein.) and *M. schencki* (Em.) (L. Peregovits et al., unpublished data). *M. rebeli* lays single eggs on leaves and buds of the gentians. Caterpillars in the ant nests are fed by workers through trophallaxis (“cuckoo” feeding) (Elmes et al. 1991a), which is considered as a more productive (Thomas and Elmes 1998) and evolutionarily advanced form of myrmecophily (Thomas et al. 1991; Fiedler 1998; Als et al. 2004).

Study site

The study area was located in the Vértes Mountains in Central Hungary (47°26'N, 18°25'E, 365 m a.s.l.). In this region *M. rebeli* occupies dry calcareous grasslands mixed with oak–hornbeam woodland scrub. The study site was a section of grassland meadow (ca. 0.8 ha) on the fringe of an oak–hornbeam forest (Fig. 1). The meadow was surrounded by pine plantation on three sides and a native oak forest on the fourth. Some oak saplings (*Quercus petraea*), hawthorn (*Crataegus* spp.) and dewberry (*Rubus* spp.) scrub were scattered throughout the meadow.

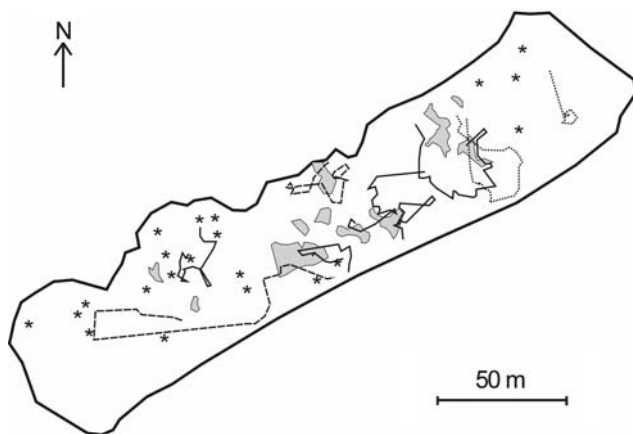


Fig. 1 Map of the study site. Asterisks indicate solitary gentian plants, grey polygons are dense gentian patches. Butterfly paths are divided into three groups: females observed to oviposit (solid lines), females observed to mate and oviposit (dashed lines) and females with no observed oviposition (dotted lines). Only nine paths out of 30 could be shown due to a high number of overlapping and/or spatially restricted (therefore not discernible) paths

Sampling method

Individual females were randomly chosen for tracking. Each female was followed until it was lost from view or stopped for >30 min. We followed at a distance of several metres to avoid influencing the butterflies’ behaviour, which was recorded on a dictaphone. Each landing point was marked with a numbered flag, which corresponds to a decision being made by the butterfly, and provides more meaningful results than the use of sampling at fixed time intervals. This method also prevents problems of over- or under-sampling due to the choice of time interval between samplings (Turchin 1991, 1998). It further allowed us to observe egg-laying behaviour. At each landing point we recorded the number of gentian shoots visited and the number of eggs laid on each shoot by the female. The distance between two consecutive landing points was classed as a move, and its length and direction were measured. We intended to avoid sampling a single individual twice, but were also concerned not to affect the butterflies’ behaviour, so individuals were captured and marked at the end of the tracking. The first and last landing points of each path were located by GPS (Trimble, Geo-Explorer3) and the distance between them was measured by a measuring tape to check the precision of measurement of successive moves on the path level. The deviation in the net displacement measured versus the displacement calculated from successive moves was within 1 m in all paths, indicating an acceptable degree of accuracy in our method. Sampling was carried out on 14 individual days between 20 June and 11 July 2005, between 1000 and 1700 hours under sunny and calm weather conditions.

We simultaneously carried out MRR sampling of *M. rebeli* adults to estimate the daily survival rate of the females. Butterflies were captured in nets, individually marked with fine-tipped waterproof pens (Edding 140S) on the underside of the hind wings and immediately released at the place of capture. Sampling was conducted on 14 days under suitable weather conditions. Four freshly eclosed, non-mated females were dissected and ova were counted in order to obtain a rough estimate of their potential egg load.

A map of the site was drawn using GPS to plot the positions of solitary gentian plants or the outlines of dense gentian patches (Fig. 1). Gentian shoots rather than plants were considered as the measurement unit of host plants, because shoots can always be distinguished. Thus the total number of gentian shoots was counted over the whole site.

Statistics

The flight paths of butterflies are typically circuitous, but can be approximated by a series of connected straight line

moves between the consecutive landing points (Kareiva and Shigesada 1983; Root and Kareiva 1984; Turchin et al. 1991; Turchin 1998). Quantitative analysis of path data was based on the discrete random walk approach, which allowed us to use only two simple parameters: move lengths and turning angles between successive moves. Correlated random walk (CRW) is a simple random walk formulation in which the distribution of turning angles is not uniform, inducing persistence in the direction of movement.

Net squared displacement (R_n^2) is a characteristic of paths and refers to the square of the net displacement of an individual after n moves. Comparing R_n^2 of observed paths with its theoretical distribution provides a test of the appropriateness of the CRW model. Observed R_n^2 was calculated for each n (number of moves) by averaging the net squared displacement after n moves for all observed paths that consisted of at least n moves. Since the length of observed paths varied in our data set, observed R_n^2 for low n is an average over all paths, but as n increases fewer paths are used. Theoretical values of R_n^2 were calculated using a simple formula of Kareiva and Shigesada (1983) that specifies the expected net squared displacement for each value of n , but does not provide a measure of variance around this expectation. It would have been straightforward to carry out an overall bootstrap goodness-of-fit (GOF) test for CRW, but we found the move length between paths significantly different (Table 1, test 3). Thus, instead of pooling data of all individuals, R_n^2 of the observed paths was compared with theoretical values for each path separately. For each observed path, 1,000 paths were simulated by keeping the move lengths fixed to observed values and sampling the turning angles from a uniform distribution (Schtickzelle and Baguette 2003). For each n , R_n^2 was calculated in all the 1,000 simulated paths and in the observed path as well. The 95% confidence limits for R_n^2 were estimated by the 25th and 975th percentiles of R_n^2 of the simulated paths.

The ratio of the net displacement and the cumulative length of moves (R_{NC}) is an indicator of movement directionality ranging between 0 and 1. If the path is a straight line, then $R_{NC} = 1$, and if the starting and end points of the path are identical it is 0. R_{NC} was calculated

for the subpaths at each number of moves of each path, and its relationship to the number of moves was assessed by a linear mixed effects model, in which paths formed the random factor, since subsequent R_{NC} values of a given path were not independent from one another. In the model the variance was weighted by the power function of the number of moves in order to fulfil homoscedasticity (Pinheiro and Bates 2000).

After checking the fit of MRR data to the Cormack–Jolly–Seber model by a bootstrap GOF test using program MARK 4.2. (White and Burnham 1999), a model selection based on Akaike’s information criterion (AIC) values was performed, and the parameter estimations of the most supported model were accepted.

Females usually probed the surface of the host plant with the apex of their abdomen before oviposition, a form of behaviour that we called “egg-laying investigation”. These investigations did not always result in oviposition. The number of eggs laid on each successful oviposition was recorded. The relationship between the number of eggs laid and other variables on the path level (number of moves, duration of path, sum of move lengths) was assessed using linear models.

Simulations were programmed into R code, and data management and analyses were performed using SciViews-R companion applications (R Development Core Team 2005; Grosjean and Lecoutre 2005). Some test results are presented in tables to offer an easy overview of the hypotheses tested on the data.

Results

Movement characteristics

We sampled 30 flight paths involving a total of 412 moves (from five to 24 moves per path, median number of moves = 14). The average tracking time was ~50 min. Move length followed a log-normal distribution (Table 1, test 1) and differed significantly between paths (Table 1, tests 2 and 3). No autocorrelation (order 1–5) between the consecutive move lengths of a given path was detected

Table 1 Statistical tests on move length (Zar 1999, p 591)

	Null hypothesis tested	Test name	Test statistic	<i>P</i> -value
Test 1	Log-normal distribution	Kolmogorov–Smirnov	$D = 0.0412$	0.479
Test 2	Equality of variance between paths	Bartlett (on log-transformed move length)	$\chi^2 = 29.76$	0.426
Test 3	Equality of means between paths	One-way ANOVA	$F = 2.3184$	<0.001
Test 4	No autocorrelation between length of consecutive moves	Pearson’s correlation coefficient on consecutive lengths (with lag = 1–5)	9 significant ($P < 0.05$) ρ out of 136	

Table 2 Statistical tests on turning angle (Fisher 1993)

	Null hypothesis tested	Test name	Test statistic	P-value
Test 1	Uniform vs. unimodal distribution with mean = 0	Rayleigh test for uniformity against a unimodal alternative with mean = 0	$R = 0.0381$	0.1452
Test 2	No autocorrelation between consecutive turning angles	Circular-circular (T-linear) correlation coefficient on consecutive turning angles (with lag = 1–4); P-value estimated by permutation test	6 significant ($P < 0.05$) ρ out of 105	

(Table 1, test 4): the length of a given move did not depend on the length of previous moves, so the first assumption of the CRW model was fulfilled.

The distribution of turning angles did not differ significantly from uniform (Table 2, test 1). Since the uniform distribution is symmetrical around 0, this implies that females did not show a preference for left or right turns, and more importantly that they turned in all amplitudes with the same probability. No autocorrelation (order 1–4) between the consecutive turning angles of a given path was detected (Table 2, test 2), so a given turning angle was not influenced by previous turning angles. The uniform distribution of turning angles suggests that there was no directional persistence in the movement of butterflies, so the assumption of CRW was not fulfilled. In the simpler uncorrelated random walk model the distribution of turning angles is assumed to be uniform. We therefore used its simplified formula to calculate the predicted values of net squared displacement (R_n^2).

Plotting the observed and expected values of R_n^2 against the number of moves provides a test of the fit of the random walk model. If the path is a straight line, R_n^2 increases following a parabola, which represents the upper limit of possible R_n^2 ; under the conditions of uncorrelated random walk R_n^2 grows linearly with n (number of moves), as is predicted by:

$$R_n^2 = n \times m_2,$$

where n is the number of moves and m_2 is the mean squared move length (Kareiva and Shigesada 1983). An upward curve in R_n^2 indicates a persistence in the direction of movement (correlated random walk), while a downward curve indicates some barrier to movement (Turchin 1998). R_n^2 averaged over all observed paths for each n increased linearly until $n = 15$, where it peaked ($\bar{R}_n^2 = 325.2 \text{ m}^2$, $\text{SE} = 172.30 \text{ m}^2$); after that it declined (Fig. 2). Apart from the divergence between predicted and observed values, we highlight the convex shape of the observed curve viewed from above.

When simulating 95% confidence intervals of R_n^2 for each number of moves for each path, and plotting them against the number of moves (Fig. 3), the observed R_n^2 fell below the simulated 95% confidence limit (at least for one move) in 13 out of 30 (43.3%) paths, while one path was

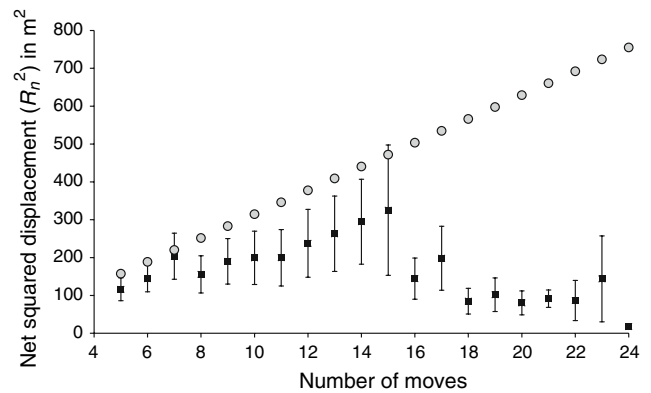


Fig. 2 Observed net squared displacement averaged over all paths (solid squares) and the predicted values of the uncorrelated random walk (grey circles) (Kareiva and Shigesada 1983) in relation to the number of moves

both above and below the confidence limits. The ten paths for which the maximum value of R_n^2 was reached at the end of the path were considered as quasi-monotonous ones. The other 20 paths were non-monotonous because the peak of R_n^2 emerged somewhere along the path (Fig. 3). Butterflies with non-monotonous paths were observed for a longer time. They made more steps but had smaller values of R_n^2 than quasi-monotonous ones (Fig. 4).

There was a significant negative relationship between the number of moves and R_{NC} values according to the linear mixed effect model ($F_{1,352} = 306.01$, $P < 0.0001$, fixed effect = -0.027 ; Fig. 5). R_{NC} equals zero when a butterfly returns to the starting point of the path predicted by the model at the ~ 22 th step. The distribution of the residuals and the random effects were normal. On Fig. 5 we fitted the fixed effect of the model to the scatterplot of the R_{NC} index and the number of moves. Since the variance of the R_{NC} index declined considerably (Fig. 5), weighting it by the power of the number of moves was appropriate in order to fulfil the homoscedasticity. The random effect explained only 5.06% of the total variance.

Egg-laying behaviour

A total of 103 investigations by 23 egg-laying females were recorded on 98 different gentian shoots. More than one egg-laying investigation was observed on five shoots,

Fig. 3 Observed net squared displacement and simulated 95% confidence intervals (CIs) for four different observed paths. *y-axis* Net squared displacement (m^2), *x-axis* number of moves. **a** Non-monotonous path, below the CI; **b** quasi-monotonous path, below and above the CI; **c** non-monotonous path, between the confidence limits; **d** quasi-monotonous path, between the confidence limits

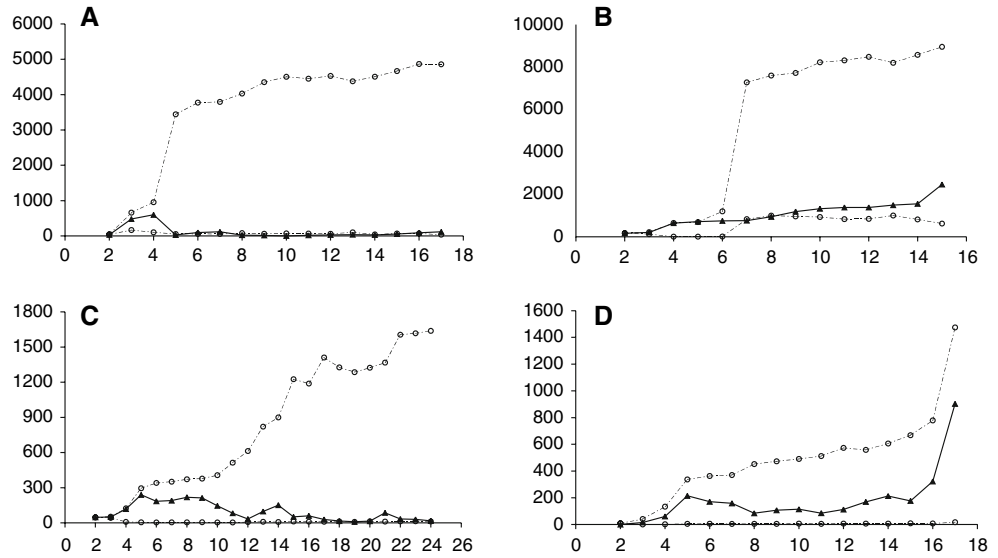


Fig. 4 A significant difference was detected between non-monotonous and quasi-monotonous paths in three variables (Wilcoxon rank sum test, $W = 48$, $P < 0.05$, $W = 27.5$, $P < 0.05$, $W = 151$, $P < 0.05$, respectively) (Zar 1999)

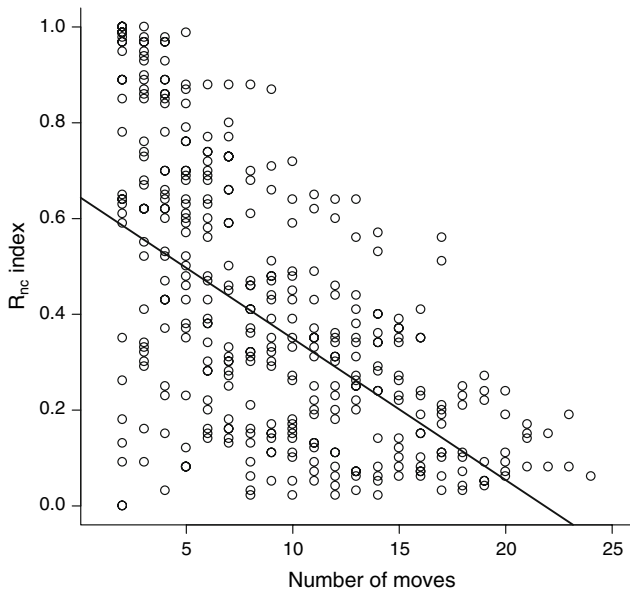
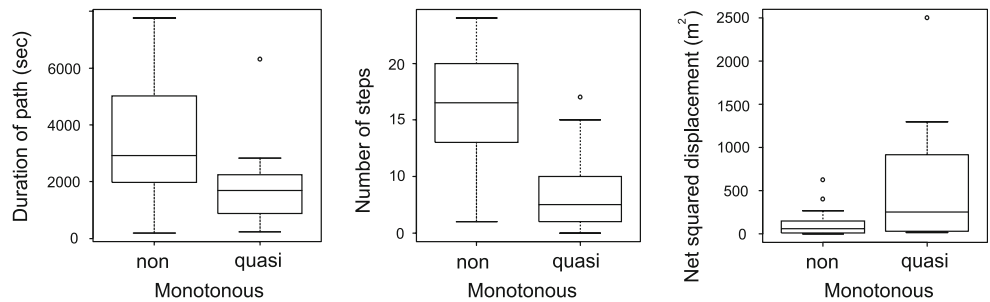


Fig. 5 The relationship between the number of moves and the ratio of the net displacement and the cumulative length of moves (R_{NC} index). The solid line indicates the fixed effect of the significant linear mixed effects model

in all cases by different females, so repeated oviposition by a female on the same shoot was never detected. Seventy-two investigations resulted in at least one egg being laid (“successful” ovipositions). Seven females did not attempt to oviposit during the observation and one individual only investigated the host plant, but did not lay any eggs. Females laid very few eggs on each occasion (for all 103 investigations, median = 2, mean = 1.92, SD = 2.21; for 72 successful ovipositions, median = 2, mean = 2.75, SD = 2.17).

We found a significant positive relationship between the duration of path and the number of eggs laid ($F_{1,28} = 5.001$, $P = 0.034$, $R^2 = 0.152$) (Fig. 6). The estimated parameter ($b = 4.763$, SE = 2.13) can be considered as an egg-laying rate (eggs/hour). R_{nc} , sum of move lengths, and maximum net displacement did not show any relationship with the number of eggs laid.

In the Cormack–Jolly–Seber model with the best fit, the daily survival rate (ϕ) and the recapture probability (P) were constant over time and identical for males and females. The estimated ϕ was 0.763 (95% confidence limit lower, 0.724; upper, 0.799). The population under examination was presumably closed in terms of movement, so the

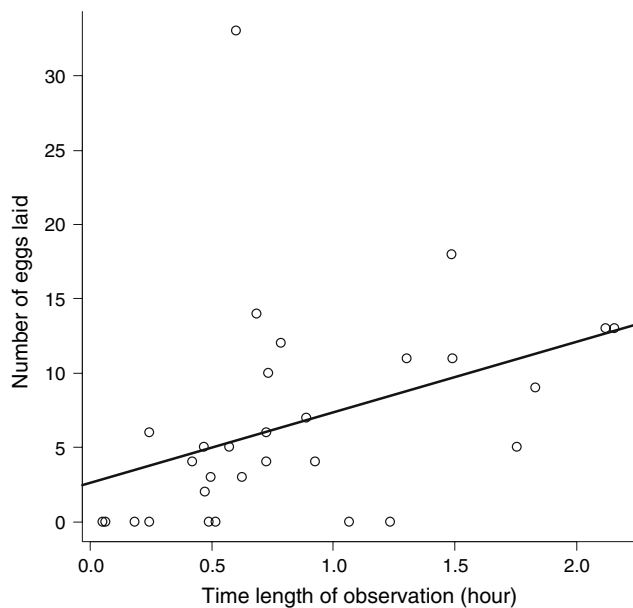


Fig. 6 Linear relationship between the duration of a path and the number of eggs laid: number of eggs = $2.57 + 4.763 \times \text{hour}$. One outlier and several females with no eggs weaken the fit of the model

average residence time (the period of time during which the population is reduced by 50%) was estimated at 2.58 days. This made it possible to estimate the total number of eggs laid per butterfly. Assuming that *M. rebeli* females are active 8 h per day, their average active lifespan is 20.6 h. Substituting this value into the equation of the linear regression of egg number and path duration, provides an estimate that an average female lays 100.9 eggs (SE = 43.9; 95% CI, 10.8–190.9). The number of ova counted in the dissected females (mean = 375.6, SD = 144.9, $n = 4$) thus greatly exceeded the estimated number of eggs laid per butterfly.

Although actual host plant distribution was not compared with theoretical distributions, we found the distribution of host plants very clumped on the sampling site: circa 82% of the gentian shoots ($\sim 1,300$ from the total of 1,585) were aggregated into a total area of 380 m² (5% of the sampling site). Thus a few gentian patches were clearly distinguished (Fig. 1).

Discussion

Our results provide a detailed description of the movements of *M. rebeli* females within a single population, including a test of the appropriateness of the random walk model. In most studies, within-habitat movement is assumed to be random (e.g. Odendaal et al. 1989; Schultz and Crone 2001; Ovaskainen 2004), but our results clearly showed that the random walk model did not describe the within-habitat

movement of *M. rebeli* females appropriately, since it overestimated the net displacement. All approaches applied in our analyses suggested that the movement of the butterflies was restricted and that they established home ranges. So far, non-random movement of butterflies has been demonstrated in the matrix and at habitat boundaries (Conradt et al. 2000; Conradt and Roper 2006), but less clearly within habitat patches. In our study, butterflies seemed to reach the boundary of their foraging range at about the 15th move, where the peak of the observed values suggested that the maximum area of the butterflies' foraging range is $325 \pm 172 \text{ m}^2$, an unexpectedly small value.

The observed value of R_n^2 was significantly smaller than predicted by the random walk model in 43.3% of the paths, indicating the inappropriateness of this model. Although the division of paths into quasi- and non-monotonous types was slightly arbitrary, the significant difference between the two in the number of moves, path duration and net squared displacement (Fig. 4) allowed us to conclude that the longer a butterfly was tracked, the more moves it made and the smaller its net displacement. This is in agreement with findings shown in Fig. 2: after the 15th move the average net squared displacement tended to decrease.

The significant negative linear relationship between the number of moves and the R_{NC} index means that the distance covered by the flight path of the butterflies increased much more slowly than the number and cumulative length of moves. At approximately the 20th move the values of R_{NC} approach zero. One possible explanation is that butterflies foraged in a restricted area, and after about 20 moves returned to the vicinity of the starting point of the path. Due to the lack of autocorrelation in the turning angles, we exclude the possibility that *M. rebeli* females had any systematic movement patterns (such as foray loops). We conclude rather that their movement was restricted primarily to the proximity of small but dense gentian patches (Fig. 1).

The females under observation never left the habitat and seldom approached its boundaries, so we rule out the possibility that frequent interferences with habitat boundaries modified their movement patterns. Furthermore, if butterflies had frequently bounced back at habitat boundaries, this would have been expressed in the distribution of turning angles, resulting in divergencies from the observed uniform distribution.

The observed movement pattern departed from that predicted by the risk-spreading hypothesis. However, the results do not disprove the other two predictions of the risk-spreading hypothesis (Root and Kareiva 1984), because *M. rebeli* females laid eggs singly and very few eggs were laid per shoot by a single female.

The estimated apparent daily survival rate is in agreement with previous studies on *Maculinea* species (Pfeifer

et al. 2000; Árnýas et al. 2005; Nowicki et al. 2005a, b). The estimated number of eggs laid per butterfly provides only a rough approximation, but it is nevertheless consistent with the results of Hochberg et al. (1992), who used a different approach. Our estimate could be imperfect if the butterflies change their egg-laying rate over time (Morales and Ellner 2002), but this is unlikely in an insect with such a short reproductive stage.

Even if our estimates of the daily survival rate and the egg-laying rate contain uncertainties, the large difference between the egg load and the estimated number of eggs actually laid by a female over its lifetime suggests that egg laying of *M. rebeli* is time constrained, which is a widespread phenomenon among butterflies (e.g. Kingsolver 1983; Doak et al. 2006).

The clumped distribution of gentians is typical of most *M. rebeli* sites (Elmes et al. 1996). Both field studies and modelling demonstrate that *Maculinea* caterpillars cause considerable damage to ant nests and reduce their competitiveness (Thomas et al. 1997). Since caterpillars depend on specific host plants for their early development, those parts of the habitat that lack gentians provide refuges for the host ants. Indeed, the long-term persistence of this butterfly on a site depends on the presence of such refuges (Elmes et al. 1996; Clarke et al. 1997; Thomas et al. 1997).

We suggest two major reasons for the restricted movement of females. First, it can be shown that even a home range of observed mean size (325 m²) can be enough for a female to avoid sibling competition, if it contains a high density of food plants. Using Hochberg et al.'s (1994) values for host ant foraging range (10 m²), Elmes et al.'s (1996) higher (30%) value for host ant incidence and Thomas and Elmes' (1998) values for the mean capacity of a *Myrmica* nest to support *M. rebeli* (5.3 pupae per nest), we can calculate that a *M. rebeli* female's mean home range contains 9.75 exploitable host ant colonies capable of rearing a total of 52 *M. rebeli* larvae to adulthood each year. Combining our values of lifetime natality (101 eggs per female) with Hochberg et al.'s (1992) values for *M. rebeli* egg and larval density-independent survival on gentians (0.758) and density-dependent larval survival on gentians, we obtain a figure of 42–54 pre-adoption larvae per female each year (see calculations in ESM). In addition, competition between siblings is further reduced due to polymorphic growth of caterpillars: 75% of the cohort take 2 years to develop per host-ant nest and 25% take 1 year (Thomas et al. 1998a, b). As described, females spread their eggs fairly evenly within their home ranges, thus even as small an area as 325 m² is sufficient to lay the maximum number of eggs in their lifetimes whilst avoiding sibling competition. However, the period of time during which our observations were made was short and we cannot be sure that females spend all of their lives within such small home

ranges. The other cause of restricted movement may be the time-constrained nature of egg laying. Time limitation increases the costs of flying, since it not only consumes energy but also time. In summary, the benefits for females of greater movement are poor due to the unpredictability of larval survival and the ease with which sibling competition can be reduced, while the costs are high: thus, restricted movement may result in a higher reproductive output per female.

Our results confirm the suggestion of Hovestadt (2005) and Hovestadt and Nowicki (2005) that *Maculinea* butterflies may establish home ranges within habitat patches. The concordance between our and their results is particularly interesting, because they employed MRR techniques, so their conclusions derive from an analysis of patterns (the spatial distribution of individuals). By tracking individuals, we gained a deeper insight into the process (movement of individuals) that generates the pattern, and we were able to combine this process with the spatial distribution of resources. It is important also to note that Hovestadt (2005) and Hovestadt and Nowicki (2005) studied populations of *M. teleius* (and *M. nausithous*), a predatory species the host plant of which (*Sanguisorba officinalis*) is abundant and evenly distributed on most of the sites.

Finally, the restricted movement of females does not allow us to infer the rate of interpatch dispersal, but only to endorse the presumption of Hovestadt (2005) that dispersal is a very rare and special event in the life of *M. rebeli* females, since the females under observation never left the habitat patch.

Both the limited within-habitat movement and the rare interpatch dispersal have implications for conservation, since they can amplify the effects of fragmentation for populations. Elmes et al. (1996) stressed that the most important factor essentially affecting the size and persistence of *M. rebeli* populations is the distribution of host plants, which was later confirmed in simulation studies (Clarke et al. 1997, 1998). Additionally, in the absence of management, suitable sites often become overgrown by scrub, making the habitat unsuitable for the butterfly (Dolek et al. 1998). We emphasize the role of linkage between gentian patches in order to decrease the spatial fragmentation of populations. The movement of butterflies between these patches should be facilitated by cutting the scrub and saplings.

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