

Climate-dependent dispersal rates in metapopulations of burnet moths

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Abstract Predicted climate change implies warmer weather and a higher frequency of extreme weather situations. The consequences of the warm July in 2003 was investigated in contrast to the cold July in 2004 in southern Sweden with focus on the dispersal rate of two species of burnet moths (*Zygaenidae*). During an extensive mark-release-recapture program in metapopulations of burnet moths substantial differences in inter habitat patch dispersal rates were observed. For two species of *Zygaena* it was 2.14 and 2.18 times higher during the warm year. Measured patch dispersal rate significantly declined towards the edges of the large study-area, suggesting that individuals disperse outside the study-area. No significant differences in dispersal rates were found between the two species studied. The dispersal rates were similar for both females and males, and no density dependent effects on dispersal or effects of amount of nectar rich flowers were found. Dispersal events appeared as distinct movements, often reaching several kilometres. We conclude that dispersal depend on climatic conditions. Exceptionally warm years may be especially important for survival of certain species in metapopulation systems and this may be crucial for the survival of populations during scenarios of climate change.

Keywords Butterflies · Climate change · Connectivity · Conservation · Habitat · Landscape · Movement · Mobility

Introduction

Dispersal rate is one of the most important traits determining the distribution of species and the structure of populations, and dispersal rates vary considerably between species and populations (Koenig et al. 1996). Several features act together and influence dispersal rates and dispersal distances; age, population density, mate-location and food distribution (Koenig et al. 1996; Thomas et al. 2000). Also landscape composition, resource distribution and the matrix can influence dispersal patterns (Dennis and Shreeve 1991; Shreeve et al. 1996; Shreeve and Dennis 2010). Dispersal behaviour, inferred from changes in local distribution, can vary considerably from 1 year to another, mainly due to weather fluctuations (Solbreck 1991; Kindvall 1995). Climate change is predicted to lead to an increased mean temperature and more frequent climatic extremes (Pollard et al. 1997; Parmesan et al. 2000). Indeed, in northern latitudes, warm weather has a positive effect on both distribution and range of many insects (Parmesan and Yohe 2003), but increased habitat destruction limits this positive weather effect (Warren et al. 2001). In fact, some species change their habitat use as a result of extreme weather conditions (Kindvall 1995; Davies et al. 2006). Climate can cause widespread synchronism of species population fluctuations (Sutcliffe et al. 1996; Raimondo et al. 2004; Powney et al. 2010), but different species show various degrees of sensitivity to climatic extremes (Pollard et al. 1997; Hill et al. 2001; Morecroft et al. 2002).

In the future some populations may face an increased extinction risk caused by increased appearance of climatic extremes (Thomas and Hanski 2004; Thomas et al. 2004).

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It is important to relate population variables to extreme weather events and examine the consequences in order to make more accurate predictions of biodiversity changes. Warm weather has been suggested to promote dispersal (Dennis 1977; Warren 1987; Dennis and Bardell 1996; Walters et al. 2006), and this patterns was recently found for two saproxylic beetles (Larsson and Svensson 2011). Long-term studies with weather extremes are required to measure direct effects of weather on dispersal, or at least observations from 2 years with weather extremes.

In this study the effects of a warm period on dispersal rate of burnet moths (*Zygaena* spp.) occurring in metapopulation systems was examined. The unusually warm July in 2003 gave a unique opportunity to directly observe weather effects on dispersal, where previous studies mainly have inferred dispersal behaviour from distribution patterns. Further, dispersal rates and the relation to the spatial configuration of habitats within the study-area, habitat characteristics, population density, sex, and whether dispersal rate differs between the two species studied were investigated.

Materials and methods

Study species

Burnet moths have declined during the last 50 years throughout Western Europe (Väisänen and Somerma 1993; Young and Barbour 2004), but are still relatively abundant in parts of southern Sweden. They occur in colonies, often small and relatively isolated, mainly at recently abandoned semi-natural grasslands rich in flowers (Tremewan 1985). They appear to be sensitive to both high grazing pressure and gradual succession from grassland to forest of suitable patches (Franzén and Ranius 2004). Mating often takes place on nectar rich flowers, in the studied area mainly on inflorescences of the herb *Knautia arvensis*. When approached the moths remain sitting exposed on the flowers, which makes them suitable for field studies. The burnets seem to occur in metapopulations, where local extinction and colonisation occurs due to the narrow habitat requirements and changing habitats between years (Tremewan 1985). In the study-area, *Zygaena viciae* appear from late June whereas *Z. lonicerae* appear from the beginning of July. In 2003 the flight period of these species lasted from 28 June to 12 August.

Study-area

The study-area in Stenbrohult parish in southern Sweden (56° 37'N, 14° 11'E) covers 81 km², including some lakes, and bordering Lake Möckeln in the west, built up areas and an exploited bog in the south and forest-dominated land to

the east and north. The study-area is typical of the wider forest-dominated landscape of the region, consisting mainly of forests, mires and lakes. Numerous small farms occur throughout the study-area, but the proportion of arable fields is low (about 1 % of land cover). There are some substantial areas of semi-natural grassland habitats (4 % of land cover), mainly pastures and recently abandoned pastures. Such habitats are centred on small farms which are separated by dense forests, mainly dominated by spruce *Picea abies*. The distances between the farms are approximately 1 km. Two nature reserves with traditionally managed hay meadows, each with about 5 ha of hay meadow, are situated in the study-area, and these have a rich associated flora (Nilsson and Nilsson 2004).

Patches

Every patch of semi-natural grassland (n = 119) in the study-area was mapped and 68 patches were occupied by one of the studied species. Patches were defined as separate if the distance between them was 100 m or more (Dennis et al. 2003). However, some patches were also regarded as distinct when separated from each other by only 75 m, if separated by tall tree stands that were assumed to provide an additional barrier to dispersal. The mean distance from the centre to the edge of an average habitat patch was approximately 40 m. Thus, we calculated the mean distance moved for all recaptured individuals, assuming a movement distance of 40 m for the individuals that were recaptured within the same patch as where marked. A within-patch movement of 40 m corresponds well with other studies of local movements on burnet moths (Bourn 1995; Kreusel 1999; Menéndez et al. 2002).

Habitat quality

Habitat quality for the burnet moths was measured using indicator herb species of semi-natural grasslands which are more valuable from a conservation point of view according to Lindahl (1997). Abundance of flowers in the grasslands was measured in 50 × 50 cm plots. At least seven plots were placed out in each patch. In larger patches the plots were placed with 100 metre intervals. Plot samples were taken along transects criss-crossing all patches, twice during the season in June and during the period 20 July–20 August. The abundance of flowers was measured as the number of flowering inflorescences of respective plant species (n_{flow}) and was counted in each 50 × 50 cm plot. The amount of nectar resources was then calculated as an index, where the plants were given different weight values depending on their attractiveness. Jennersten (1984) ranked the importance of different plant species depending on the frequency of butterfly visitations (rank) and our index was

calculated as the rank multiplication with the abundance of the plant in respectively patch. The mean of the nectar index for each patch (mean/plot in each grassland patch) was used in the statistical analyses by dividing the values with the number of squares sampled in each patch (n_{sqr}) (Eq. 1). We observed similar flower preferences in our study-area as Jennersten (1984).

$$\text{Nectar index} = \frac{\sum (n_{\text{flow}1} * \text{rank}_{\text{flow}1} + n_{\text{flow}2} * \text{rank}_{\text{flow}2} + \dots)}{n_{\text{sqr}}} \quad (1)$$

Vegetation height was measured in each 50×50 cm plot described above, using a plate horizontally placed on the vegetation and the height was measured between the ground and the plate. The plate was an A4 sized piece of plastic weighing 14 g. The mean of the vegetation height for each patch (mean/grassland patch) was used in the statistical analyses (Stewart et al. 2001).

Mark-release-recapture

In order to study dispersal, an extensive mark-release-recapture (MRR) programme for burnet moths was carried out in the periods 26 June–31 July 2003 and 23 June–9 August 2004. Every single patch was visited in approximately 3-days interval when there was suitable weather, and all individuals of *Zygaena* spp. encountered were captured with a butterfly net. Each individual was identified as to species and sex and marked with a fine-point permanent ink pen, receiving a unique code for that marking event. Date, sex, activity and site of capture were recorded during each marking occasion. We prioritised working in a larger area in order to also find long-distance dispersal and it was, due to the large numbers marked, therefore impossible to mark all moths individually. Hence, all individuals were marked with a unique code at each patch and occasion, making it possible to detect between-patch movements and estimate dispersal rates.

Recaptures on the marking day were not included in the analyses to avoid underestimating dispersal (Gall 1984). Recaptured individuals that had moved between patches were subsequently individually marked according to Kreusel (1999). The distance of all movements between patches was recorded (the number of marked individuals that moved between patches more than once were only three). Marking and handling individuals may affect their mobility (Morton 1984) and therefore each insect was handled with care.

Dispersal rate

The overall frequency of dispersal was calculated as the number of individuals recaptured in patches other than in the patch where they were marked (individuals

transferring), divided by the total number of marked individuals recaptured anywhere in the system, expressed as a percentage. Due to the marking method, it was impossible to separate individuals when recaptured from the same marking occasion at the same patch repeatedly. Individuals recaptured more than once in the patch marked were treated as the same individual so as not to overestimate the number of individuals moving. Using the minimum number of individuals recaptured in the analysis of dispersal rate, the effect of time spent in the field was eliminated as a confounding factor.

Dispersal frequency for each patch was calculated as the number of individuals moving to a new patch (n_{mov}) divided by the number of recaptured individuals at the original patch (n_{recep}), subtracting individuals recaptured at other sites (n_{reco}) (Eq. 2).

$$\text{Dispersal frequency} = n_{\text{mov}} / (n_{\text{recep}} - n_{\text{reco}}) \quad (2)$$

The percentage of transferring individuals per patch was calculated as the number of individuals dispersing to a new patch each year (n_{dis}) divided by the estimated minimum number of recaptured individuals that year (n_{rec}) (Eq. 3).

$$\text{Patch dispersal rate (\%)} = n_{\text{dis}} / n_{\text{rec}} * 100 \quad (3)$$

Connectivity

Dispersal data near the edge of the study-area can be expected to be biased, with some individuals being undetected or simply dispersing outside the study-area in unexamined habitats (Barrowclough 1978; Franzén and Nilsson 2007). Thus, in the statistical analyses a measure was included to examine if the dispersal rate was related to the distance to the edge of the study-area. The distance was measured from the centre of the study-area to each patch where burnets were recaptured. The distance from the centre was highly correlated (Pearson $r = 0.83$) with the connectivity index calculated for all patches of semi-natural grasslands (cf. Moilanen and Hanski 2001). In finite areas the connectivity index suffers the same problem of bias as dispersal data, since patches were not included outside the study-area. For between-patch dispersal rate we concluded that it is more relevant to determine if it was related to the distance from the centre of our study area than to a connectivity index, which is more useful when examining occupancy patterns and survival probabilities (Tischendorf and Fahrig 2000; Moilanen and Nieminen 2002; Cabeza 2003). The study-area is adjacent to a large lake in the west, built up areas and an exploited bog in the south and to coniferous forests to the north and east. Thus, the areas surrounding the landscape has a low proportion of suitable grassland habitats that in our case might bias the connectivity measure suggested by Moilanen and Hanski (2001).

Statistics

Daily mean maximum temperatures were obtained from the weather station in Vaxjo, 50 km north of the study-area for the years 1873–2004 (Tuomenvirta et al. 2001; SMHI 2002; SMHI 2003; SMHI 2004). Paired samples *t* test was used to compare the mean maximum temperature in July 2003 to the mean maximum temperature in July 2004. Dispersal frequency was treated as the dependent variable and analysed against nectar resources (index), distance from centre of study-area (connectivity), density (of each burnet species), and habitat patch size (area). Density of burnets in a patch was calculated as the number of individuals per hectare. Population sizes were calculated for each patch using the POPAN module in the program MARK (White and Burnham 1999). Dispersal rates between 2003 and 2004 were compared with a χ^2 test using the number of individuals recaptured that had not moved to another patch and the number of individuals transferring between patches. We also used a χ^2 test to see if there was any difference in dispersal rates between the two species. We used a Mann–Whitney U-test to analyse if there was any difference in the number of dispersal events between the sexes and *t* test was used to analyse if dispersal events were related to the flight season (early, middle or late). GLM analyses of dispersal rate in relation to habitat and population characteristics was performed for *Z. viciae* in 2003. The number of recorded dispersal events was too low for *Z. lonicerae* in 2003 and 2004 and for *Z. viciae* in 2004 for this analysis. For statistical analyses SPSS 11.0 was used.

Results

In 38 patches ten or more burnet moths per patch were marked, and in total 7301 burnet moths were marked in 68 patches. For a map over the patch network see Franzen and Nilsson (2007). The number of marked, recaptured, and transferring individuals together with dispersal distance data are presented in Table 1. Mean dispersal distance was

<100 m for both species in both years. A difference in between patch dispersal rate was shown between the years, with a significantly higher dispersal rate of 8.5 % in the warmer 2003 compared to 3.9 % in 2004 for *Z. viciae* ($df = 1$, $\chi^2 = 5.65$, $P = 0.018$). For *Z. viciae* the dispersal rate was thus 2.18 times higher in 2003 than in 2004, and for *Zygaena lonicerae* it was 2.14 times as high in 2003 compared with 2004. July in 2003 showed a significant higher mean maximum temperature (mean max 22.9 °C) compared with 2004 (mean max 18.8 °C) ($P < 0.001$, $t = 4.62$). The normal July mean maximum temperature in Vaxjo is 21.0 °C (based on mean maximum temperature data from 1961 to 1990). No significant difference in dispersal rate between the two species was found in 2003 ($df = 1$, $\chi^2 = 0.03$, $P = 0.31$), or in 2004 ($df = 1$, $\chi^2 = 1.12$, $P = 0.18$).

For *Z. viciae* the dispersal rate between patches significantly decreased towards the edges of the study-area in 2003 (Table 2, Fig. 1). The dispersal rate was unrelated to abundance of flowers, habitat patch size, and population density (Table 2). No difference in the proportion of dispersal events between sexes were found (Mann–Whitney U-test, $P = 0.26$), neither was any relationship found between dispersal events nor the time of the flight period (*t* test, $P = 0.54$).

Discussion

Increased dispersal rate between patches in the warmer year 2003 was evident compared to the relatively cold year 2004. Long-term weather data from a nearby weather station show that both years studied deviate about 2 °C from normal July mean maximum temperatures. Climate predictions for large parts of Europe suggest that such years as warm as 2003 will become more frequent in the future (Easterling et al. 2000; Parmesan 2001). Since many insects, including burnet moths, are likely to be favoured by warm weather in northern Europe (Roy et al. 2001; Hill et al. 2002; Davies et al. 2006) the effect on dispersal rate may be a general effect among thousands of species. There

Table 1 Summary of mark-release-recapture studies in 2003 and 2004 for the two study species

Species and year	Individuals marked	Individuals recaptured	Individuals transferring	Mean transfer distance (m)	Maximum dispersal distance (m)
<i>Zygaena lonicerae</i>					
2003	554	117	10	540	3,499
2004	184	25	1	494	494
<i>Zygaena viciae</i>					
2003	4,202	944	80	1,078	5,561
2004	2,361	232	9	1,805	4,062

Table 2 GLM analyses of dispersal rates of *Z. viciae* in 2003 in relation to patch size, the patch distance from the study area centre, the density of *Z. viciae* and the density of flowers in the patch

Source of variation	B	P
Patch size	−0.28	0.75
Distance from centre	−0.32	0.01
Density of <i>Zygaena viciae</i>	−2.798	0.633
Density of flowers	4.28	0.78

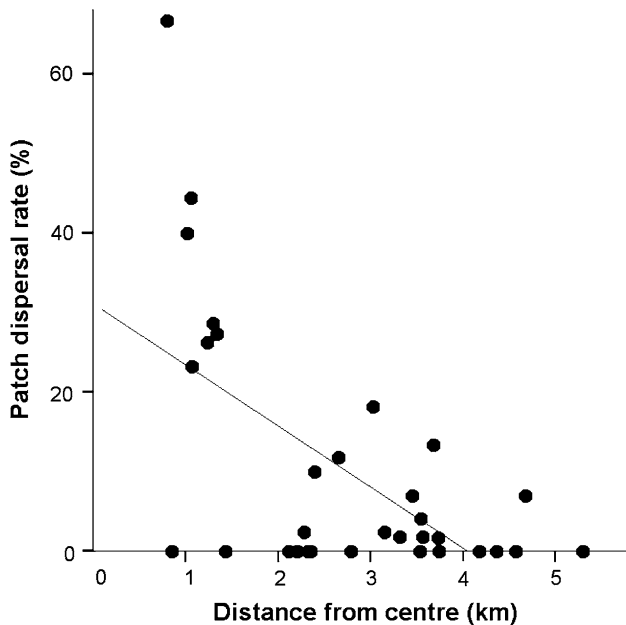


Fig. 1 Patch specific dispersal rates of *Z. viciae* in 2003 in relation to the patch distance from study-area centre (x). Dispersal rate = $0.31 - 0.08x$, $r^2 = 0.36$

is also evidence that climate conditions influence vertebrate dispersal (Walls et al. 2005) as well as plant dispersal (Kuparinen et al. 2009). Our results only cover 2 years and two species, and therefore the conclusions are preliminary but indicative. To solve this, in the future studies using dispersal distances from species over several years with different weather should be performed.

An important question is how an increased dispersal rate will affect population survival and in particular the survival of species similar to the species investigated in this study, which occurs in metapopulations. Theoretical studies indicate that, dependent on parameter values, metapopulation survival can increase, remain unaffected or decrease with increased dispersal rates (León-Cortés et al. 2003). Many British butterflies occur in warm habitats, and many species have avoided extinction by moving into warm refugia habitats (Thomas 1993). If summer temperatures increase, these species would also survive in later seral stages that are more common and less dependent on man (Thomas 1993). Warm

weather will probably be of major importance in areas close to the northern range for metapopulation survival because dispersal rate increases substantially in favourable weather. Close to the southern range margins warmer weather might be disadvantageous because habitats are not able to buffer increased warming (Roy and Thomas 2003; Davies et al. 2006; Visser 2008). Smolis and Gerken (1987) found burnet moths more mobile than expected in 1983, also a summer with warm weather. In Great Britain *Z. filipendulae* has colonised areas over 10 km from the nearest populations in years with suitable and warm weather (Owen 1954; Leverton 2002). There is also strong evidence that other moths that are active at higher temperatures are able to cover greater distances compared with species active at colder temperatures (Sparks et al. 2005; Dennis and Sparks 2006; Betzholtz and Franzén 2011). Our study demonstrates that two burnet species are more mobile at higher than lower temperatures.

It is very difficult to obtain unbiased estimates of dispersal using traditional MRR studies (Barrowclough 1978; Shreeve 1992; Wilson and Thomas 2002; Stevens et al. 2010). As shown in this study, patch dispersal rate estimates for edge localities of a study-area are underestimated. The dispersal rate intercept at zero distance from the centre of our study-area (Fig. 1) may provide the most unbiased estimate of dispersal rate, since few dispersal events from the centre of the study-area reach outside this area (Franzén and Nilsson 2007). Thus, in the extremely warm year 2003, about 31 % of the individuals of *Z. viciae* moved to a new habitat patch, as defined in this study. In the following cold year, the patch dispersal rate was approximately one-third of this value. Such large differences may have important consequences for long term survival and influence metapopulation dynamics.

It is noteworthy that all six species in the family *Zygaenidae* in southern Sweden are red-listed, showing that their long-term survival is insecure (Gärdenfors 2010). A higher frequency of extremely warm summers may increase the survival if the amount of suitable habitat remains above the critical threshold for population survival. However, we suggest that this critical habitat threshold may be affected by weather. Indeed, when predicting distribution changes and expected range expansions, it is important to consider the variation in dispersal between years (Hill et al. 2002). A current phenomenon is that suitable habitat for burnet moths, and other insects dependent on semi-natural grasslands with low nutrient levels, is changing rapidly in agricultural/forest mosaics in Europe. The pace of landscape change is a challenge to these species which may have evolved a low dispersal rate in the traditional more temporal stable landscapes, and the new situation provides new selection pressures. Warm years as 2003 may be especially important in the colonization process. It is important to understand the dynamics

of different species and identify critical habitats for long-term survival. Problems arise if the accuracy of predictions decreases when habitat preferences, dispersal rates, patch-specific extinction and recolonization change as a result of unusual weather conditions (cf. Takekawa and Beissinger 1989; Solbreck 1991).

Conclusion

Evidence that dispersal propensity could be attributed to weather and study-area is important in many ways. In practice, knowing how weather affects dispersal could be helpful when estimating the viability of a population. Models built to study survival over longer period of times should account for weather-situations and consider how a warm period may influence colonisation and extinction patterns. Global warming may alter colonisation rates, as exceptionally warm years appear to be affecting the dispersal propensity. Unusual weather situations and the size of the study-area should be taken into consideration when dispersal is studied.

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