Absence of forest mantles creates ecological traps for *Parnassius mnemosyne* (Papilionidae)

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Abstract. During an intensive mark-recapture study of a woodland population of *Parnassius mnemosyne*, we observed dozens of butterflies occurring at intensively farmed wheat fields that adjoined the wood but clearly did not constitute their habitat. Worn individuals prevailed at the field, suggesting that they arrived there during dispersal. Behaviour of the individuals occurring at the field did not differ from behaviour within the wood, suggesting that the butterflies did not recognise unsuitability of the farmland biotope. This implies that *P. mnemosyne* assesses suitability of its habitat using broad landscape features, rather than detailed clues. Such assessment fails to perform in modern landscapes, where sharp woodland edges replaced wide mantels of a past. We advocate restoration of wide and structurally rich woodland mantels as a conservation tool that may, besides of maintenance of open conditions in forest interiors, contribute to survival of this species.

Introduction

Parnassius mnemosyne (Linnaeus, 1758) is an endangered butterfly in most of Central Europe (Kudrna & Seufert 1991; van Helsdingen et al. 1996; Benes et al. 2002). It has declined due to substantial changes in woodland management practices, such as coniferisation and demise of short-rotation coppicing (Konvicka & Kuras 1999; Kuras et al. 2000). In the Czech Republic, it has disappeared from over two thirds of its historical distribution and became limited to fourteen population systems, most of which are small and isolated (Benes et al. 2002; Konvicka & Benes 2005).

While studying demography of one of the largest Czech population using mark-recapture methods, we observed a striking phenomenon of dozens of butterflies occurring at large and intensively farmed crop fields outside of their woodland habitat. The fields were clearly unsuitable for such activities as nectaring or patroling of males. In this report, we discuss the implications of the phenomenon for our understanding of butterfly ability to recognise suitable habitats, as well as for conservation of the species in modern landscapes.

Material and methods

P. mnemosyne depends on presence of open structures, such as clearings, wide and sunny rides and roadside verges, within deciduous forests. Its females limit egg-laying to host plants growing at such sites (Konvicka & Kuras 1999; Konvicka et al. 2000) and larval development slows down under closed canopy (Bergström 2005; Valimaki & Itamies 2005). The larval host plants include several species of *Corydalis*: *C. solida*, *C. fabacea* and *C. pumilla* are used in the study area. Males patrol over woodland

Fig. 1. Male *Parnassius mnemosyne* (wing wear 2) settling on blades of wheat amidst of a vast wheat field.

openings in search for fresh females (Konvicka & Kuras 1999; Konvicka et al. 2000), multiple insemination is prevented via a solidified male-derived *sphragis*.

In May and June, 2005, we carried out a mark-recapture study of a large *P. mnemosyne* population that inhabits the Milovicky wood, a large (24 km^2) complex of Pannonian oak-hornbeam forests in southernmost corner of Moravia, Czech Republic (48°49'N, 16°42'E, altitude 250 m). The wood used to be low coppice ("Niederwald") until the World War II, has been allowed to overgrow afterwards and now is used as a deer enclosure. Two of us marked the butterflies on everyday basis between May 11 and June 11, 2005, covering eleven distinct colonies within a central part (ca 3 × 3 km) of the wood. For each capture, sex, position, wing wear (4-grade scale from mint to heavily worn) and behaviour prior to capture were recorded; 1,873 individuals (1320♂, 553♀) were captured in total.

Detailed demography results will be reported elsewhere. Here, we refer to captures made in May 21 and 22, when the senior author conducted some additional marking in peripheral parts of the wood. At those peripheral sites, 164 butterflies (138♂, 26♀) were marked during 229 capture events (202♂, 27♀). These records are compared with same-days records by the two other recorders from central part of the wood (marked: 158♂, 69♀; capture events: 328♂, 105♀). The single-day estimates of population sizes are based on assumed Poisson's distribution of frequencies of recaptures per individual (details in Thomas et al. 1983).

Results

In afternoon hours of May 21 and 22, dozens of butterflies occurred at wheat fields adjoining the wood (Fig. 1). Field-forest edge is sharp and abrupt there (Fig. 2), interrupted only by a mouth of a sunny ride. Outside of the wood, intensive crop fields stretch to vast distance, the closest woody structure (a windbreak hedgerow) being 2 km apart (Fig. 3).

The butterflies occurred within a strip ca 200 m wide that reached to some 1 km along the field-forest boundary. Zigzagging this area returned 45 new captures and 10 recaptures (42/10♂, 3/0♀) between 14:30 and 15:30 h (May 21), and 19 captures / 8 recaptures (14/8♂, 5/0♀) between 12:00 and 13:30 h (May 22). A crude single-day estimates of numbers of butterflies at the field, sexes combined, were 240 (± 80 SE) for May 21, and 60 (± 20 SE) for May 22. Within the wood, the respective estimates were 1,780 (± 342 SE) and 2,420 (± 624 SE).

Males prevailed at the field, constituting 90.2% of capture events, compared to 72.8% within the wood ($\chi^2 = 6.08$, d.f. = 1, $P < 0.05$). Majority of males exhibited characteristic patrolling behaviour, flying back and forth in a low height above the crop, rather than in a straightway manner as during dispersal. Activities prior to capture (i.e. frequencies of patrolling, nectaring and basking) did not differ between the field and the wood ($\chi^2 = 0.61$, d.f. = 2, $P = 0.74$; analysis restricted to records between 14:00 and 16:00 h). These observations suggest that the butterflies perceived the field as their habitat, rather than as a hostile non-habitat.

The individuals captured at the field were more heavily worn than those captured in the wood. Mean wing wears of males were 2.30 (±0.893 SD) (field) compared to 1.72 (±0.810 SD) (wood), the difference being significant ($t = 4.43$, d.f. = 192, $P < 0.0001$). In females, the respective means were 2.00 (±0.000 SD) and 1.32 (±0.455 SD) ($t = 4.42$, d.f. = 52, $P < 0.0001$). All females handled at the field were inseminated. Limiting the analysis to records by the same recorder and thus avoiding personal bias in wear assessment gave less pronounced differences, still significant for males (2.30 ±0.893 SD vs. 1.68 ±0.850 SD, $t = 3.45$, d.f. = 95, $P < 0.01$) but not for females (2.00 ± 0.000 SD vs. 1.73 ± 0.647 SD, 1.18, d.f. = 17, $P = 0.25$).

It was unlikely that the butterflies visited the field for nectar. The proportions of handled butterflies that nectared before capture (field: 24 records/ 10.5% of capture events, wood: 64 records / 14.8 % of capture events) did not differ ($P = 0.07$). There were very few flowers available at the field and only two species were used there (*Viola arvensis*: 18, *Lamium purpureum*: 6). Within the wood, seven plant species were used, the most frequent being *Ajuga reptans* (35), *Lithospermum purpureocoreuleum* (10) and *Lamium maculatum* (N: 10). *V. arvensis* was the only plant used in both biotopes (one record in the wood).

Discussion

The main day-round activity of males of *P. mnemosyne* is search of females, which are most likely encountered at sites of their emergence, i.e. at woodland openings containing *Corydalis* plants (Konvicka et al. 2001). Patrolling outside such habitats

Fig. 2. Woodland-forest edge at the Milovicky wood locality, adjoining wheat fields where multiple individuals of *Parnassius mnemosyne* occurred. Note that the edge is narrow and shady and that nitrophilous weedy grass, *Agropyron repens*, prevails in its herbaceous vegetation.

clearly decreases reproductive output of individual males. As the butterflies could not have developed at the fields, it is reasonable to assume that they arrived there during dispersal. This is supported by the fact that they were more heavily worn (i.e., older) than those encountered within the wood – dispersal of individuals that already invested into reproduction at their native locality is a logical bet-hedging strategy in insects. The same should apply for inseminated females.

Although based on limited data, our observation suggests that patrolling males of *P. mnemosyne* cannot distinguish habitat from non-habitat. Cognitive clues influencing selection of patrolling sites were never examined in detail in this butterfly, but there are indices that the species relies on coarse landscape patterns, such as canopy cover, plus presence of conspecifics (e.g., Valimaki & Itamies 2003; Luoto et al. 2001; Heikkinen et al. 2005). If general appearance rather than such resources as host plants or nectar guide behavioural decisions, than any open space within and/or near occupied woodland can attract dispersing males, despite unsuitable local conditions. We found some supportive evidence from another locality in the Czech republic, the Bori wood (45°44’N, 16°49’E), where we observed males patrolling over clearings that had been freshly ploughed and planted by conifers. Because ploughing totally destroys forest floor vegetation, including *Corydalis*, chances to encounters females at such sites are close to zero (Fig. 4).

Fig. 3. View of the field-woodland transition, Milovicky wood locality of *Parnassius mnemosyne*.

It is notable that host plant density acts as an important predictor of movements in two related species, *Parnassius clodius* (Ménétriés, 1855) and *P. smintheus* (Doubleday, 1847) (cf. Auckland et al. 2004; Matter & Roland 2002). A difference between these species and *P. mnemosyne* stems from the fact that host plants of *P. mnemosyne* are already senescent in time of adult flight (Konvicka & Kuras 1999; Bergström 2005). Considering, further, that larval development is more constrained by microclimate than by host abundance (Valimaki & Itamies 2005), relying on broad biotope features is quite expectable, at least for males.

Such simple habitat-detecting clues likely sufficed the species in ancient European landscapes. These were dominated by sparse woodlands, maintained in open conditions by large animals and/or natural disturbances (cf. Vera 2000). It is presumable that after fragmentation of primeval landscapes restricted populations of *P. mnemosyne* to individual forest fragments, short-rotation coppicing maintained the openness of remaining woods, whereas traditional farming rendered separating matrix considerably less hostile than it is in present. Individual forests were surrounded by wide and sunny mantles ("softe edges" *sensu* Duelli et al. 1990), providing the species both safe dispersal routes and breeding habitats. In modern landscapes, such mantles practically ceased to exist. Falloffs of farm nutrients promote vigorous nitrophillous vegetation there, whereas foresters manage every bit of their land for the highest possible yields. The

Fig. 4. Ploughed and recently coniferised clearing in the Bori wood, Czech Republic. A single individual of *Primula elatior* remained from a formerly rich forest ground vegetation. Males of *Parnassius mnemosyne* patrolled at this clearing, apparently not recognising its inhospitable state.

replacement of wide and structurally diverse mantles of a past by "sharp edges" typical for intensively used landscapes constitutes a widely recognised threat to biodiversity (Duelli et al. 1990; Hanski 2005: 35–36).

From a point of view of *P. mnemosyne*, and perhaps other woodland butterflies (e.g., Greatorex-Davies et al. 1993; Konvicka et al. 2005), sharp forest-farmland edges represent ecological traps. When dispersing males encounter such an edge, they may perceive the adjoining crop field as a grassland or forest opening, a biotope that should "normally" be there. While attempting to locate females at crop field, they are effectively lost for reproduction. The same applies for hostile sites within the wood, such as ploughed clearings. In terms of reproductive output and genetic diversity, such losses are probably not too high, especially because they mainly affect already worn individuals. Still, detrimental effect can arise in already weakened populations (i.e., Meglecz et al. 1999).

The message for conservation is clear: besides of maintaining open conditions in forest interiors, restoring wide and structurally rich woodland mantels may contribute to sustaining sensitive species of open woodlands. Available measures include setting aside of strips of fields bordering the woods, opening the mantels via shrub removal and canopy thinning, or establishment of coppiced borderline strips. Such measures may considerably increase the areas inhabitable by endangered woodlands species, thus contributing to halting their declines.

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