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# Dispersal, colonization power and metapopulation structure in the vulnerable butterfly *Proclissiana eunomia* (Lepidoptera: Nymphalidae)

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## Summary

1. Mark–release–recapture (MRR) surveys of *Proclissiana eunomia* conducted in 1992 and 1993 in the Belgian Ardennes, and in 1993 in the Pyrénées revealed that 8–16% of recaptures occurred after a movement of more than 200 m on unfavourable habitat.

2. The spread of *P. eunomia* following its introduction in Morvan (central France) 20 years ago shows a colonization speed of 1–3 km per favourable year (i.e. sunny weather during the imago flying season) and average 0.4 km year<sup>-1</sup> over a 25-year period.

3. Both MRR and introduction studies suggest a hierarchical nested metapopulation structure, movements being free within habitat patches, common between neighbouring patches and significant between river basins, ensuring population cohesion at the regional scale.

4. The establishment of a network of populations (metapopulation) within 5 years of the original introduction shows that (re)colonization of empty habitat patches around refuge/introduction sites may be effective and quick. High dispersal rate as well as the dynamics of *P. eunomia*'s metapopulations suggest that a network of suitable habitat patches is necessary for the long-run conservation of this vulnerable species.

*Key-words:* butterfly conservation, habitat patchiness, introduction.

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## Introduction

'Throughout the world natural habitats are being cut up, cut down and cut off. The fragmentation isolates pieces of habitat and surrounds them with ever-rising seas of inhospitable terrain' (Soulé & Wilcox 1980). This is a challenge posed to all conservation biologists at the end of the twentieth century. Theoretical research on the effect of this man-induced patchiness has led to the rise of two new important paradigms in population biology: (i) the application of the Theory of Island Biogeography (MacArthur & Wilson 1963, 1967) to biological conservation (Game 1980; Shafer 1991), and (ii) the emergence of the metapopulation concept (Levins 1969; Gilpin & Hanski 1991). These approaches have emphasized that the probability of extinction depends on habitat area and population

size, and that the colonization of an empty habitat depends on its isolation from existing populations. Although considerable debate has surrounded the applicability of the theories to the field (Gilbert 1980), these generalizations are widely supported by empirical data (Simberloff 1988). For several butterfly species, Thomas, Thomas & Warren (1992) showed how small populations are more likely to become extinct than large ones, and how habitats close to occupied patches are more likely to be colonized. In particular, stepping stone habitats proved to be crucial in the creation and maintenance of a metapopulation system of the butterfly *Plebejus argus* (Thomas & Harrison 1992).

In many European countries, there is a growing concern about the conservation of threatened butterflies. Many countries have published 'Red lists' of

their butterfly faunas, identifying why many European butterfly species have declined. Threatened butterflies often have narrow ecological requirements (British fauna: Hodgson 1993; Belgian fauna: M. Baguette, unpublished), and populations of these species are prone to extinction, particularly as habitat fragments become smaller. As habitats also become isolated from one another, specialist species fail to recolonize following a local extinction, and surviving populations are subject to selection against dispersal, as has been suggested for *Papilio machaon* and *Maculinea arion* in Britain (Dempster 1991), and *Parnassius mnemosyne* in southern France (Descimon & Napolitano 1993). This scenario leads to the on-going disappearance of specialist species from small and isolated habitat patches (Soulé 1987; Hanski 1991). Even large populations may be subject to occasional extinction due to unusual local climatic conditions or habitat change, and these localities would not be recolonized either if they remain isolated from surviving populations which could supply colonists (Murphy & Weiss 1988). This has been suggested as the cause for the extinction of *Colias palaeno* on the Hautes-Fagnes Plateau, Belgium (Sarlet 1965) and of *Parnassius apollo* from various parts of its range, e.g. Vosges and part of Massif Central, France (Braconnot, Descimon & Vesco 1993). The specialization of *Proclossiana eunomia* (Esper) and its vulnerable status in France and in Belgium (Baguette & Goffart 1991) prompted us to investigate the population biology of this species, taken as an example of specialized declining species.

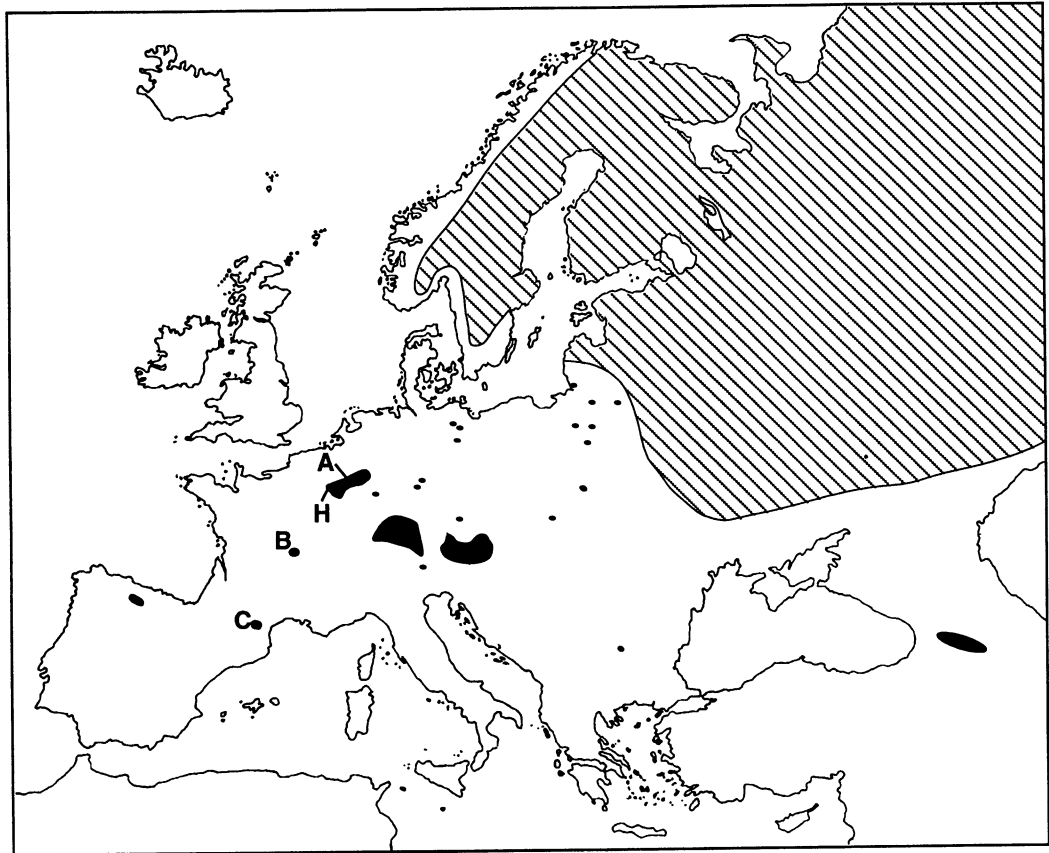
This paper reports a study of the effect of habitat patchiness on the population ecology of *P. eunomia*. Although a Mark-Release-Capture (MRR) study conducted in 1992 has already shown that this species disperses readily between populations separated by just a few 100 m (Baguette & Nève 1994), its ability to disperse over longer distances remained unknown. Recolonization of previously extinct populations, a key factor in metapopulation dynamics, needs effective long-distance dispersal ability. We have therefore expanded our study. (i) In 1993, all other suitable sites of the Lienne valley (Belgium), within a 6-km radius, were included in the MRR study in order to investigate dispersal power over longer distances than those previously published. (ii) An MRR study was launched in the Quérigut area (French Pyrénées). (iii) We present data on the colonization of the Morvan (central France) since the introduction of *P. eunomia* there in the 1970s. This artificial situation (colonization was man-induced) may be taken as an example of what could happen if populations go extinct in a large area, and are recolonized from refuge populations; this is a typical metapopulation process acting after a massive disturbance causing local extinctions (Harrison, Murphy & Ehrlich 1988; Thomas & Jones 1993). The present paper aims at assessing the importance of a network of patches for metapopulation processes in the specialist butterfly *P. eunomia*.

## The species

*P. eunomia* is a specialist univoltine Nymphalid butterfly inhabiting wet hay meadows where the bistort (*Polygonum bistorta* L.) is its only larval food plant in middle and southern Europe (Mairlot 1932; personal observation). On a continental scale, *P. eunomia* shows a disjunct distribution (Fig. 1), typical of glacial relicts (Warnecke 1942). *P. eunomia* is a good example of a boreo-montane species (*sensu* Udvardy 1969). The northern taxon *P. eunomia ossianus* Herbst s.l. displays a markedly distinct morphology, karyotype (haploid chromosome number is 28 for *P. eunomia ossianus* and 30 for *P. eunomia eunomia*; Higgins 1975), and ecology (it feeds on other food plants: *Viola palustris*, *Polygonum viviparum*, *Andromeda polifolia*, Henriksen & Kreutzer 1982; Marttila *et al.* 1990). It was therefore ranked by Kudrna (1990) as a semi-species. Several subspecies have been described from southern mountain ranges: *P. eunomia campurrianensis* Gómez Bustillo, Odriozola & Eizaguirre from the Cordillera Cantábrica, *P. eunomia ceretanensis* Deslandes from the Pyrénées, *P. eunomia diluta* Heydemann from Germany; and isolated populations in Bulgaria and the Caucasus may also deserve subspecific rank. At a regional scale, the distribution is also patchy, as hay meadows and bogs where *P. bistorta* grows are found mainly along valleys. The distribution in Belgium has not changed since 1960 in terms of occupied 10 × 10 km grid squares, but the number of occupied individual sites has significantly decreased (Baguette, Goffart & De Bast 1992). This denotes an increase in the local patchiness of *P. eunomia*'s distribution. If the trend continues, will this species be able to persist? To answer this question requires knowledge of *P. eunomia*'s dispersal power and population structure, as well as its habitat requirements. The long-term ability of a species to survive in patchy habitats depends on its ability to disperse, allowing gene flow and (re)colonization of habitat patches (Harrison *et al.* 1988; Gilpin & Hanski 1991).

## Study systems

In Belgium, intensive MRR surveys were conducted in the Lienne valley (Liège Province, 50°18'N, 5°49'E; Fig. 2) in 1992 and 1993. Totals of 656 and 402 imagines, respectively, were marked individually with a thin-point permanent pen on the underside of the left hind wing before being released at the location of capture. The sex and the wear of the wings on a scale from 1 (fresh) to 4 (extensive wing wear) were recorded for each individual at each capture, as well as the coordinates of the location of capture. Small patches of unfertilized wet meadows with *Polygonum bistorta* are scattered on both sides of the Lienne river, separated by single-age Norway spruce *Picea abies* (L.) Karst. plantations (some of them with trees more than 20 m high) or fertilized pastures. The sites were



**Fig. 1.** European distribution of *Procllossiana eunomia*: A, Lienne valley study site (Belgium); B, introduction sites in Morvan (France); C, Quérigut valley study site (French Pyrénées); H, Hargnies (France), site of origin of introduced specimens. Hatched: *P. eunomia ossianus*, and closely related forms. Distribution map compiled from Aagaard & Gulbransen (1976), Abadjiev (1995), Ebert & Rennwald (1991), Fernández-Rubio (1991), Henriksen & Kreutzer (1982), Kudrna (1994), Marttila *et al.* (1990), Meyer & Pelles (1981), Reichl (1992), Schreiber (1976), Šulcs & Viidalepp (1973), Verity (1950), from information supplied by Yu. P. Nekrutenko, S. Beshkov, J. Buszko, J. Patočka and A. Weidner, and from personal observations. The southern limit of the Eastern range remains unprecisely known, as the species is widely but very locally distributed in most of the Ukraine.

visited daily – weather permitting – during the flight season (28 May–29 June 1992; 22 May–26 June 1993), totalling 14 and 20 capture days. The first year (1992) of the MRR study in the central sites of the Lienne valley (Belgium) showed that the species was more mobile than hitherto thought (Baguette & Nève 1994); thus, in 1993 all other suitable sites within a 6-km radius were also visited daily. Further details on the site and methods are to be found in Baguette & Nève (1994).

In 1993, the Quérigut valley (42°41'N, 2°4'E, Ariège Département, France) was investigated for the presence of *P. eunomia*, and the four suitable sites were regularly visited from 4 June to 7 July (19 capture days) to conduct an MRR study on *P. eunomia*. The sites of the Quérigut area were more scattered than those of the Lienne river, the minimum distance between two sites being 1.2 km, while some sites of the Lienne valley are only 200 m apart. The Carcanières site (D, Fig. 3) was located along the Quérigut river itself, while the other sites are found along two of its tributaries. A total of 779 imagines were marked individually. The four sites were visited consecutively; a tour of all sites lasting three capture days.

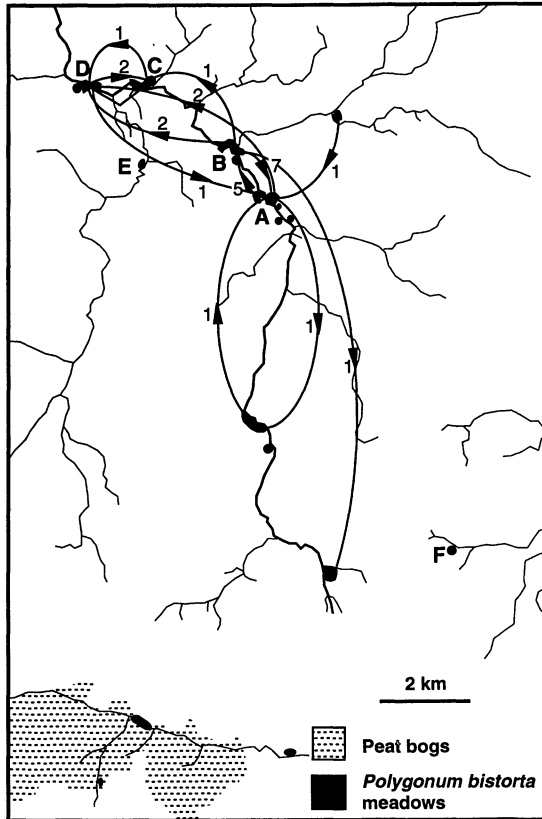
*P. eunomia* was introduced in Morvan in 1970 and 1973 (Descimon 1976) and detailed studies of its spread have been conducted ever since, but the progression of the colonization was followed less regularly in the 1980s. Care was taken to visit potential habitats scattered throughout Morvan, so that no major colonization could escape our attention. All released specimens come from Hargnies (French Ardennes, 50°01'N, 4°48'E, site H, Fig. 1). Four females were released in June 1970 at Saint-Brisson (47°16'N, 4°04'E, site A, Fig. 4), 14 females were released at Lavault-de-Frétoy (47°6'N, 4°04'E, site B) in 1973. On 25 June 1977, four females from the colony A were released at Alligny (47°12'N, 4°10'E, site C).

Population estimates used the Jolly–Seber method, as applied to open populations (Seber 1982; Hines 1988). All other statistical analysis used SAS package (SAS 1990).

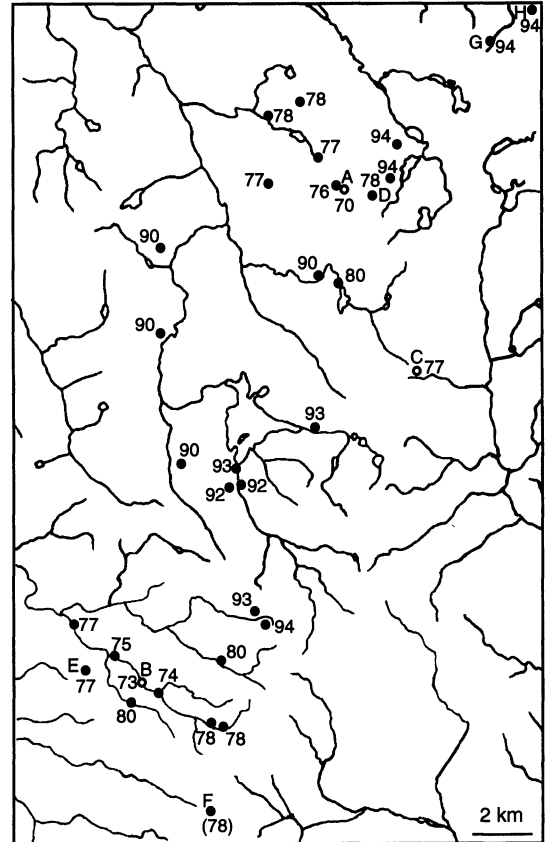
## Results

### MRR STUDIES: BELGIAN ARDENNES

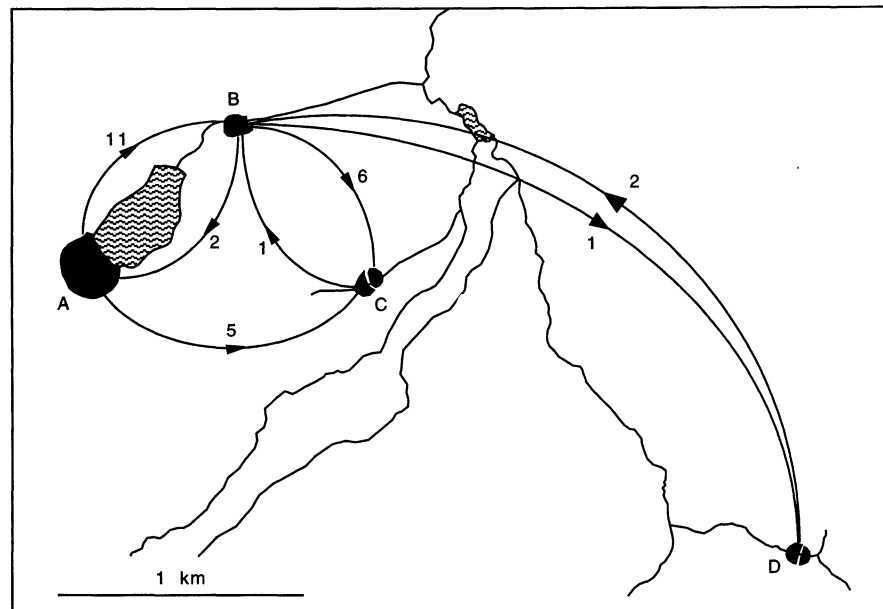
From 692 and 344 recaptures recorded in 1992 and 1993 within the Lienne river system (Fig. 2: Sites A



**Fig. 2.** Movements of *P. eunomia* observed in the Lienne valley (Belgium) in 1993. Only movements including a crossing of more than 200 m of unfavourable habitat are drawn. Fourteen such movements between patches of site A were omitted from the figure. Arrows symbolize movements between patches, and figures indicate numbers of observed movements. Letters indicate sites referred to in the text.



**Fig. 4.** Colonization in Morvan by *P. eunomia*, following introductions: open circles, introduction sites A–C; closed circles, observed colonization. Figures give year of introduction or observed colonization. Brackets indicate the observation of a single individual, with no establishment of population. Letters indicate sites referred to in the text.



**Fig. 3.** Movements of *P. eunomia* observed in the Quérigut valley (France) in 1993. Only movements between sites are drawn. Arrows symbolize movements between patches, and figures indicate numbers of observed movements. Letters indicate sites referred to in the text.

and B), 58 and 30 (8 and 9%), respectively, involved a crossing of more than 200 m of unsuitable habitats, such as fertilized pastures and Norway spruce *Picea abies* plantations. In 1992 females moved more often than males: 42 of the 285 recaptures of females (14.7%) included a movement of more than 200 m on unsuitable habitat, whereas only 16 of the 407 recaptures of males (3.9%) did so. In 1993 the tendency is reversed, with 3 of 64 recaptures of females further than 200 m (4.7%), and 27 of 280 recaptures of males (9.6%). The maximum recorded movements were 4.6 km for males and 2.5 km for females. A lack of suitable sites on 2 km downstream from site D (Fig. 2) seems to lower considerably the probability of movements to the next available site. Despite search in neighbouring valleys, no individual has ever been found to have emigrated to or from the Lienne river basin. The population of the core area (sites A and B) may fluctuate between years. It was estimated to amount to 1374 and 644 individuals in 1992 and 1993, respectively; the small difference between this 1992 estimate and the one published (Baguette & Nève 1994) is due to the fact that an improved version of Jolly's estimate was used (Hines 1988). Such differences in abundance between years have commonly been reported for butterfly species (e.g. Pollard 1991). Numerous movements between patches prevented the estimation of populations in each habitat patch.

Some sites of very small size (< 1 ha) were not occupied every year: no imago could be found despite regular visits (site E in 1992, presence in 1991 and 1993; site F in 1991, presence in 1989, 1992 and 1993).

#### MRR STUDIES: FRENCH PYRÉNÉES

Of the 174 recorded recaptures, only 18 were of females, because of bad weather conditions during their main flight period, and the normal lower capture rate of females. It was thus possible to estimate only the male population, which amounted to 1741 individuals. In Belgian populations of *P. eunomia*, the sex ratio is balanced (Baguette & Nève 1994; M. Baguette, Chr. Vansteenwegen & G. Nève, unpublished), and the same is probably true here, in which case the total population of the area was in the range of 3500 imagines in 1993. Of the 174 recaptures, 28 (16%) involved a crossing of at least 1.2 km of unfavourable habitat, and the maximum distance covered was of 2.9 km, between sites B and D. The high percentage of observed emigration, twice as high as in Belgian populations (see above) despite the sites being further apart, is most probably due to a bias, as each site was visited at 2–7 days interval, thus enhancing the probability of recording emigration/immigration.

#### COLONIZATION OF MORVAN (FIG. 4)

In June 1970, a first introduction of four females from Pont Collin was made in a clearing of Bois au Saint

(Saint Brisson, Site A Fig. 4). Its area was rather small (< 1 ha), and the surrounding forest was composed mainly of introduced conifers such as Norway spruce *Picea abies* and Douglas fir *Pseudotsuga menziesii* (Mirb.) Franco. The day of the release was sunny, as were the next few days. Visits in 1971 and 1972 did not yield any observation of *P. eunomia*, and the introduction was assumed to have failed. On 11 June 1973, 14 females were collected at Pont Collin, in order to make two new releases, one in the former place, and one further south. But as it was then observed that the first introduction had finally been successful, all the captive stock was released 20 km away, near Lavault de Frétoy (Site B Fig. 4), also in fine weather.

The original locations of release have not been occupied at least since 1990, due to afforestation. The colonization of site E, completely isolated in an old beech *Fagus sylvatica* L. forest indicates that founder individuals may fly over the canopy. One female was observed on site F in 1978, but if a local population was established it did not survive because this site has now been subject to heavy disturbance. The colonization of locality D in 1978 is of particular importance, as it is part of a different river basin; this involved a jump of only 1 km, but included the crossing of a ridge c. 50 m higher than the original place of release; in 1994, this locality was also destroyed, but two small populated patches were observed west of Champeau, in the same basin. The same year, it appeared that *P. eunomia* performed a much larger jump, which implied crossing into the Tournesac watershed (sites G and H). Although the latter place was very favourable, the butterflies were not numerous and some downstream bistort patches were not occupied. It is therefore likely that colonization is recent here.

After the initial introduction events, neighbouring sites were colonized within 5–10 years, creating two complexes of populations (Fig. 4), nearly all available habitats in northern Morvan were occupied within 20 years, but the depression of Arleuf (on the southern part of Fig. 4), which separates northern Morvan from the Haut Folin massif was still not crossed in 1994. Colonization first included patches close to introduction sites (Fig. 5), then a 6-km gap had to be crossed to expand further. Within the first decade, there is no correlation between the distance from the source and the time needed for establishment ( $P > 0.4$ ); all colonized sites are within the maximum distance that could be achieved by one individual colonist. When all colonization events are taken into account the relationship between distance and time to colonize becomes significant (Spearman rank correlation = 0.54,  $n = 30$ ,  $P < 0.01$ ) and the average speed of colonization is 0.4 km year<sup>-1</sup>. It seems thus that, in the short term, colonization speed and direction are unpredictable, whereas stepping-stone processes may be detected at a larger space-time scale.

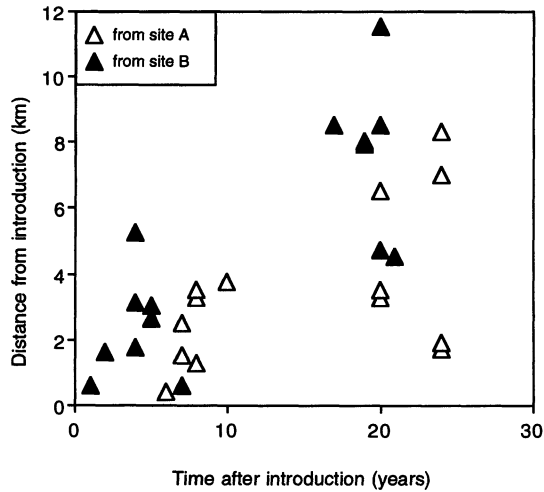


Fig. 5. Spread of *P. eunomia*, after introduction events in 1970 and 1973.

## Discussion

### MRR AND COLONIZATION

Both MRR studies showed that *P. eunomia* individuals may move across several km of unfavourable habitats. Small sites around important densely populated biotopes may be occupied only by a few individuals, and not necessarily every year. These sites may nevertheless be important as stepping-stone sites for dispersing individuals and for reproduction in 'good years'. Local hydric conditions may have an effect on the suitability of such sites for reproduction. The distribution of the suitable sites thus changes slightly from year to year. Despite the fact that grazed meadows are not suitable for reproduction, adults were occasionally observed feeding on bistort flowers growing there, some of which were subsequently recorded in optimal habitats. Thus it seems that small and localized bistort patches may act as temporary foraging sites for dispersing individuals. On the other hand, sites placed under grazing pressure during or after the flight season of *P. eunomia* may be considered as traps for dispersing individuals, as has been observed in the Pyrénées.

Further evidence of *P. eunomia*'s dispersal capacity was revealed by its colonization of the Morvan region. Following its release at two localities, it spread to occupy virtually all suitable habitat patches in a 200 km<sup>2</sup> area in under 25 years. The habitat in Morvan was patchily distributed, and several colonization steps of over 4 km were required to achieve this. The detailed record of the spread of *P. eunomia* in Morvan discloses valuable information about the colonization abilities of the species. From the slowness of the start of the colonization, it may be inferred that a temporarily low abundance may later nevertheless develop into a core area from which colonization occurs. The effect of weather conditions on the abundance of the butterflies, and hence on colonization

should be noted: June 1974 was cold and rainy in the Morvan, and June 1975 was closer to average but cloudy; these led to no colonization being observed in 1975, and limited colonization in 1976. The latter year, however, being very favourable to *P. eunomia* (hot and sunny in June and July), resulted in the high colonization rate observed in 1977; this included a 3 km jump, and flight over several hundred metres of high beech forest canopy. The high abundance of *P. eunomia* at any given location may only be transitional if the site does not remain suitable to the species, and this is particularly the case for the two original locations of release, where the species could not be relocated in 1993.

The disjunct distribution of *P. eunomia* in France, where it naturally occurred only in the Ardennes and the Pyrénées, has led us to question why the species is absent in other seemingly suitable areas, such as the Morvan where such habitats are abundant. A similar situation occurs in other areas of the Massif Central, and in the French and Swiss Alps. In the latter area, however, the Nymphalid *Clossiana titania* Esper is a potential competitor, as it also feeds on *Polygonum bistorta*. In Morvan, ecogeographical studies suggest that, under natural vegetation dynamics, no suitable habitats would be available for either species (Descimon, Dutreix & Essayan 1980). Indeed, the only open spaces which would subsist permanently are peat bogs and moors. For this reason, the only boreo-montane butterflies naturally occurring in the region are *Boloria aquilonaris* Stichel (Nymphalidae) and *Coenonympha tullia* Müller (Satyridae), which are linked to these habitats. Under a natural regime, *Polygonum bistorta* would be confined to shrubby sheltered locations, where it is not used by *P. eunomia*. The present abundance of *P. bistorta* is obviously due to human action and landscape opening; it forms dense colonies in the more moist parts of meadows. When heavily grazed, such places are not favourable to bistort-eating butterflies; but when herbivorous pressure is released, the resulting plant formation appears very hospitable to many specialist butterflies (e.g. *Palaeochrysophanus hippothoe* L., *Clossiana selene* Denis & Schiffermüller and two bistort-associated species: *P. eunomia* and *Lycaena helle* Denis & Schiffermüller).

In the 1960s *P. eunomia* was not protected by law, allowing free capture and release experiments. Codes of conservation practice on insect re-establishment, agreed in the 1980s, recommend that introduction of butterflies should only be carried out in the known historical range of the species (Thomas 1992). The introduction in Morvan took place before such discussions arose in entomological circles, but it seems unlikely that it would have had deleterious effects on the region's ecosystems.

### POPULATION STRUCTURE

The populations of *P. eunomia* are organized in a hierarchical way. Inside habitat patches individuals

move freely. Movements are frequent between neighbouring patches, particularly if these patches are situated in the same river basin. Such a complex of populations therefore functions as a metapopulation system. Movements between river basins, albeit infrequent, are sufficient to ensure genetic cohesion. At the European scale, the disjunct areas of *P. eunomia*'s distribution, particularly in the south of its range, may be taken as a complex of metapopulations. The spread in the Morvan shows that new complexes may be created *de novo*. The colonization of a large area from such a low number of introduction events (2), as well as a low number of individuals (18) is a spectacular success, which was unexpected as, at that time, *P. eunomia* was thought to have closed populations. However, movements of *P. eunomia* are limited: movements of a few kilometres over unfavourable habitats are exceptional, and this would render patches of habitat isolated by 10 km from occupied patches unlikely to be colonized, as it is still absent in southern Morvan. A similar situation has been described for *Plebejus argus*, for which 1 km is the limit of distance covered by dispersive individuals (Thomas & Harrison 1992). In such cases the existence of a dense network of suitable habitats is necessary.

The success of the *P. eunomia* introduction and its quick spread in Morvan is a rare event in butterfly introductions (Oates & Warren 1990). Butterfly populations with an open structure do not easily naturalize, because a limited number of released individuals tend to disperse and 'evaporate' into the area of release without being able to initiate a nucleus (Descimon 1976; Thomas 1984). On the other hand, a sedentary species, such as *Strymonidia pruni*, hardly colonize and the site of reintroduction would lead to the establishment of very few colonies (Thomas 1984; Thomas *et al.* 1992). One factor resulting in the quick colonization of the Morvan area may be the absence of any specific parasite, as only adult females were introduced. Ford & Ford (1930) have shown that parasitism may cause up to 90–95% mortality in *Eurodryas aurinia* caterpillars at high density. However, there is no known parasitoid in *P. eunomia* caterpillars: from 104 last instar caterpillars captured in May 1994 in the Belgian Ardennes and kept until imago emergence, no parasitoid could be found (M. Waeyenbergh, personal communication). The rôle of the release of population size control by specific parasites is not obvious in the present case; we noticed that the density observed in the new colonies was comparable to that of the original ones. However, if density-dependent dispersal occurs as soon as population density oversteps a certain threshold, then the observed rapid occupation of neighbouring habitats could be explained by an accelerated proliferation of the original nuclei.

From a conservation point of view, the way *P. eunomia*'s metapopulation systems work is at the same time a hope and a danger for the conservation of the species. Restoration or creation of suitable habitats

may be sufficient to establish new local populations, enhancing networks of existing patches; on the other hand, some habitats may act as sinks for dispersing individuals, if local reproduction rate is insufficient to balance local mortality (Pulliam 1988; Howe, Davis & Mosca 1991), such as seems likely to be the case for some Pyrénées sites. On a large scale, however, if patches of suitable habitats disappear, colonization processes no longer balance natural and man-induced extinctions, as shown in the case of *Eurodryas aurinia* in Britain (Warren 1994).

For several butterfly species, dispersal has been shown to be density-dependent (Shreeve 1992). At the landscape scale the metapopulations are usually not at equilibrium because of habitat dynamics (Harrison 1994). Therefore, metapopulation dynamics models recently developed by Hanski (1994a, 1994b) are not directly applicable to *P. eunomia*, nor probably to many other butterfly species, unless modified to account for the effect of density (M. Baguette *et al.*, unpublished) and for habitat change (Thomas 1994). The extinction of *M. cinxia* from many islands of the Finnish archipelago and from mainland Finland is probably due to the fact that the network of suitable sites went below a critical threshold, resulting in the collapse of populations (Hanski, Kuussaari & Nieminen 1994). This is probably also the case for other species that have disappeared from part of their range despite the continued presence of suitable habitats.

If *P. eunomia* and other specialist species showing similar metapopulation structures are to be conserved in the long term, the protection of large core sites would not be a sufficient prerequisite; the presence of small sites, necessary for stepping-stone processes and recolonization, are essential for the regional distribution dynamics. In heavily modified landscapes, the (re)introduction of butterflies to new areas is now recognized as an integral part of wildlife conservation, especially as wildlife sites become fewer, smaller and more isolated (Morris & Thomas 1987). Precise recording and monitoring of (re)introduction events are necessary in order to improve their success. In only a very few cases do reintroduction events lead to the efficient colonization of habitats and to the establishment of a new metapopulation (review in Oates & Warren 1990; discussion of the *Plebejus argus* case: Thomas & Harrison 1992). For migrant species and species with good dispersal power, whole regions may be colonized from a few refuges, but species with low dispersal power will not recolonize previously occupied patches if the unoccupied habitats are too far away from refuge populations (Thomas *et al.* 1992; Thomas & Jones 1993). In the latter case a man-induced colonization, i.e. reintroduction, could be justified (Morris & Thomas 1987; Oates & Warren 1990).

## Conclusions

The maintenance of *P. eunomia* depends on a delicate balance between ecological factors: a narrow range in



grazing intensity and a space–time dynamic in the distribution of transient habitats. The long-term survival of *P. eunomia* depends both on large sites for reproduction and on a network of smaller sites, essential as stepping stones allowing recolonization. The survival of such a specialist species is thus dependent on land management at regional and local scales. The habitat of *P. eunomia* in the lowlands of western Europe consists mainly of secondary vegetation, due to extensive grazing pressure or regular hay mowing, and this is the situation for about 50% of west European butterfly species (Erhardt & Thomas 1991). Our observations have shown that modern fertilization leads to the disappearance of *P. eunomia* and other bistort-linked butterflies (*Lycaena helle* and *Palaeochrysophanus hippothoe*). Therefore, the survival of *P. eunomia* and other species related to secondary vegetation is linked with the continuing management of their habitat, the paramount factor of long-term survival being habitat suitability both in quality and in spatial structure.

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### References

- Aagaard, K. & Gulbrandsen, J. (1976) *Prikkart over norske dagsommerfugler*. Kgl. Norske Videnskabers Selskab Museet, Universitet i Trondheim.
- Abadjiev, S. (1995) *Butterflies of Bulgaria*. Volume 3. *Nymphalidae: Apaturinae & Nymphalinae*. Abadjiev, Sofia.
- Baguette, M. & Goffart, P. (1991) Liste rouge des Lépidoptères Rhopalocères de Belgique. *Bulletin et Annales de la Société Royale Belge d'Entomologie*, **127**, 147–153.
- Baguette, M. & Nève, G. (1994) Adult movements between populations in the specialist butterfly *Proclissiana eunomia* (Lepidoptera, Nymphalidae). *Ecological Entomology*, **19**, 1–5.
- Baguette, M., Goffart, P. & De Bast, B. (1992) Modification de la distribution et du statut des Lépidoptères Rhopalocères en Belgique depuis 1900. *Mémoires de la Société Royale Belge d'Entomologie*, **35**, 591–596.
- Braconnot, S., Descimon, H. & Vesco, J.-P. (1993) La conservation des *Parnassius* de France: état des populations de 1990 à 1992. *Alexandria*, **18**, 1–44.
- Dempster, J.P. (1991) Fragmentation, isolation and mobility of insect populations. *The Conservation of Insects and their Habitats* (eds N. M. Collins & J. A. Thomas), pp. 143–153. Academic Press, London.
- Descimon, H. (1976) L'acclimatation de lépidoptères: un essai d'expérimentation en biogéographie. *Alexandria*, **9**, 195–204.
- Descimon, H. & Napolitano, M. (1993) Enzyme polymorphism, wing pattern variability, and geographical isolation in an endangered butterfly species. *Biological Conservation*, **66**, 117–123.
- Descimon, H., Dutreix, C. & Essayan, R. (1980) Esquisse écologique et biogéographique des Rhopalocères de la Bourgogne. *Bulletin de la Société d'Histoire Naturelle d'Autun*, **93**, 13–61.
- Ebert, G. & Rennwald, E. (eds) (1991) *Die Schmetterlinge Baden-Württembergs. Band 1. Tagfalter I*. Ulmer, Stuttgart.
- Erhardt, A. & Thomas, J.A. (1991) Lepidoptera as indicators of change in the semi-natural grasslands of lowland and upland Europe. *The Conservation of Insects and their Habitats* (eds N. M. Collins & J. A. Thomas), pp. 213–237. Academic Press, London.
- Fernández-Rubio, F. (1991) *Guía de Mariposas diurnas de la Península Ibérica, Baleares, Canarias, Azores y Madeira. Lybhyteidae, Nymphalidae, Riodinidae y Lycaenidae*. Pirámide, Madrid.
- Ford, E.H. & Ford, E.B. (1930) Fluctuation in numbers and its influence on variation in *Melitaea aurinia* Rott. (Lepidoptera). *Transactions of the Entomological Society of London*, **78**, 345–351.
- Game, M. (1980) Best shape for nature reserves. *Nature*, **287**, 630–632.
- Gilbert, F.S. (1980) The equilibrium theory of island biogeography: fact or fiction? *Journal of Biogeography*, **7**, 209–235.
- Gilpin, M. & Hanski, I. (eds) (1991) *Metapopulation Dynamics: Empirical and Theoretical Investigations*. Academic Press, London.
- Hanski, H. (1991) Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society*, **42**, 17–38.
- Hanski, I. (1994a) A practical model of metapopulation dynamics. *Journal of Animal Ecology*, **63**, 151–162.
- Hanski, I. (1994b) Patch-occupancy dynamics in fragmented landscapes. *Trends in Ecology and Evolution*, **9**, 131–135.
- Hanski, I., Kuussaari, M. & Nieminen, M. (1994) Metapopulation structure and migration in the butterfly *Melitaea cinxia*. *Ecology*, **75**, 747–762.
- Harrison, S. (1994) Metapopulations and conservation. *Large-Scale Ecology and Conservation Biology* (eds P. J. Edwards, R. M. May & N. R. Webb), pp. 111–128. Blackwell, Oxford.
- Harrison, S., Murphy, D.D. & Ehrlich, P.R. (1988) Distribution of the Bay Checkerspot Butterfly, *Euphydryas editha bayensis*: evidence for a metapopulation model. *American Naturalist*, **132**, 360–382.
- Henriksen, H.J. & Kreutzer, I. (1982) *The Butterflies of Scandinavia in Nature*. Skandinavisk Bogforlag, Odense.
- Higgins, L.G. (1975) *The Classification of European Butterflies*. Collins, London.
- Hines, J.E. (1988) *Program 'Jolly': User Instructions (Draft)*. US Fish and Wildlife Service, Patuxent Wildlife Center, Laurel, Maryland (USA).
- Hodgson, J.G. (1993) Commonness and rarity in British butterflies. *Journal of Applied Ecology*, **30**, 407–427.
- Howe, R.W., Davis, G.J. & Mosca, V. (1991) The demographic significance of 'sink' populations. *Biological Conservation*, **57**, 239–255.
- Kudrna, O. (1990) Conservation of butterflies in Fen-

- noscandia: aims and priorities from an European point of view. *Entomologist's Gazette*, **41**, 167–176.
- Kudrna, O. (1994) Kommentierter Verbreitungsatlas der Tagfalter Tschechiens. *Oedippus*, **8**, 1–137.
- Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, **15**, 237–240.
- MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373–387.
- MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- Mairlot, M. (1932) *Argynnis apherape* Hbn. en 1931. *Lam-billionea*, **31**, 142–145.
- Marttila, O., Haahtela, T., Aarnio, H. & Ojalainen, P. (1990) *Suomen Päiväperhoseet*. Kirjayhtymä Oy, Helsinki.
- Meyer, M. & Pelles, A. (1981) *Atlas provisoire des insectes du Grand-Duché de Luxembourg. Lepidoptera (première partie)*. Travaux Scientifiques du Musée d'Histoire Naturelle de Luxembourg, Luxembourg.
- Morris, M.G. & Thomas, J.A. (1987) Re-establishment of insect populations, with special reference to butterflies. *The Moths and Butterflies of Great Britain and Ireland*, Vol. 7, Part 1 (eds A. Maitland Emmet & J. Heath), pp. 22–36. Harley Books, Colchester.
- Murphy, D.D. & Weiss, S.B. (1988) Ecological studies and the conservation of the Bay Checkerspot butterfly *Euphydryas editha bayensis*. *Biological Conservation*, **46**, 183–200.
- Oates, M.R. & Warren, M.S. (1990) *A Review of Butterfly Introductions in Britain and Ireland*. World Wide Fund for Nature, Godalming.
- Pollard, E. (1991) Monitoring butterfly numbers. *Monitoring for Conservation and Ecology* (ed. F. B. Goldsmith), pp. 87–111. Chapman & Hall.
- Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652–661.
- Reichl, E.R. (1992) *Verbreitungsatlas der Tierwelt Österreichs. Band 1: Lepidoptera – Diurna, Tagfalter*. Forschungsinstitut für Umweltinformatik, Linz.
- Sarlet, L.G. (1965) *Colias palaeno* L. Ce joyau disparu de Belgique! (Lepidoptera Pieridae). *Revue Verviétoise d'Histoire Naturelle*, **22**, 2–83.
- SAS Institute Inc. (1990) *SAS/STAT® User's Guide*, Version, **6**, 4th edn. SAS Institute Inc., Cary, NC.
- Schreiber, H. (1976) *Lepidoptera. Familien Papilionidae, Pieridae und Nymphalidae. Fundorkataster der Bundesrepublik Deutschland*. Universitaet des Saarlandes, Saarbruecken.
- Seber, G.A.F. (1982) *The Estimation of Animal Abundance and Related Parameters*. 2nd edn. Griffin, London.
- Shafer, C.L. (1991) *Nature Reserves: Island Theory and Conservation Practice*. Smithsonian, Washington.
- Shreeve, T.G. (1992) Monitoring butterfly movements. *The Ecology of Butterflies in Britain* (ed. R. L. H. Dennis), pp. 120–138. Oxford University Press, Oxford.
- Simberloff, D. (1988) The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics*, **19**, 473–511.
- Soulé, M.E. & Wilcox, B.A. (eds) (1980) *Conservation Biology: An Evolutionary-Ecological Perspective*. Sinauer, Sunderland (Mass.).
- Soulé, M.E. (ed.) (1987) *Viable Populations for Conservation*. Cambridge University Press, Cambridge.
- Šulcs, A. & Viidalepp, J. (1973) Verbreitung der Großschmetterlinge im Baltikum. I Tagfalter (Diurna). *Deutsche Entomologische Zeitschrift*, **21**, 353–403.
- Thomas, C.D. (1992) The establishment of rare insects in vacant habitats. *Antenna*, **16**, 89–93.
- Thomas, C.D. (1994) Difficulties in deducing dynamics from static distributions. *Trends in Ecology and Evolution*, **9**, 300.
- Thomas, C.D. & Harrison, S. (1992) Spatial dynamics of a patchily distributed butterfly species. *Journal of Animal Ecology*, **61**, 437–446.
- Thomas, C.D. & Jones, T.M. (1993) Partial recovery of a skipper butterfly (*Hesperia comma*) from population refuges – lessons for conservation in a fragmented landscape. *Journal of Animal Ecology*, **62**, 472–481.
- Thomas, C.D., Thomas, J.A. & Warren, M.S. (1992) Distributions of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia*, **92**, 563–567.
- Thomas, J.A. (1984) The conservation of butterflies in temperate countries: past efforts and lessons for the future. *The Biology of Butterflies. Symposium 11 of the Royal Entomological Society* (eds R. I. Vane-Wright & P. R. Ackery), pp. 333–353. Academic Press, London.
- Udvardy, M.D.F. (1969) *Dynamic Zoogeography*. Van Nostrand Reinhold, New York.
- Verity, R. (1950) *Le Farfalle Diurne d'Italia*, Vol. 4. Casa Editrice Marzocco, Firenze.
- Warnecke, G. (1942) *Argynnis apherape* Hb. als Eiszeitrelikt in Europa (Lep. Rhop.). *Entomologische Zeitung*, **103**, 50–59.
- Warren, M.S. (1994) The UK status and suspected metapopulation structure of a threatened European butterfly, the marsh fritillary *Eurodryas aurinia*. *Biological Conservation*, **67**, 239–249.

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### Note added in proof

In 1995, the parasitoid *Cotesia vestalis* Haliday (Hymenoptera, Braconidae) was recorded on 92% of 112 last instar larvae found in the field in the Plateau des Tailles area (Belgian Ardennes; M. Waeyenbergh, D. Maas & M. Baguette, unpublished). Its impact on the local population dynamics of *P. eunomia* is still unknown, but likely to be important, as parasitism by *Apanteles bignelli* was for the dynamics of *Euphydryas aurinia* (Porter 1983).

### REFERENCE

- Porter, K. (1983) Multivoltinism in an *Apanteles bignelli* and the influence of weather on synchronization with its host *Euphydryas aurinia*. *Entomologia Experimentalis et Applicata*, **34**, 155–162.