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Adult dispersal and genetic structure of butterfly populations in a fragmented landscape

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Abstract

Metapopulation theory is a powerful tool to predict the future of populations within a fragmented landscape. By coupling demographic and genetic studies on such a set of populations of the butterfly *Proclissiana eunomia*, we show that adult dispersal was oriented along river basins. The comparison of allelic frequencies of populations from different river basins revealed that the presence of stepping stone habitats allows effective gene flow. This leads to a hierarchical system of populations where stepping stone habitats and topographical barriers are the major factors determining their differentiation. Isolation by distance plays a minor part at the spatial scale considered here.

Keywords: Metapopulation structure, allozyme electrophoresis, spatial structure, *Proclissiana eunomia*, Mark-Release-Recapture.

Résumé

La théorie des métapopulations est un outil puissant pour la prédiction du devenir des populations dans un paysage fragmenté. En couplant des études écologiques et génétiques sur un ensemble de populations du papillon *Proclissiana eunomia*, nous montrons que la dispersion des adultes est orientée au sein des bassins versants. La comparaison des fréquences alléliques de populations de différents bassins versants met en évidence la structure en pas japonais des habitats, permettant un flux effectif de gènes. La structure des populations est donc hiérarchisée, dans un système où les pas japonais et les barrières topographiques sont les facteurs principaux déterminant le degré de différenciation des populations, alors que l'isolement par la distance ne joue qu'un rôle mineur à l'échelle spatiale considérée.

INTRODUCTION

Habitat loss and fragmentation are the main threats to biodiversity in Europe. In this context, the emergence of metapopulation theory has provided a new framework for understanding population persistence in fragmented landscapes (e.g. HANSKI & GILPIN, 1991; HANSKI, 1994). Because of their links with particular

host-plants and habitats, and their observability, butterflies have been the subject of several metapopulation studies (*e.g.* HANSKI & THOMAS, 1994). Moreover, most butterfly species are specialists, have suffered from environmental changes and have displayed severe declines over their range (*e.g.* NEW *et al.*, 1995). At the landscape scale, populations of specialist butterflies occur in discrete patches in suitable habitats (THOMAS *et al.*, 1992). For many species, individuals are rarely, if ever, encountered outside of these habitats, and their populations are often described as closed (*e.g.* THOMAS, 1984; WARREN, 1992). Several recent field studies have revealed individual movements between populations in a patchy network of habitats (*e.g.* HANSKI *et al.*, 1994; WARREN, 1995; NÈVE *et al.*, 1996), and it is now thought that most butterflies that were formerly described as having closed populations actually function as metapopulations (THOMAS *et al.*, 1992; HANSKI & THOMAS, 1994; THOMAS, 1995).

However, individual movements do not necessarily imply gene flow within the metapopulation. We report here on the investigation of a patchy population coupling two different approaches: (1) the actual rate of dispersal, as estimated from Mark-Release-Recapture surveys; and (2) the genetic relationship of populations which is a consequence of effective dispersal.

MATERIAL AND METHODS

The Bog Fritillary (*Proclissiana eunomia* ESPER; Lepidoptera, Nymphalidae) was chosen as a model of species with typically disjunct populations. This species occurs in wet hay meadows and peat bogs along rivers where Bistort (*Polygonum bistorta* L), its only food plant in Middle Europe, grows. The Plateau des Tailles system (ca 20 km × 20 km, in southern Belgium, 50° 14' N, 5° 47' E) consists of a network of small suitable patches separated by Spruce (*Picea abies* (L) KARST) plantations with some trees more than 20 m high and fertilised pastures. Within the system, the Lienne valley (50° 18' N, 5° 49' E, 12 km length) was chosen to conduct a mark-release-recapture study; all other suitable patches in a radius of 6 km around the valley were included. Suitable patches were visited daily – weather permitting – during the flight season in 1993 and 1994. 536 and 613 adults respectively were marked individually using a thin point permanent-pen on the underside of the left wing. Further details on the study system and field methods can be found in BAGUETTE & NÈVE (1994) and in NÈVE *et al.* (1996).

Allozyme electrophoresis on cellulose acetate plate (RICHARDSON *et al.*, 1986; WYNNE *et al.*, 1992) was conducted on the three locally polymorphic loci out of the 10 polymorphic loci known to exist in Europe (Adenylate kinase E.C. 2.7.4.3, Phosphoglucomutase E.C. 2.7.5.1 and 6-Phosphogluconate deshydrogenase E.C. 1.1.1.44). Within the Plateau des Tailles system, 286 individuals captured between 1991 and 1993 from five samples were scored for these enzymes. Genetic differentiation was assessed by the GENEPOP software (RAYMOND & ROUSSET, 1995*a* & *b*). Comparisons of the three allelic frequencies between couples of populations were computed using the Fisher exact test. Genetic distances were computed with the BIOSYS-1 software (ver. 1.7; SWOFFORD & SELANDER, 1981) and Mantel tests between geographic and genetic distances matrices were performed with the "R" package (LEGENDRE & VAUDOR, 1991).

RESULTS

In 1993 and 1994, 39 and 51 of the 514 and 692 recaptures (8% and 7%) respectively involved a flight across at least 200 m of unsuitable habitats (table I). Some of these flights exceeded 1 km, and the recorded maximum movement was

TABLE I. – Movements recorded in *P. eunomia* during MRR studies conducted in the Plateau des Tailles area. All movements of more than 200 m are between patches movements.

Distance between two successive captures	1993	1994	Total
0-100 m	402	548	950
100-200 m	73	93	166
200-1000 m	29	46	75
> 1000 m	10	5	15
Maximum distance recorded	4600 m	2400 m	$\Sigma = 1206$

4.6 km (from Lierneux to Hébronval populations; fig. 1). With one exception (from Petit Sart to Hébronval), all flights took place within a single water basin. No movements between Bihain and Hébronval were ever recorded.

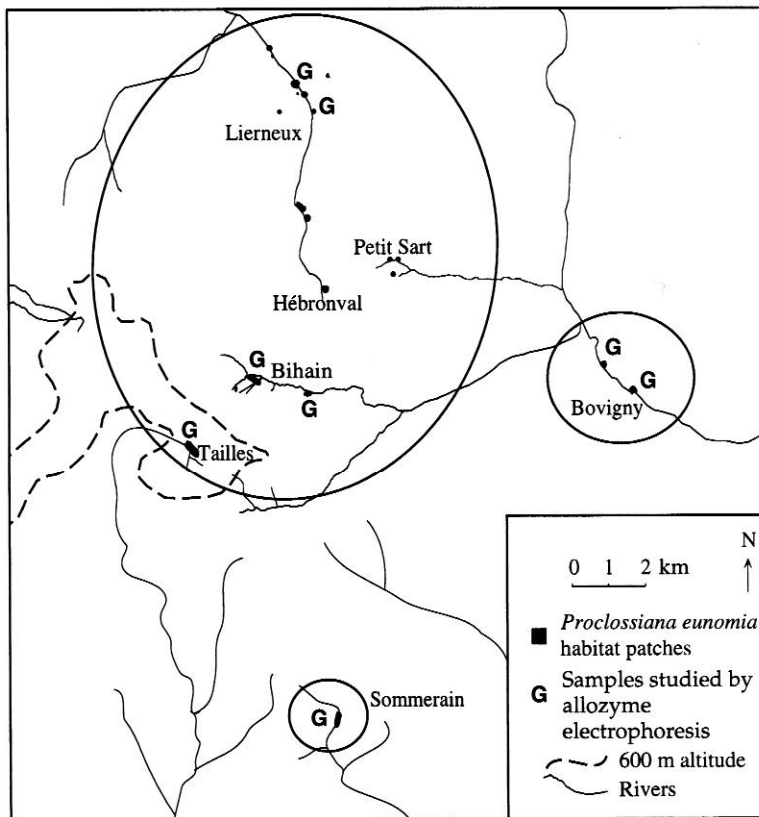


FIG. 1. – Populations of *P. eunomia* within the Plateau des Tailles system. Ellipses group patches which were shown to form single genetic units.

When pairs of samples were taken from the same valley, the samples always proved to be not significantly different from one another (Lierneux 1 vs 2: $P=0.23$; Bihain 1 vs 2: $P=0.83$; Bovigny 1 vs 2: $P=0.37$); these were therefore grouped as three populations. Allelic frequencies of the three polymorphic loci vary greatly between the 5 study populations (table II). The genetic distance (Rogers' Modified distance; WRIGHT, 1978) between the 5 study populations is not significantly correlated with the geographical distances between them (Mantel test, $P>0.05$). Results of paired population comparisons (table III) revealed significant differences in 8 cases out of 10. The two populations located in the bogs on the upland (Tailles and Bihain) have similar allelic frequencies. When individuals belonging to these two populations are pooled, allelic frequencies of two populations (Bovigny and Sommerain) were significantly different from this group ($P<0.01$), while the population of Lierneux no longer showed significant differentiation ($P>0.05$).

TABLE II. – Allele frequencies in *P. eunomia* populations of the Plateau des Tailles area.

Code	Locality	Number of specimens	Frequencies of alleles in polymorphic loci						
			PGM		6PGD			AK	
			A	B	A	B	C	A	B
1	Lierneux	45	.667	.333	.644	.356	0	.767	.233
2	Bihain	103	.772	.228	.510	.466	.024	.733	.267
3	Tailles	31	.694	.306	.548	.387	.065	.806	.194
4	Bovigny	76	.711	.289	.855	.145	0	.434	.566
5	Sommerain	31	.677	.323	.339	.629	.032	.548	.452

TABLE III. – Population differentiation between all pairs of populations of *P. eunomia* in the Plateau des Tailles area: Probability levels of Fisher's test to combine tests done on the 3 polymorphic loci. NS: not significant; *: $P<0.05$; **: $P<0.01$; ***: $P<0.001$.

From	2. Bihain	3. Tailles	4. Bovigny	5. Sommerain
To				
1. Lierneux	0.048*	0.263 NS	< 0.001***	< 0.001***
2. Bihain		0.212 NS	< 0.001***	0.003**
3. Tailles			< 0.001***	0.005**
4. Bovigny				< 0.001***

DISCUSSION

The distribution of *P. eunomia* is patchy at the scale of the study system (BAGUETTE & NÈVE, 1994). Moreover, individuals were shown to be able to move up to 4.6 km between habitat patches, and population turnover was detected in small patches (NÈVE *et al.*, 1996). This suggests the existence of only one metapopulation for the whole system. However, we found that dispersal movements were oriented: we detected only one movement between two adjacent river basins during our 2-year investigation. A gap of several kilometres without suitable

habitats seems to decrease sharply the gene flow between populations; the isolated populations of Sommerain and Bovigny are both very different from one another and from the Bihain and Lierneux populations. Scarcity of exchanges between habitat "archipelagoes" is confirmed by the analysis of genetic polymorphism of allozymes: allelic frequencies in populations separated by unsuitable habitats were significantly different, while nearby habitat patches did not reveal significant differences. We identified three genetic units within the study system which emphasises the low level of gene flow between these populations.

The study system of *P. eunomia* is thus likely to function as several networks of small connected populations. As the habitat of *P. eunomia* is wet hay meadows, suitable patches are usually distributed along rivers within water basins. Within these groups of habitat patches, each *P. eunomia* population has a certain probability of survival and recolonisation, according to its size and history, especially since female dispersal behaviour, and thus (re-)colonisation, is linked with male density (BAGUETTE *et al.*, 1996). Because dispersal is oriented along river valleys, small metapopulations are more or less isolated from each other, according to the presence or absence of suitable stepping stone habitat patches. This corresponds to a hierarchical system of populations where the differences between populations depend on the overall distribution of habitats rather than on the distance *per se*. Coupling demographic and genetic studies of population structures appears to be a good strategy to separate superficially metapopulation-like systems, such as "patchy populations" and "non-equilibrium metapopulations" (HARRISON, 1994) from systems in which between-population processes are of crucial importance for their viability. A further study using this strategy was launched in 1995 on an insular-like system.

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