

Metapopulation structure and conservation of the cranberry fritillary *Boloria aquilonaris* (Lepidoptera, Nymphalidae) in Belgium

Luc Mousson, Gabriel Nève, Michel Baguette *

Université catholique de Louvain, Unité d'Ecologie et de Biogéographie, Croix du Sud 4, B-1348 Louvain-la-Neuve, Belgium

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Abstract

The spatial structure and dynamics of local populations of an endangered specialist butterfly, the cranberry fritillary *Boloria aquilonaris* living on peat bogs was studied in Southern Belgium. Seventeen populations on the Ardenne uplands (Plateau des Tailles, Hautes-Fagnes, Plateau de Recogne, Plateau de St-Hubert) and one population in the forested lowlands of Lorraine were monitored in 1996. The population structure and dynamics were investigated on the “Plateau des Tailles”, the most important area for *B. aquilonaris* in Belgium with 12 distinct populations. A mark–release–recapture survey was carried out on four sites in 1995 and 1996 within an area of 85 km². An unexpectedly high degree of interchange was detected between sites. This connectivity, together with the asynchrony of local dynamics suggest that populations act as a single metapopulation within the whole study area. We observed that adult butterflies were less prone to move out of their natal patch when this patch was small (< 1 ha), isolated and sheltered. Therefore, such patches must also be taken into account when planning the conservation of the species. © 1998 Elsevier Science Ltd. All rights reserved.

Keywords: *Boloria aquilonaris*; Mark–release–recapture; Habitat fragmentation; Conservation strategy; Metapopulation; Migration

1. Introduction

Many butterfly species have severely declined in industrialized countries in recent decades and in all types of habitats (Ehrlich, 1984; Heath et al., 1984; Thomas, 1989; Baguette and Goffart, 1991; Warren, 1993; New et al., 1995). Numerous specialist species, with narrow ecological requirements, have been listed in red data books in many countries. This process of species loss is mainly due to man-induced destruction and fragmentation of suitable habitats, leading to isolation of local populations. Past efforts to reduce extinctions by maintaining local nature reserves have not always succeeded in conserving threatened species at a regional scale (J.A. Thomas, 1989; C.D. Thomas, 1995).

At the landscape scale, the variability and temporal dynamics in habitat quality of patches, the composition and structure of the surroundings, and the connectivity among patches will influence the future of remaining populations. The metapopulation concept, coined by Levins (1970), has been developed as a predictive tool of population survival in a fragmented landscape (Gilpin

and Hanski, 1991; Hanski and Gilpin, 1997). In such a system, each local population has its own probability of extinction and (re)colonization. Occupied patches within the landscape are connected by occasional migration.

Most butterflies are closely related to particular habitats for their larval development and large scale movement between sites was thought to be very rare (Baker, 1969; Ehrlich, 1984; Warren, 1992); such species were expected to display closed and isolated populations (Thomas, 1989, 1991; Warren, 1992). However, recent studies have shown that specialist butterflies are more mobile than previously expected. Field studies indicate that their populations are connected by individual movements across unsuitable habitats, leading to a metapopulation structure (Thomas and Jones, 1993; Hanski and Kuussaari, 1995; Nève et al., 1996). The biased impression of population isolation may be caused by the lack of large-scale mark–release–recapture studies (Dempster, 1991; Hanski and Kuussaari, 1995).

Conservation priorities in fragmented landscapes may therefore require the establishment of a network of suitable habitats (Fahrig and Merriam, 1994). If such a

* Corresponding author. E-mail: baguette@ecol.ucl.ac.be

conservation strategy is to be effective, an accurate knowledge of population structure at different spatial scales is necessary. A knowledge of dispersal power of threatened species is of crucial importance for the long-term persistence of its populations at the regional scale, as this parameter will determine how the network must be configured and which local population should be considered within a single conservation programme (Hanski, 1991; Warren, 1992; Stacey et al., 1997).

In Belgium, the cranberry fritillary *Boloria aquilonaris* was widely distributed but has declined dramatically over the last 25 years. Populations inhabit wet acid peat bogs where the principal larval hostplant *Vaccinium oxycoccos* is abundant (Crosson du Cormier and Guérin, 1947). The natural patchiness of bogs has been increased by drainage and planting of Norway spruce *Picea abies* since the end of World War II. In this paper, (1) we assess the population structure of *Boloria aquilonaris* at the landscape scale, (2) we infer the population structure and dynamics of the species at the regional scale and (3) we suggest a background for landscape management to allow the conservation of remnant populations of this threatened species.

2. Material and methods

2.1. The species

The cranberry fritillary is univoltine, with adults flying in June and July, the period depending on altitude and latitude (Higgins and Riley, 1984). Adults were observed nectaring on the flowers of marsh cinquefoil *Comarum palustre*, marsh thistle *Cirsium palustre*, cross-leaved heath *Erica tetralix* and arnica *Arnica montana*. In northeastern Switzerland, Jutzeler (1989) also mentioned brown knapweed *Centaurea iacea* and hawkweed *Hieracium* sp. as nectar plants.

Suitable localities can be found from lowland bogs at sea level (in Normandy, France, and in The Netherlands) to subalpine flushes at altitudes of up to 2000 m (Haute Engadine, Switzerland). The distribution of *B. aquilonaris* in Europe is typical of a boreo-montane species as defined by Udvardy (1969). It is most widespread and abundant in Fennoscandia (Henriksen and Kreutzer, 1982; Kudrna, 1990; Marttila et al., 1990), where it is not threatened. Although it is critically endangered in most of western and central Europe, its distribution here is naturally fragmented (Fig. 1) and it is not protected by the Bern Convention (Mikkola, 1991).

In Belgium, the cranberry fritillary has declined substantially from 104 recorded localities before 1970 to 18 after 1970, although this is not obvious when mapped on 10 km grid squares (Fig. 2; Baguette et al., 1992).

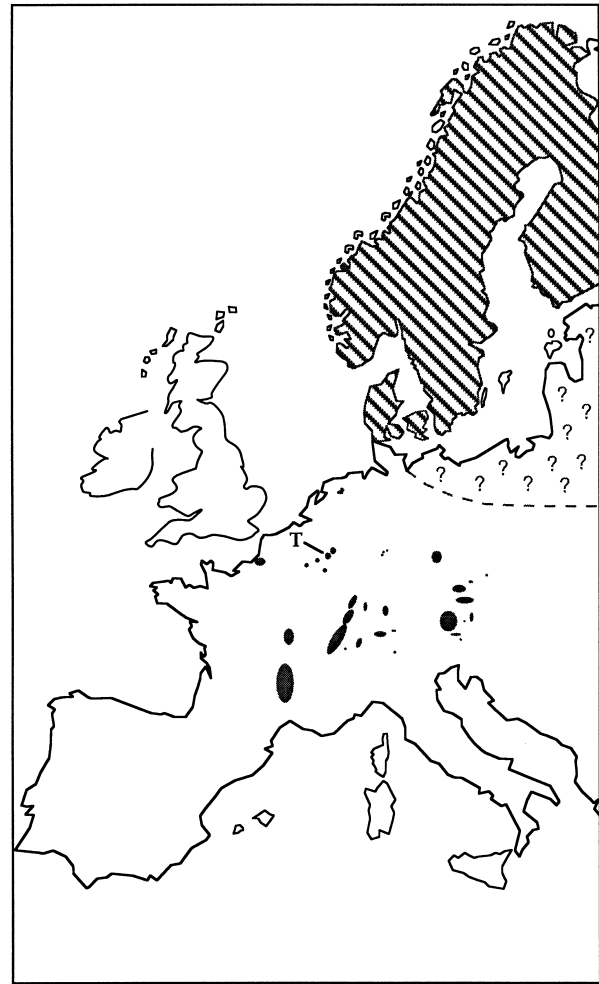


Fig. 1. European distribution of *Boloria aquilonaris*. MRR study system in the Plateau des Tailles and surroundings is indicated by 'T'. Distribution records were collected from Ebert and Rennwald (1993), Henriksen and Kreutzer (1982), Ivinskis (1993), Kudrna (1993), Kudrna (1994), L.S.P.N. (1987), Marttila et al. (1990), Reichl (1992), Wynhoff et al. (1990) and WWF (1994). Eastern distribution is not well known (represented by '?').

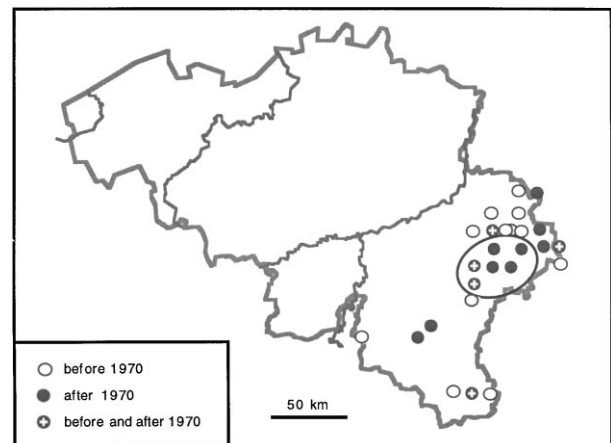


Fig. 2. Past and present distribution of *B. aquilonaris* records in Belgium, plotted by 10-km grid squares (UTM). The ellipse indicates the Plateau des Tailles and surroundings.

The species was listed as “vulnerable” in Belgium according to IUCN criteria (I.U.C.N., 1983; Baguette and Goffart, 1991). Remnant populations are located on the four Ardenne uplands (Plateau des Tailles, Hautes-Fagnes, Plateau de Recogne, Plateau de St-Hubert) and in one small isolated site in Lorraine.

2.2. Study areas

In Belgium, all suitable habitats with *Vaccinium oxycoccos* (24 sites on the Ardennes uplands and in Lorraine) were monitored during the flight season in 1996. A mark–release–recapture experiment was carried out at two sites (GF and FM areas) on the Plateau des Tailles (area T in Fig. 1, 220 km², southern Belgium) in 1995. Two other sites (CO and QV areas) were added in 1996. These sites are separated by 5–6 km of agricultural landscape and spruce plantations (Fig. 3).

The “Grande Fange” complex (GF, 50°14'N 5°47'E), with 262 ha, is referred to in the European CORINE site classification system (code 500 260 101). It consists of bogs and marshes (active raised bogs, drying bogs invaded by *Molinia caerulea*, transition mires, wet heaths, acidic fens), woodland clearings and scrub (birch, willow, etc.). In this site, suitable habitats with abundant cranberry, are scattered in 24 patches varying between 0.02 and 1.5 ha, with a total area of 7.5 ha. The distance between neighbouring patches vary from 20 to 290 m and maximum distance between two patches is about 1.6 km.

The other three sites, “Fange de Mirenne” (FM, 50°15'N 5°52'E), “Quatre-Vents” (QV, 50°16'N 5°57'E) and “Commanster” (CO, 50°15'N 6°00'E), were located in the eastern part of the Plateau des Tailles. Each consisted of acid fens, wet heaths and woodland clearings with 0.15–0.2 ha of suitable habitat, surrounded by birch forests, Norway spruce plantations or fertilized pastures.

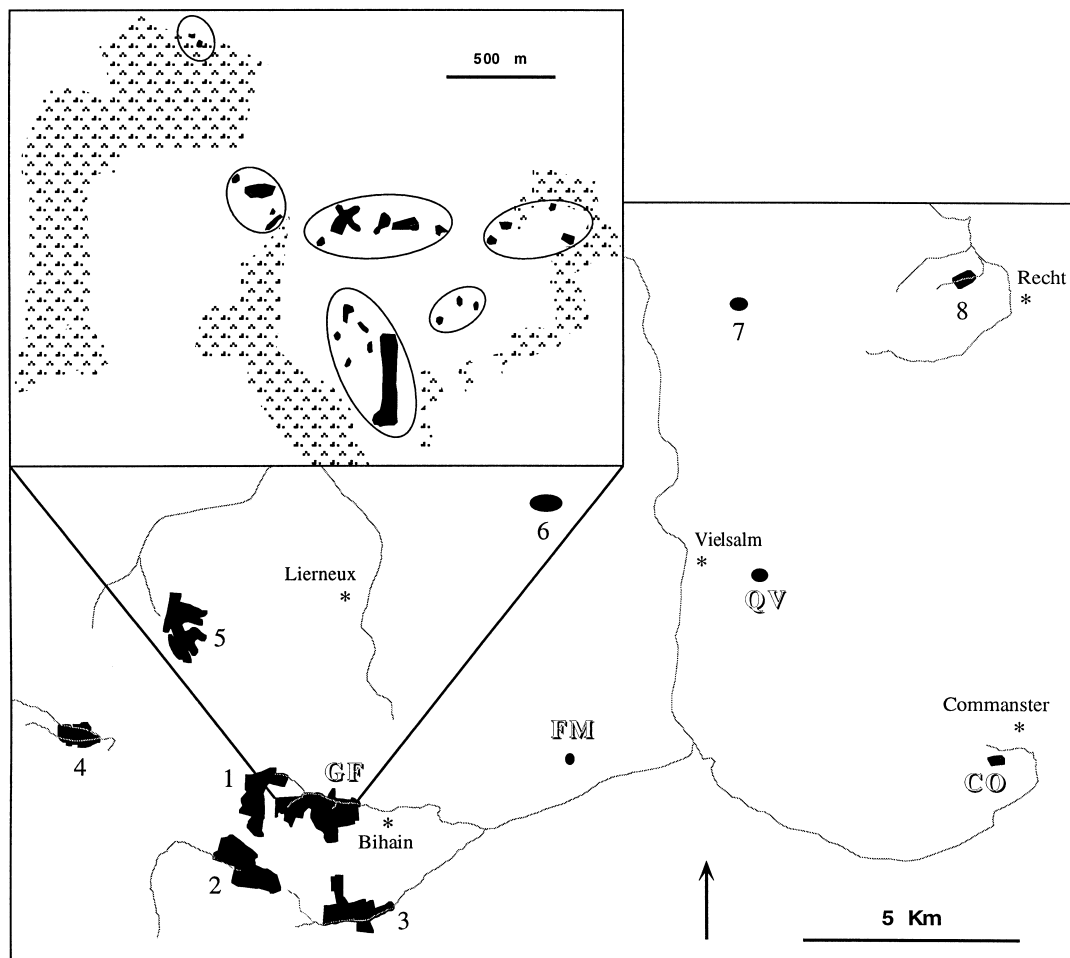


Fig. 3. Distribution of populations (in black) of *B. aquilonaris* in the Plateau des Tailles and surroundings. Mark–release–recapture sites are indicated in shaded letters: Grande Fange (GF), Fange de Mirenne (FM), Commanster (CO), Quatre-Vents (QV). Other sites are numerated: Sacrawé (1), As Massotais–Grand Passage (2), Pisserotte (3), Robiëfa (4), La Crépale (5), Arbrefontaine (6), Logbiermé (7), In Der Eicht (8). Insert represents the distribution of habitat patches in the Grande Fange. Shaded areas indicate Norway spruce plantations. Ellipses show six groups of patches separated by > 200 m of unsuitable habitats.

2.3. Estimation of population parameters

The GF and FM sites were visited daily, weather permitting, during the flight season of *B. aquilonaris* in 1995 (from 2 until 30 July) and all four sites in 1996 (from 1 July until 8 August). Within study sites, standard transects were performed at each visit. Butterflies were netted and marked with an individual number and site code on the underside of the left hindwing with a thin-point permanent pen (Staedler Lumocolor S or Schwan Stabilo Universal S) and immediately released at the location of their capture. This allowed the immediate detection of movements between sites. For each observation, the time, individual code, sex, wing wear and local habitat patch were recorded. The wing wear, giving information about butterfly age and activity, was estimated on a scale from 1 (perfect conditions) to 4 (damaged wings). The numbers of marked adults and capture sessions for each site are summarized in Table 1.

Demographic parameters (daily population size, sex-ratio and average residence time of populations) were estimated using the Jolly-Seber method as applied to open populations (Seber, 1982; Hines, 1988). Other statistical analyses were performed using SAS (SAS Institute, 1990).

3. Results

Of the 24 suitable sites recorded in Belgium, 18 supported populations of *B. aquilonaris* in 1996. Among these remnant populations, 12 were located on the Plateau des Tailles and its surroundings (Fig. 3), where the MRR experiments were performed. The six other sites were unoccupied in 1996.

Estimates of daily population size and standard deviation are shown in Fig. 4 for GF and FM, and in Fig. 5 for CO and QV populations. As is frequently observed in butterfly species (Wiklund and Fågerström, 1977), protandry was evident. The time lag between male and female maximal abundance varied between 4

and 13 days depending on the year and the study site (Table 2).

Estimates of total population size and densities for each sex were highly variable between sites (Table 3). Over the 2-year period, the GF population increased and FM population decreased. The highest density (> 3000 butterflies ha^{-1}) was observed at FM.

At the GF site, all habitat patches were used by adult butterflies which actively moved between them (Fig. 6). The proportion of recaptured males was more than twice as great as for females (Table 4). Over these recaptures, most individuals moved to other patches. The tendency to stay in natal patch was low for both sexes. As movements between neighbouring patches occurred commonly, clustering were made for patches separated by < 200 m of unsuitable habitats. In 1995, movements between groups of patches were observed for 19 males and nine females (respectively 14.6 and 27.3% of the recaptured individuals). In 1996, these movements occurred for 32 males (29.6%) and one female (11.1%).

Maximum distances moved by marked individuals during their lifetime in 1995 and 1996 were 1020 m and 1270 m for males and 970 and 775 m for females. In 1995, the female mean flight distance was more than twice as great as for males (226 m, $n=37$ for females; 87 m, $n=184$ for males; Kruskal–Wallis, $\chi^2=8.08$, $p<0.01$). In 1996, mean flight distance did not differ significantly between sexes (160 m, $n=12$ for females; 209 m, $n=149$ for males; Kruskal–Wallis, $\chi^2=0.31$, $p=0.58$). The difference between years was significant only for males for which the mean flight distance was higher in 1996 than in 1995 (Kruskal–Wallis, $\chi^2=6.73$, $p<0.01$). The proportions of individuals flying certain distances are shown in Fig. 7.

The proportions of marked individuals that were observed more than once ranged from 9.2 females ha^{-1} at GF to *c.* 70 males ha^{-1} at CO and QV (Table 4).

Nine butterflies were detected moving between sites (see Fig. 3): four males from GF to FM (5 km), one male and one female from FM to GF, one female from FM to CO area (11 km) in 1995; one male from FM to GF and one female from FM to QV in 1996 (6 km).

4. Discussion

The “Plateau des Tailles” upland (220 km^2), with 12 populations, was identified as the key area for the conservation of the species in Belgium. The question whether these can be considered as a single metapopulation may be addressed by using the four propositions coined by Hanski et al. (1995): (1) habitat patches support local breeding populations, (2) no single population is large enough to ensure long-term survival,

Table 1
Number of capture sessions and total marked imagines of *Boloria aquilonaris* for each study site in 1995 and 1996^a

Site	1995			1996		
	Males	Females	Capture sessions	Males	Females	Capture sessions
GF	341	181	20	352	98	18
GFp	88	46	20	26	9	18
FM	294	180	22	191	86	24
CO	–	–	–	97	50	17
QV	–	–	–	35	17	15

^a ‘GFp’ represents a patch in GF complex of similar size as the other study areas (0.2 ha).

(3) patches are not too isolated to prevent recolonization, and (4) local dynamics are sufficiently asynchronous to make extinction of all populations unlikely. The answers are crucial in order to propose an efficient conservation strategy for the species: whether it should emphasize the management of a habitat network or the conservation of all local populations.

4.1. Local breeding populations

Suitable habitats for *B. aquilonaris* are structured into discrete patches, supporting local breeding populations and most individuals spend their lifetime in their natal patch. However, recaptures within the GF area show that a few individuals fly between patches so this area

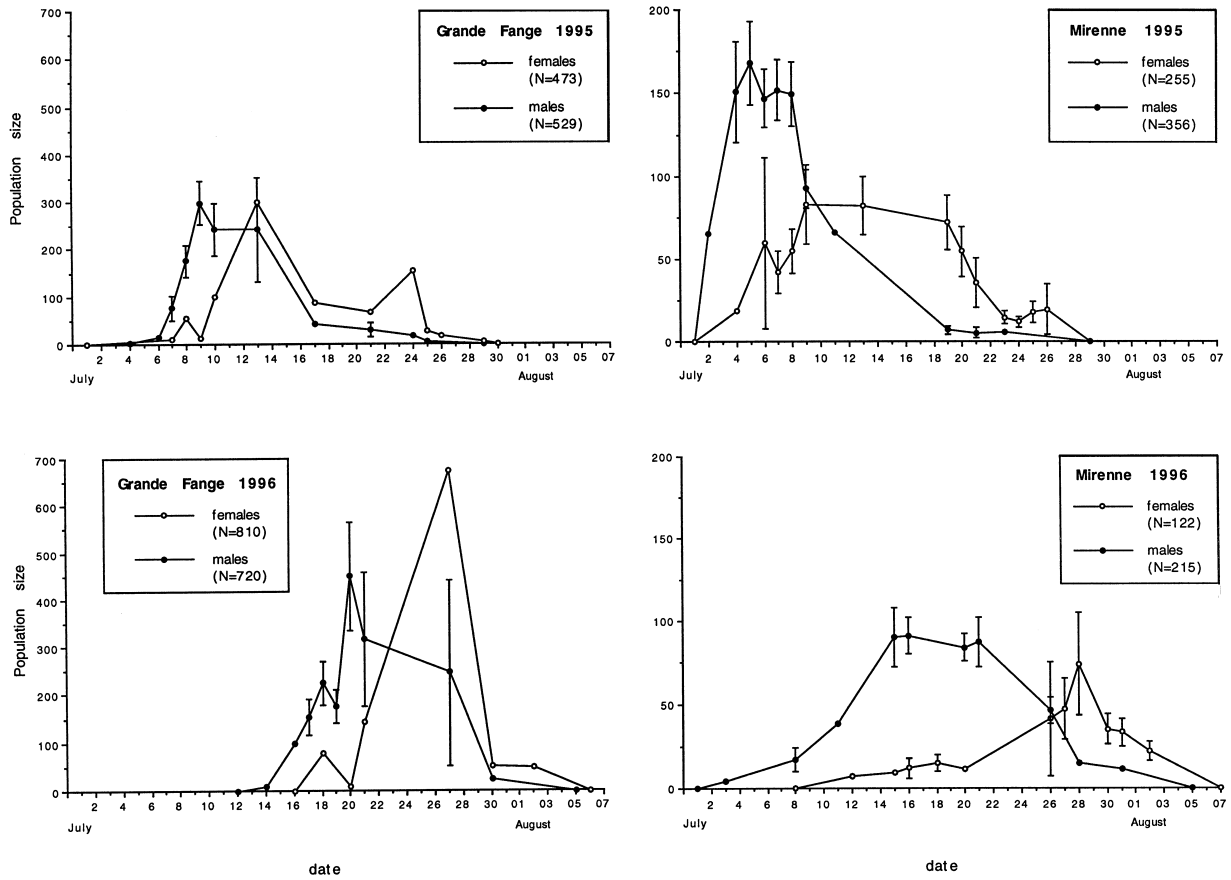


Fig. 4. Daily population sizes of *B. aquilonaris* in the Grande Fange and the Fange de Mirene (Jolly estimates, mean and SE): comparison between 1995 and 1996.

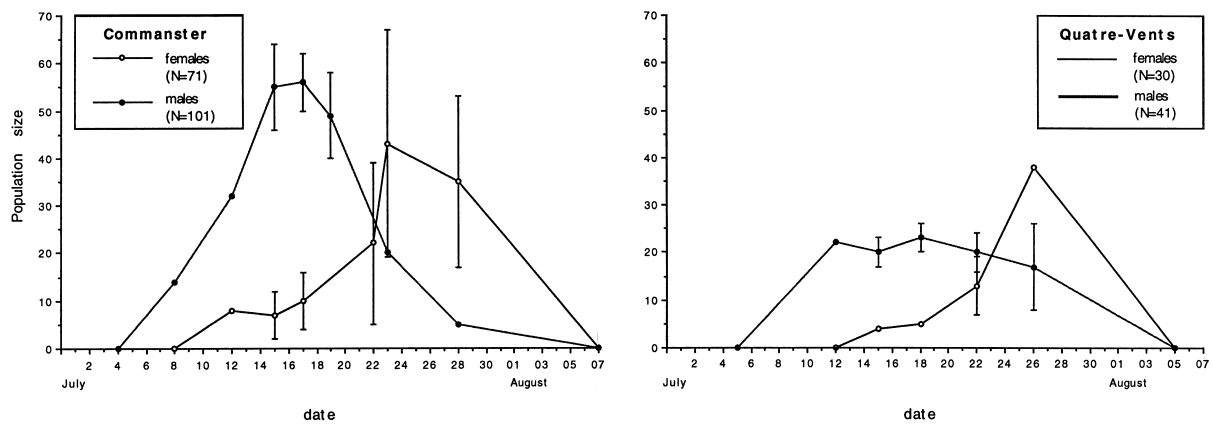


Fig. 5. Daily population sizes of *B. aquilonaris* in the Commanster and the Quatre-Vents in 1996 (Jolly estimates, mean and SE): comparison between 1995 and 1996.

may be considered as supporting one single large patchy population. The proportion of adults staying in the patch where they were marked was higher in the three smallest patches (CO, QV and FM) than in the large GF population (Table 4). Such a higher fidelity to small patches has been observed in other butterfly species (see

Table 2

Time lag (in days) between male and female abundance peaks for each study site in 1995 and 1996

Year	GF	FM	CO	QV
1995	4	4	–	–
1996	7	13	6	8

Table 3

Total population size and density (butterflies per ha of suitable habitat) estimates for each study site in 1995 and 1996^a

	1995			1996		
	Males	Females	Total	Males	Females	Total
GF	529 (71)	473 (63)	1002 (134)	720 (96)	810 (108)	1530 (204)
FM	356 (1780)	255 (1275)	611 (3055)	215 (1075)	122 (610)	337 (1685)
CO	–	–	–	101 (673)	71 (473)	172 (1146)
QV	–	–	–	41 (205)	30 (150)	71 (355)

^a Jolly estimates.

review in Hanski and Kuussaari, 1995; Thomas and Hanski, 1997). Two factors may explain this pattern: (1) butterflies are reluctant to fly out of isolated patches, separated by unsuitable habitats over long distances, and (2) as such patches were surrounded by trees, they have clearly discernible margins which might enable the butterflies to remain within favourable habitat. Other study systems with higher residence time in large than in small patches (Sutcliffe et al., 1997) suggest that patch isolation and edge structure have unexpected effect on population dynamics. Compared to these three small, sheltered and isolated sites (CO, FM, QV), a patch of similar size in GF (GFp, 0.2 ha) showed a much lower density of adults (Table 3) and a lower proportion of individuals captured more than once within the patch (Table 4). This suggests that adults are more prone to move away from their natal patch when direct surroundings are open areas rather than forested areas, as shown for *Melitaea cinxia* by Kuussaari et al. (1996). Therefore, physical barriers appear to be important factors in preventing emigration and must be preserved.

4.2. Risk of local extinction

The largest local population was estimated to 1530 adults (1996 GF population). Several hundred adults

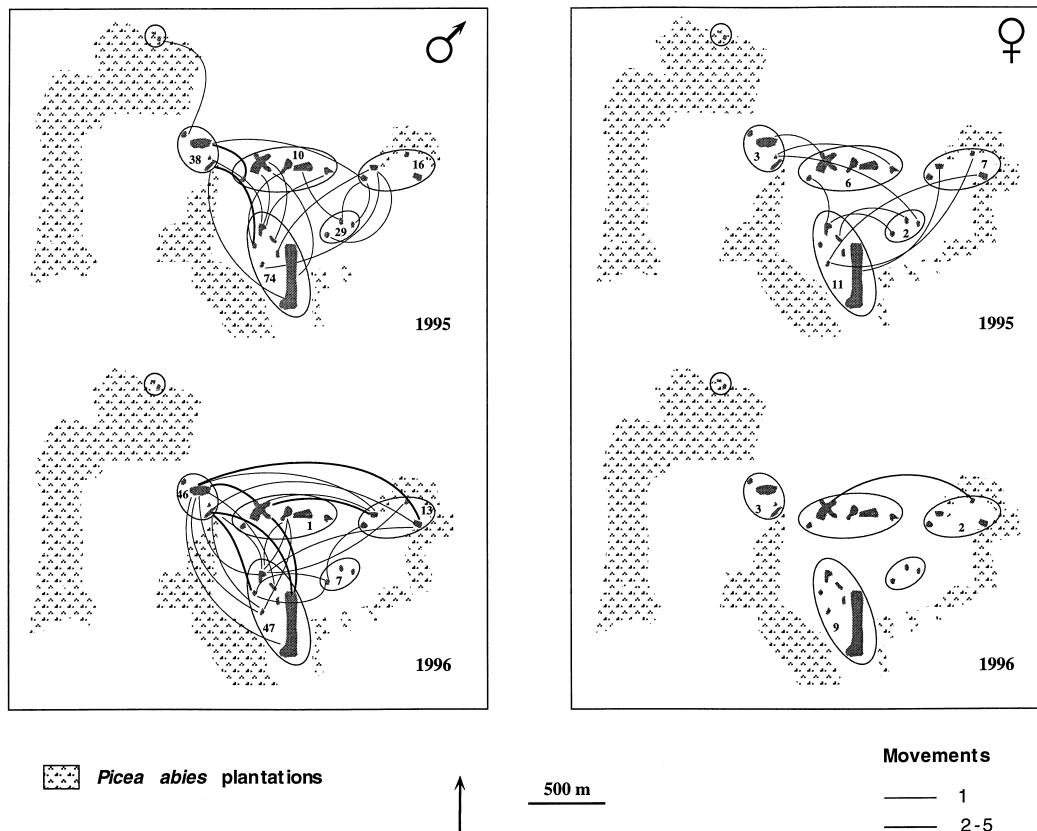


Fig. 6. Movements of males and females of *B. aquilonaris* within and between groups of patches of habitat in the Grande Fange in 1995 and 1996. The ellipses represent groups of patches separated by > 200 m of unsuitable habitats. Numbers in the ellipses represent movements within groups.

are not enough to prevent local extinctions in nymphalid butterflies. Hanski and Kuussaari (1995) document such extinctions for the related fritillary *Melitaea cinxia* in Finland. In Belgium, an isolated population of another fritillary, *Eurodryas aurinia* dropped from 135 larval nests in 1994 (each nest producing about 4–5 adults) to 0 in 1997, without apparent change in the habitat quality (unpublished pers. obs.).

4.3. Dispersal and recolonization within the network of suitable habitats

The mark–release–recapture experiment demonstrated that local populations are not isolated: individual

movements of several km have occurred between all study sites. Moreover, a recolonization event was recorded in 1997 when a new population was founded in a suitable habitat which was empty in 1995 and 1996.

4.4. Asynchronous local dynamics

The survey in GF and FM showed asynchronous local dynamics between the 2-year period. Such asynchrony may be explained by two main factors: climatic and biotic effects in relation with habitat structure (Sutcliffe et al., 1996). For example, weather conditions (heat, humidity, wind,...) act differently on caterpillars, pupae and adult butterflies in large open areas than in small isolated and sheltered patches (Hanski et al., 1995; Weiss et al., 1993). Extreme climatic conditions can even lead to extinction of the metapopulation (Thomas and Hanski, 1997). On the other hand, biotic effects such as predation or parasitism may cause large fluctuations in population size. Specific parasitoids have been implicated in density-dependent changes of fritillary populations (Ford and Ford, 1930; Porter, 1981, 1983; Warren, 1994; Lei and Hanski, 1997).

Table 4

Numbers and proportions (butterflies per ha of suitable habitat) of butterflies which were observed more than once in 1995 and 1996^a

	1995			1996		
	Males	Females	Total	Males	Females	Total
GF	129 (37.8)	31 (17.1)	160 (30.7)	108 (30.7)	9 (9.2)	117 (26.0)
GF p	14 (15.9)	6 (13.0)	20 (14.9)	4 (15.4)	1 (11.1)	5 (14.3)
FM	177 (60.2)	92 (51.1)	269 (56.8)	114 (59.7)	54 (62.8)	168 (60.6)
CO	–	–	–	67 (69.1)	18 (36.0)	85 (57.8)
QV	–	–	–	25 (71.4)	8 (47.1)	33 (63.5)

^a ‘GF p’ represents a patch in GF complex of similar size as the other study areas (0.2 ha).

5. Conclusion

Taken together, these results show that the *Boloria aquilonaris* populations on the “Plateau des Tailles”

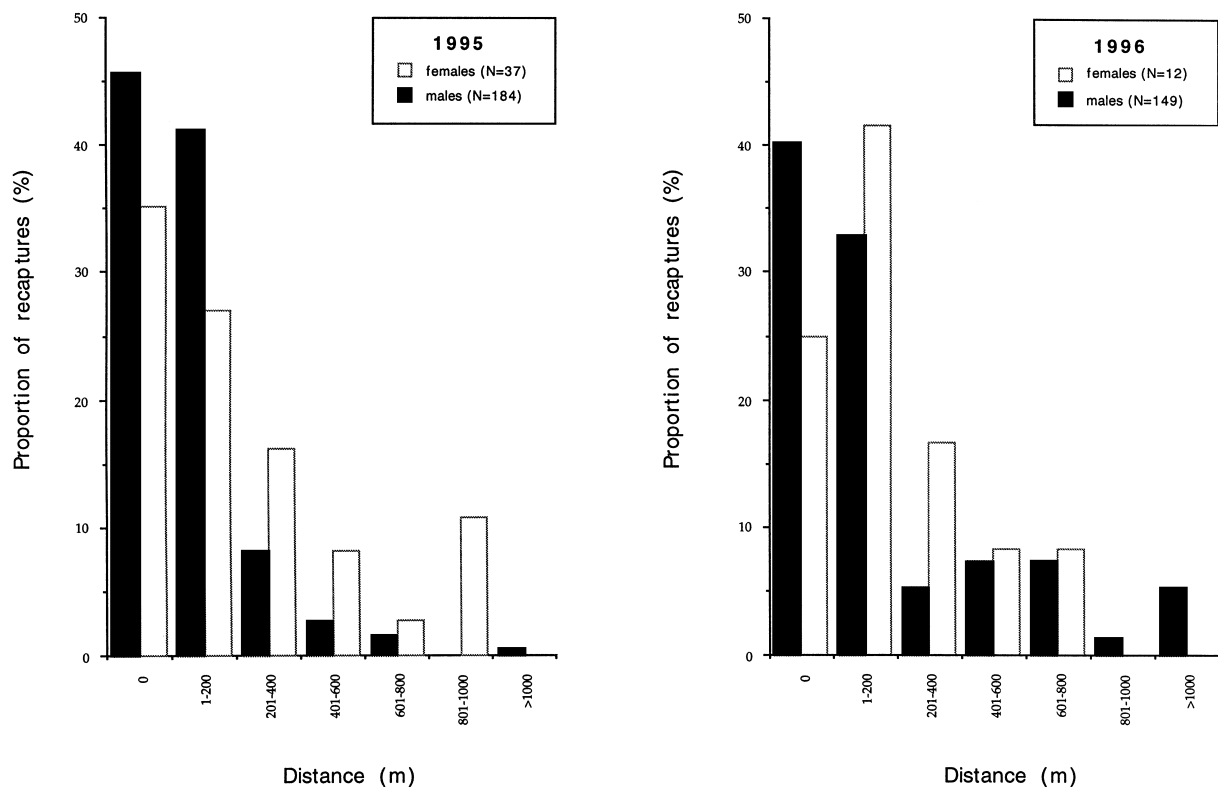


Fig. 7. Proportion of individuals flying certain distances in the Grande Fange in 1995 and 1996.

upland form a single metapopulation and its long-term persistence at this landscape scale therefore requires “connectivity” between local populations. This means that small patches must be taken into account as they may contribute significantly by allowing long-distance (re)colonizations by a stepping-stone process. Finally, physical barriers against migration in small and isolated habitat patches may be more important than expected. Forested margins to these patches must be preserved.

On the “Plateau des Tailles” upland, most *B. aquilonaris* populations are located in reserves. Until now, no empirical data have been available to predict the minimum area or number of patches required for the conservation of the metapopulation. Spatially explicit simulation models can be used to estimate the probability of metapopulation persistence after extinction of some patches. Such a study is now in progress; it will allow us identify which habitat patches are required to contribute to the regional conservation of this butterfly.

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