

Baguette, M. & Nève, G. 1994. Adult movements between populations in the specialist butterfly *Procllossiana eunomia* (Lepidoptera, Nymphalidae). *Ecological Entomology*, 19: 1-5.

Abstract

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2. An unexpected high level of adult movements between habitat patches was detected by a mark-release-recapture technique. Local populations were connected by adult movements across unsuitable habitats, leading to a metapopulation structure.
3. This evidence of the metapopulation structure of a specialist butterfly challenges the supposed relationship between habitat specialization and closed, isolated populations.
4. Males and females of *P.eunomia* exhibited different spatial behaviours; females were more likely to emigrate and dispersed further than males. These differences in spatial behaviour are related to the mating system.

Adult movements between populations in the specialist butterfly *Proclrossiana eunomia* (Lepidoptera, Nymphalidae)

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Abstract. 1. The structure of local populations of a monophagous butterfly, the bog fritillary *Proclrossiana eunomia*, was studied in a complex of suitable habitat patches separated by spruce plantations or fertilized pasture.

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Key words. Conservation, protandry, dispersal, movements, metapopulation, butterflies, mark–release–recapture, *Proclrossiana eunomia*.

Introduction

Most butterfly species are declining in industrialized countries (Thomas, 1984). This trend is generally explained by the combination of (1) the destruction of suitable habitat and (2) the human-induced patchiness of formerly continuous habitats. Habitat destruction is due primarily to changes in land use, leaving a smaller total surface of suitable habitats (Thomas, 1984, 1991; Kudrna, 1986; Blab *et al.*, 1988), and secondarily to indirect effects due to man-induced climatic changes which may become important in the future (Dennis & Shreeve, 1991). Furthermore, human activities have an important effect on the distribution of the remaining suitable habitats, which are becoming increasingly more isolated and smaller (Ehrlích, 1984; Thomas, 1984, 1991). On a local scale, the dispersal power of most butterfly species, and especially specialized ones, has been thought to be low (Ehrlích, 1984; Thomas, 1984, 1991; Warren, 1987, 1992); moreover, the increasing isolation of populations seems to coincide with the selection of less mobile individuals (Dempster, 1991).

Baker (1969) developed a model showing that the rate of movements out of natal patches (Baker's 'voluntary displacements') depends (1) on the rate of formation of new larval foodplants, (2) on the difference between the optimal habitats for larvae and adults, and (3) on the distance between larval foodplant sites. According to this model, specialist butterflies living in long-lived habitats which are suitable for both larvae and adults should show a relatively low dispersal rate. Since Baker's model was formulated, most authors have accepted that butterflies with highly specialized habitat requirements, which are restricted to local patches, are more prone to isolation mechanisms than regionally ubiquitous species (Brussard & Ehrlich, 1970). Such species are said to form closed populations (Thomas, 1984, 1991; New, 1991; Warren, 1992). This reasoning has suggested a scenario of butterfly decline based on small, discrete local populations becoming more and more isolated and thereby threatened with extinction (Thomas, 1984), although cases of between-sites dispersal in several specialist species have been reported (e.g. Watt *et al.*, 1977; White, 1980).

In this paper we report on the spatial structure of local populations of the bog fritillary *Proclrossiana eunomia* (Esper). This univoltine species has a very restricted habitat in Belgium: it is found in unfertilized wet meadows

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where *Polygonum bistorta*, the only larval food plant of *P. eunomia* in the region, grows. The natural patchiness of this habitat has been increased by the plantation of Norway spruce (*Picea abies*) and the transformation of hay meadows into fertilized pastures. We focus on the movements of adult butterflies between habitat patches which are assumed to be an important factor in the extinction scenario for species living in subdivided 'closed' populations. We compare, therefore, the level of movements within and between patches. This species was chosen because of its specific habitat requirements and local abundance in suitable habitats, which are typical ecological characteristics of most vulnerable butterfly species in Belgium (Goffart *et al.*, 1992).

Methods

The study area (1 km long, max. 300 m wide) was located along the Lienne river, southern Belgium (50°18'N, 5°49'E). Small patches of unfertilized wet meadows with *Polygonum bistorta* were scattered on both sides of the river, separated by single-age spruce plantations (some of them with trees more than 20 m high) or fertilized pastures. This complex of suitable habitat patches of various sizes (totalling about 10 ha, Fig. 1) was isolated from other patches downstream by continuous spruce plantations for 1 km, and upstream by fertilized pastures and a village. On both sides of the study area, other river basins with suitable habitat are at least at 3 km away. In 1992 the study site was visited as often as possible, weather permitting, during the

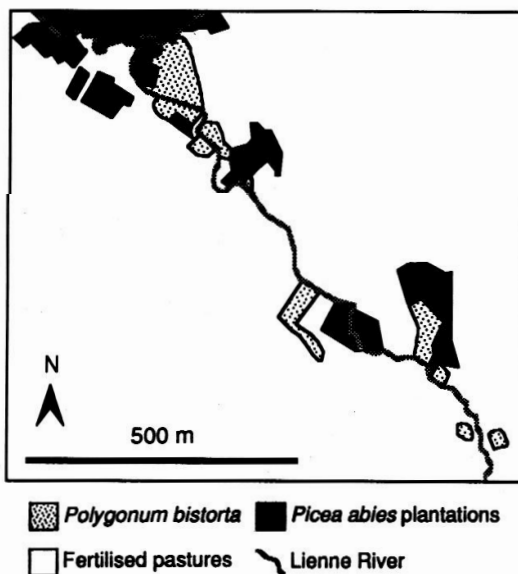


Fig. 1. Study site of *Proclissiana eunomia* in the Lienne Valley, Belgium.

flight period of *P. eunomia* (from 28 May to 29 June). A total of 656 butterflies were captured and individually marked with a number written using a thin-point permanent pen on the underside of the right hindwing. The butterflies were 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.

As numerous movements between patches were observed (see below), the Jolly-Seber method, as applied to open populations, was used to estimate the size of the *P. eunomia* population (Seber, 1982; Krebs, 1989). Average residence time was computed following Watt *et al.* (1977).

Spermatophore counts were performed on twenty females sampled on 10 June 1993 at Elsenborn (50°29'N, 6°15'E).

Results

Dispersal

The numbers of marked individuals which were subsequently recaptured were 181 of the 304 marked males, and 178 of the 352 females. Butterflies actively moved between the different patches. On a few occasions individuals were seen flying straight across fertilized pasture or flying above mature spruce plantations. Butterflies were never observed to follow the river banks. Therefore, the unsuitable habitats (managed pastures and spruce plantations) were not absolute obstacles to adult dispersal. No preferred direction of movement could be detected, with as many individuals moving downstream as upstream. The sexes displayed different spatial behaviours: independently of the time elapsed between two captures of an individual, females moved further than males ($F_{1,688} = 23.35$, $P < 0.001$). Between two successive catches, females moved twice as much as males (female mean 123 m, $n = 285$; male mean 59 m, $n = 407$), whereas the time elapsed between those catches was more similar (males 3.0 days, females 3.9 days). The maximum recorded distances were 920 m for females, and 730 m for males. Females thus tended to emigrate more than males, which was confirmed by the fact that 42 of the 285 recaptures (15%) of females took place in a patch of *Polygonum bistorta* separated by at least 200 m of unsuitable habitat to the one in which they had been captured before, whereas only 16 of the 407 recaptures of males (4%) did so, and the difference is significant ($\chi_1^2 = 25.5$, $P < 0.001$). The proportion of individuals involved also varied, as 14 of the 304 males (4.6%) proved to have moved to a non-adjacent patch of habitat, whereas 37 of the 352 marked females (10.5%) did so ($\chi_1^2 = 7.9$, $P < 0.01$).

Both sexes showed a significant relationship between distance and time between consecutive captures (males: $R^2 = 0.0135$, $n = 407$, $P < 0.05$; females: $R^2 = 0.0619$, $n = 285$, $P < 0.001$); this suggests that the capture had little effect on movements of the individuals. Furthermore, this relationship varied with the sex ($F_{1,688} = 8.75$, $P < 0.01$),

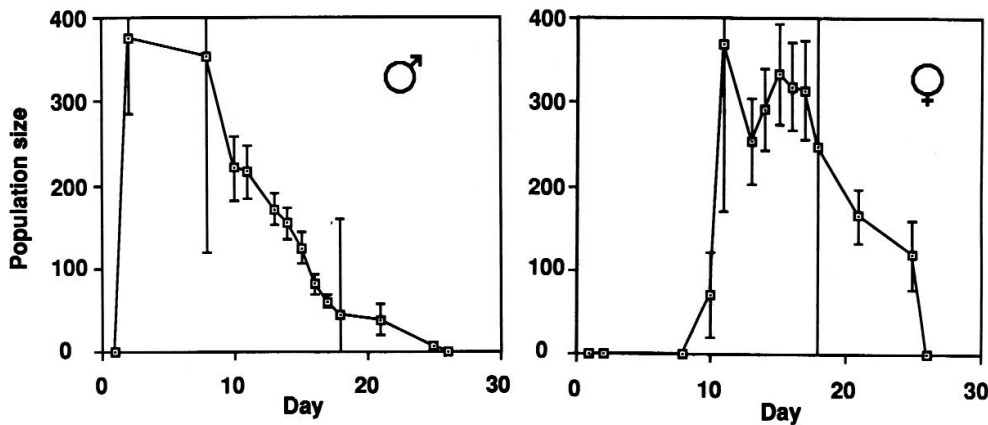


Fig. 2. *Proclissiana eunomia* daily population sizes (Jolly estimates, with 95% confidence intervals) in the Lienne Valley, Belgium; Day 1 is 30 May 1992.

which means that more females than males 'chose' to move away from their patch of first capture, and that when they moved, they went further away than males.

Among the individuals which were captured at least three times, 35% of the males (37/107) had been observed on the same patch as a previous capture after having been seen on another patch, whereas only 9% (7/79) of the females showed such a space-time capture pattern.

These results indicate that the sexes had different spatial behaviours, with females being more likely to emigrate, but neither sex being restricted in movement to its native patch.

Demographic parameters

The daily population size for the study area taken as a whole was estimated separately for both sexes. Results (Fig. 2) show that adult males emerged before adult females: male maximum population size occurred 8 days before the peak of females. This pattern of adult emergence occurs frequently in butterfly species and is referred to as protandry (Wiklund & Fågerström, 1977). However, the time course of population size was similar for males and females: the peak of individuals occurred suddenly and the high level of abundance lasted for about 10 days. Afterwards the population size decreased slowly for males, and faster for females. This difference in population size decrease allowed some males to be on the wing up to the end of the female flight period. At this time, however, the few remaining males were old, with damaged wings: 100% of males ($n = 7$) were in wing wear class 3 or 4 on the last occasion of capture (29 June 1992) compared with 74% of the females ($n = 23$).

Within the whole study area, the total population size amounted to 635 males and 734 females. The average residence time was 4.75 days for males and 7.18 days for females. However, the maximum residence time was much

longer; 18 days for males and 21 days for females (see also Warren, 1992). The dependence of population parameters on weather conditions is shown by the effect of bad weather during the first 6 days of June on the male residence time, which fell to 0.76 days during this period. The weather was fine during the rest of the month, which may explain the higher female abundance and average residence time. Therefore the time disjunction of male and female peaks of abundance, due to protandry, suggests that males' and females' maximum levels of abundance would occur under different weather conditions.

Spermatophore counts

From dissection of 20 females, one was virgin and all the others had only one spermatophore. The mean number of ripe eggs was 34 (minimum 15, maximum 64).

Discussion

Populations of *Proclissiana eunomia* were connected by adult movements across unsuitable habitats, leading to a metapopulation structure (Levins, 1969; Hanski & Gilpin, 1991). The high level of between-patch displacement (observed percentage of emigration: males 4.5%, females 10.5%) contradicts previously reported population structures of specialist butterflies (Ehrlich, 1965, 1984; Brussard *et al.*, 1974; Ehrlich *et al.*, 1975; Gall, 1984; Thomas, 1984, 1991; Warren, 1992). However, such a pattern of movement has been described in *Mellicta athalia*, a specialist butterfly inhabiting short-lived woodland clearings (Warren, 1987), albeit with a lower rate of movement between nearby colonies (males 1.7%, females 1.3%). Other specialized butterflies have shown a high level of movements between habitat patches (e.g. *Colias* spp., Watt *et al.*, 1977; *Euphydryas anicia*, White 1980). In *Euphydryas*

phaeton these movements caused the persistence of high levels of genetic variability in local small populations (Brussard & Vawter, 1975).

In *P.eunomia*, males and females differ in temporal occurrence and mobility. Protandry has been demonstrated to be an evolutionary stable strategy (ESS) both for males and for females if (1) males are able to mate more than once and (2) females mate about once (Zonneveld & Metz, 1991). Spermatophore counts show that *P.eunomia* females usually mate only once. As some males were observed patrolling and attempting courtship after having copulated, they may mate several times. This is the case in *Atrophaneura alcinous* where males mate up to five times whereas 60% of the females mate only once (Suzuki & Matsumoto, 1992). According to these predictions, males should search actively for females and try to mate at each encounter, while virgin females should mate soon after emergence and then should avoid males to maximize the time available for selection of good oviposition sites. Differences in mobility must therefore be related to these differences in predicted behaviour: at high female density, males should not invest time in movement between habitat patches since, 'by the time dispersing males reach another population, females there will probably have been serviced already' (Burns, 1968). On the other hand, at high male density, mated females should increase their movements to avoid ardent males. Another possible reason for dispersal is to find a better quality habitat for feeding or laying eggs, or both. The choice to go or stay within a patch depends on a combination of factors including inter-patch distances, cost of migration between patches and the portion of the individual's reproductive potential still to come (Baker, 1984). As in the present study it seems that females move more than males, the between-patch dispersal of females is assumed to be the main factor in gene flow in such a metapopulation structure, allowing regional panmixy and (re)colonization of unoccupied patches.

The evidence of *P.eunomia* metapopulation structure challenges the strict duality of specialized species with closed local populations as opposed to ubiquitous species with open distribution (Warren, 1992), as the links between population structure and habitat specialization are not as strong as formerly thought. However, some specialist butterfly species inhabiting long-lived habitats, such as *Strimonidia pruni* or *Cupido minimus* (Lycaenidae), have been shown to be sedentary species with closed populations (Shreeve, 1992).

Descimon (1976) and Descimon & Napolitano (1992) reported the results of two introduction experiments of *P.eunomia* in the Morvan (Nièvre, France). From a stock of four females from the Ardenne released in a suitable habitat in 1970, the population increased up to c. 100 individuals in 1973 and to at least 10,000 individuals in 1985; from a stock of fourteen females introduced in another location in 1973, *P.eunomia* has colonized the valley upstream up to 1 km within a year. Moreover, a morphometric analysis of wings of *P.eunomia* at a regional scale reveals that its populations do not differ significantly within Belgium (Nève *et al.*, 1993); this has to be related to

the high dispersal power of adults allowing gene flow between populations.

P.eunomia is thus a species with relatively strong colonization capabilities at a local scale. However, due to its restricted and regionally shrinking habitat, this species is classified as 'vulnerable' in Belgium, according to the I.U.C.N. criteria (I.U.C.N., 1983; Baguette & Goffart, 1991). The regional distribution of the species, as expressed by the number of 10 × 10 km squares, has not changed since 1950, but the total number of occupied sites has significantly declined (Baguette *et al.*, 1992). The high level of movement between patches, at least in years of rather good weather conditions like 1992, could therefore explain why this species has so far persisted widely despite a local decline in distribution due to habitat loss.

We have shown here that the persistence of specialized species such as *P.eunomia* needs effective emigration and immigration to occur. Hanski *et al.* (1994) recently showed this to be of particular importance between habitat patches occupied by *Melitaea cinxia* populations. This process would be possible only with the persistence of a regional network of suitable habitats (Thomas *et al.*, 1992). Therefore we emphasize the need for precise data on the population structure of threatened species as a first step in designing an effective conservation strategy.

Acknowledgments

Professor Ph. Lebrun showed constant support and interest; Professor J. Blondel, Ph. Goffart and M. Waeyenbergh made invaluable comments on the manuscript; Dr R. R. Baker and an anonymous referee provided useful comments; V. de Tillesse, L. Renier, M. Waeyenbergh and A. K. de Caritat contributed to the field work; I. Convié performed the spermatophore counts; G.N.'s research is supported by a grant from the Institut pour l'Encouragement de la Recherche Scientifique dans l'Industrie et l'Agriculture (IRSIA); a special capture licence was issued by the Ministère de la Région Wallonne, which allowed us to work on this protected species, and access to the site was granted by Dr J.-M. Dumont.

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Accepted 5 October 1993