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Distribution and dispersal patterns of the ringlet butterfly (*Aphantopus hyperantus*) in an agricultural landscape

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Summary

1 The spatial structure and dynamics of local populations of the butterfly species *Aphantopus hyperantus* were studied in a Swiss agricultural landscape to investigate how the population structure and dispersal of this species are affected by habitat attributes, and whether there is a metapopulation structure.
2 The study took place in the Reussebene (Canton Aargau), an area that is intensely used but that contains semi-natural and natural elements (hedges, canal embankments), which form a network of connected linear structures within the agricultural landscape.
3 A presence-absence mapping showed that *A. hyperantus* is widely distributed along canal embankments. It was found in nearly all spots whose vegetation structure, exposition and species composition suggest that they are suitable habitats for this species.
4 A mark-release-recapture study suggested that site occupancy and migration patterns of *A. hyperantus* are influenced by the landscape structure. The well-connected canal system of the study area permitted a continuous interchange of individuals between suitable patches. The habitat quality and size of habitat patches affected the migration rate and the abundance of the species.
5 Our results suggest that the population structure of *A. hyperantus* can be considered a metapopulation structure and that the species depends on well-connected habitat systems for dispersal. Low connectivity can lead to the isolation of populations.

Zusammenfassung

Verbreitung und Ausbreitungsmuster der Schmetterlingsart *Aphantopus hyperantus* in einer Agrarlandschaft

1 Die räumliche Struktur und die Dynamik von lokalen Populationen der Schmetterlingsart *Aphantopus hyperantus* wurden in einer Schweizer Agrarlandschaft untersucht, um deren Abhängigkeit von der Landschaftsstruktur zu verstehen.
2 Das Untersuchungsgebiet lag in der Reussebene (Kanton Aargau), ein intensiv genutztes Landwirtschaftsgebiet welches aber auch natürlichere Elemente (Hecken, Grabenränder) enthält, die ein Netzwerk von miteinander verbundenen linearen Strukturen bilden.
3 Eine Kartierung zeigte, dass *A. hyperantus* entlang der Grabenränder sehr verbreitet ist. Die Art kam praktisch überall dort vor, wo die Vegetationsstruktur, Einstrahlung und das Blütenangebot den Bedürfnissen der Art entsprachen.

4 Eine Fang-Wiederfang-Untersuchung wies darauf hin, dass das Vorkommen und die Bewegungen von *A. hyperantus* von der Landschaftsstruktur abhängig sind. Das vernetzte Grabensystem des Untersuchungsgebiets erlaubte einen regelmässigen Austausch von Tieren zwischen günstigen Habitaten. Die Häufigkeit der Tiere innerhalb der günstigen Habitate und deren Migrationsraten hingen von der Grösse, der Sonneneinstrahlung und dem Blütenangebot der Habitate ab.
5 Aufgrund der Ergebnisse kann die Populationsstruktur von *A. hyperantus* in der Reussebene als Metapopulationsstruktur betrachtet werden. Die Ausbreitung der Art scheint von gut vernetzten Habitatsystemen abzuhängen. Geringe Vernetzung kann zur Isolation von Populationen führen.

Keywords: connectivity, fragmentation, habitat quality, mark-recapture study, metapopulation

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Introduction

The loss and fragmentation of natural and semi-natural habitat due to human activities is a major threat for many animal and plant species (Hanski 1997). Specialist species with low mobility are particularly restricted to few discrete patches of suitable habitat surrounded by a more or less unsuitable matrix area. In this context a key concept for the understanding of population dynamics is that of metapopulations. A metapopulation is a set of local populations within a fragmented landscape, whose long-term survival depends on the balance between local extinctions and recolonizations (Hanski 1999). The size of habitat patches and their isolation from each other are the main parameters determining the structure and persistence of populations. Patch size mostly influences population turnover and local extinction rates; isolation affects the probability of (re)colonisation of suitable but currently vacant habitats. In fragmented landscapes the occurrence of metapopulation structures is favoured by increasing patch area and decreasing isolation (Thomas & Jones 1993; Hanski *et al.* 1995; Nieminen 1996). A third important parameter is habitat quality, which may strongly determine the patterns of site occupancy (Thomas *et al.* 2001).

The metapopulation concept is relevant for species conservation because particular conservation measures may be required by species whose persistence depends on the migration of individuals outside their habitat patches. For butterflies it is known that the rates of population extinction have been nearly as high in nature reserves as in the rest of the landscape (Thomas 1984; Warren 1994). Even great efforts to protect and manage the nature reserves could not ensure the long-term persistence of populations of both rare and common species. Possible reasons for this failure include insufficient knowledge about the habitat requirements of butterflies, and therefore inadequate management, but also changes in the surrounding landscape which lead to an increased isolation of the populations (Thomas 1984). For example, *Argynnis aglaja* and *Thecla betulae* vanished from Monks Wood Nature Reserve because the neighbouring farmland became unsuitable for breeding (Thomas 1984). This illustrates the importance of suitable habitat in the surroundings of protected areas to prevent the isolation of populations of species that present a metapopulation structure (Thomas & Hanski 1997).

Previous studies on butterfly population structure were often carried out within more or less 'ideally' structured landscapes such as very large nature protection areas or true island systems (Hanski *et al.* 1995; Sutcliffe & Thomas 1996; Sutcliffe *et al.* 1997a,b). However, these ideal landscapes do not completely mirror the situation of butterflies in the common agricultural landscape. In Switzerland, about 37% of the land surface is dedicated to agriculture, but only 2% of the land is maintained as terrestrial nature reserves (www.statistik.admin.ch). These nature reserves are extremely important for the preservation of endangered species and plants, but due to their isolation and relatively small size, they can not ensure the long-term persistence of species living mainly in the agricultural landscape. However, some of these species can find suitable habitats outside nature reserves within the agricultural landscape. Depending on land use intensity and landscape structure, field boundaries such as hedgerows, forest edges or grass banks as well as grasslands may provide suitable habitat patches within the unsuitable matrix of arable land. These habitats can be very important for maintaining butterfly biodiversity in the countryside (Dover 1996). However, as they are often small and scattered across the landscape, it is likely that many butterfly species that depend on them present a metapopulation structure in the extremely fragmented modern agro-ecosystems.

This study was concerned with the population structure of the common ringlet butterfly, *Aphantopus hyperantus* (L.), within the Reussebene, a typical agricultural landscape in the Swiss lowlands. Previous studies of dispersal in butterfly metapopulations have focused on species that are rare, or at least locally rare, e.g. at their range margins (Hanski *et al.* 1995; Baguette & Nève 1994; Nève *et al.* 1996). The results of these studies may not apply to less endangered species, such as *A. hyperantus,* that live in agricultural landscapes. In this study special attention was paid to the differences between female and male butterflies. Female butterflies may have very high demands on oviposition sites, which results in further dispersal of female individuals (Baguette & Nève 1994; Bergman & Landin 2001). Therefore, male and female butterflies may be influenced differently by fragmentation.

The main questions of our study were as follows:

- How does landscape structure influence the distribution and dispersal pattern of *A. hyperantus?*
- Do males and females differ in their dispersal behaviour?
- Is there any evidence for a metapopulation structure?

Materials & Methods

STUDY SPECIES

Aphantopus hyperantus (L.) occurs in most of Europe, except for the northernmost regions and parts of southern Europe. It is a common species of moist meadows, hedgerows and forest edges with sunny exposition. The species has one generation flying from June to August with a clear maximum in July. Adult butterflies feed mainly on *Cirsium arvense, Valeriana officinalis* and *Rubus* sp. For oviposition females use a wide range of grass species. Eggs are simply scattered above grass stands (Carter & Hargreaves 1987). The caterpillar feeds at the tussock base of a range of grass species such as *Dactylis glomerata* and *Poa* sp. (Carter & Hargreaves 1987, Phillips & Carter 1991). *A. hyperantus* is generally considered to have a closed population structure, occurring in small, well-defined populations (Heath *et al.* 1984; Pollard & Yates 1993).

STUDY SITE

The Reussebene is a flat area of 27 km^2 situated in the Swiss lowlands. It has a temperate climate with an annual mean temperatures of 8 °C and an annual precipitation of 1100 mm (Kirchhofer 1982, 1984, 2000). It is a former floodplain that has been heavily drained and meliorated (Canton Aargau 1982). Nowadays the landscape is characterised by a net of ditches and hedgerows and several remnant wetlands, which form the major habitats for wildlife and show a high connectivity. Forest only takes up a small fraction of the area (Table 1). The Reussebene is one of the study sites of the European project "Greenveins", which is concerned with biodiversity in the agricultural landscape. In this study we surveyed an area of 4.6 km^2, representing 17% of the Greenveins study site (Table 1).

Table 1. *Distribution of landscape structures (% of area) within the Reussebene, for the whole "Greenveins" study site and for the area surveyed in the present study.*

	Whole site (27 km^2)	Study area (4.6 km^2)
Grassland	39.6%	40.0%
Arable land	33.8%	41.8%
Forest	9.7%	5.3%
Settelements	6.7%	4.2%
Wetlands	4.9%	5.2%
Canal embankments	3.3%	2.0%

HABITAT MAPPING AND PRESENCE/ ABSENCE SURVEY

Suitable habitat for *A. hyperantus* was mapped in the field using three criteria based on literature (e.g. Dennis 1992) and our own observations:

- presence of nectar plants such as *Cirsium arvense, Valeriana officinalis* and *Rubus* sp.;
- vegetation composed of tall herbs and grasses, which creates a more or less moist microclimate and permits oviposition (Dennis 1992);
- direct sunshine during the day (no shade).

All wood edges, hedgerows and other natural and semi-natural elements present in our study areas were searched and checked for these criteria.

During the flight activity season of the species, presence surveys were conducted along all suitable habitats between 10:00 and 16:00 under sunny weather conditions. Suitable habitats were visited twice on different days. Each butterfly observation was mapped.

MARK-RELEASE-RECAPTURE STUDY (MRR)

Based on the results of the habitat mapping and presence survey, a T-shaped canal system was chosen for the MRR (Fig. 1). The canal system was divided into four segments of suitable habitat (OS, MS, LS, RS) separated by short intervals of habitat considered unsuitable due to a high percentage of shade or missing nectar flower sources (see criteria above). These segments were divided into 10 m-long numbered plots (Dover 1996), and habitat quality was mapped for every plot. We recorded the presence of flowering nectar plants such as *Cirsium arvense, Valeriana officinalis, Rubus* sp., of graminoid species (used for oviposition), and of trees casting shade on the plots (Table 2).

The MRR was carried out from 3 to 12 July on eight days with sunny weather. Segments were walked slowly starting from each end. All butterflies encountered were captured and numbered on the ventral hind wing using a permanent pen. For each individual caught, the following data were collected: date of capture, sex, id number, and plot of capture. If the individual was already marked, day and plot of recapture were noted. Each marked

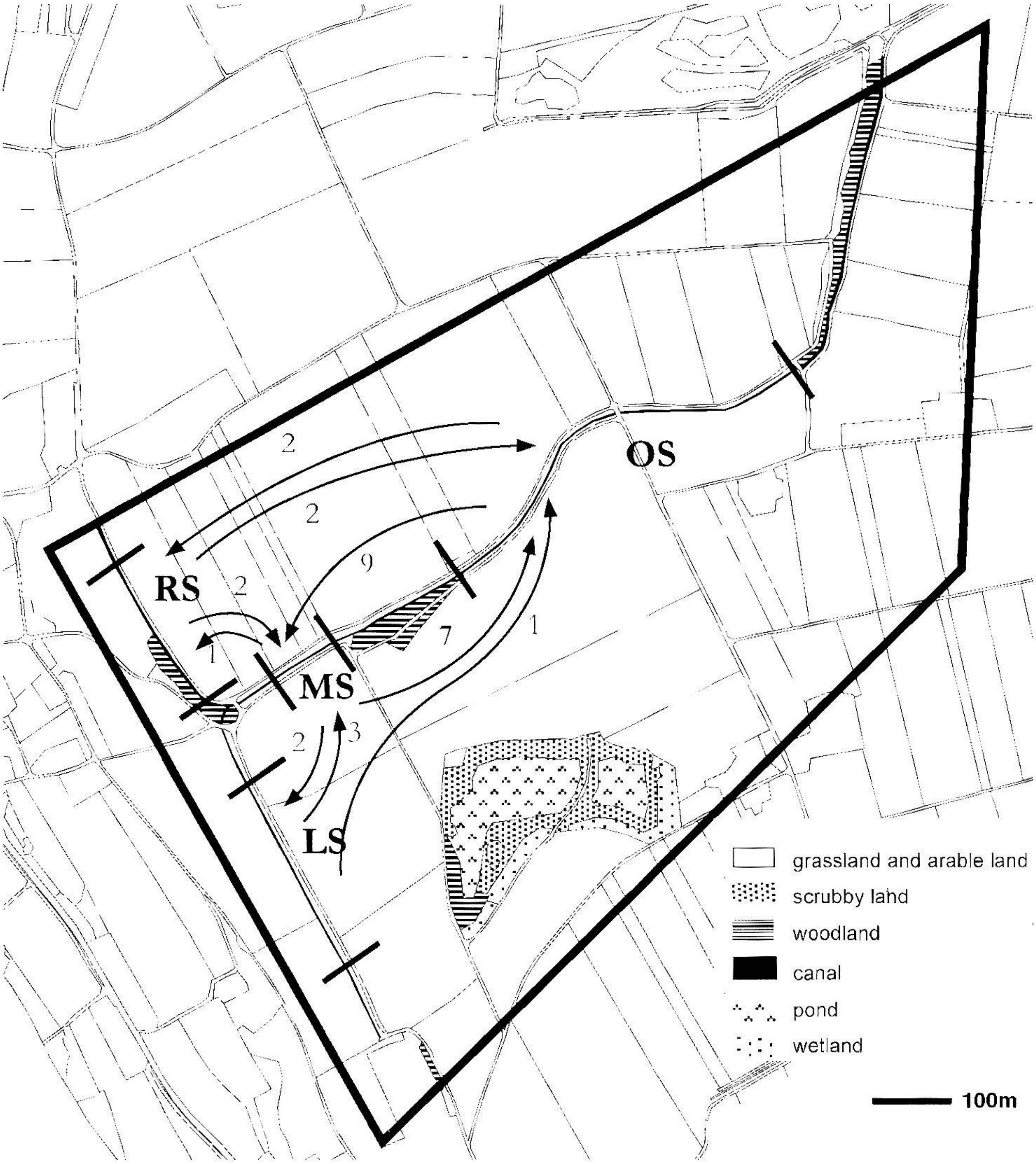

Fig. 1. *Number of recaptured individuals of* A. hyperantus *moving between the four canal embankment segments surveyed in the mark-release-recapture study. Arrows show the direction of movements for which numbers are given.*

Table 2. Length and habitat quality of the four canal embankment segments included in the mark-release-recapture study. Habitat quality was defined by the percentage of 10-m plots within these segments that was or was not shaded by trees and that did or did not contain flowering nectar plants, such as Cirsium arvense, Valeriana officinalis *or* Rubus *sp.*

Segment	OS	MS	LS	RS
Length (m)	770	170	290	270
Shaded by trees	35%	53%	72%	67%
Unshaded, without nectar flowers	45%	18%	21%	29%
Unshaded, with nectar flowers	20%	29%	7%	4%
Habitat quality	high	high	low	low

Table 3. Number of males and females of A. hyperantus *newly marked on each date of capture in four canal embankment segments (total length: 1500 m) in the Reussebene. Recaptured individuals are not included in counts.*

Date of first capture	3.7.	4.7.	5.7.	7.7.	8.7.	9.7.	11.7.	12.7.
Number of males	49	11	35	16	16	16	18	8
Number of females	19	8	11	10	16	14	17	14

individual was released immediately at its position of capture. To avoid that released individuals flee in panic from the canal into the surrounding arable land, they were placed in the vegetation.

Based on the MRR results, the daily flight distance was calculated as the sum of all straight line distances between consecutive recaptures divided by the number of observation days of the individual. The dispersal range was calculated for all individuals that were recaptured at least twice, as the greatest distance between any two captures of one individual. We are aware that for a more robust estimate of daily flight distances and dispersal ranges more observations would be preferable (Samietz & Berger 1997), but this was not possible within the time-frame of this study. Numbers of residents, emigrants and immigrants were calculated such that each capture was counted. Each time an individual was recaptured, it was hence counted either as a resident (previous capture within the same patch) or an immigrant (previous capture within another patch). An immigrant in one patch is at the same time an emigrant in the patch where it migrated from.

STATISTICAL ANALYSIS

Changes in butterfly density with time were analysed using linear regressions. Differences between daily flight distances and dispersal ranges of female and male butterfly individuals and the influence of habitat quality on butterfly density were analysed using a Wilcoxon rank-sum test. All analyses were carried out using JMP 5.

Results

HABITAT MAPPING AND PRESENCE/ ABSENCE SURVEY

Suitable habitat runs mainly along the canal embankments and also along nature protection areas and small forest patches. *A. hyperantus* was widely distributed and inhabited nearly all suitable habitat (Appendix 1). There were only two suitable patches in which no individual was found within 250 m (the mean female dispersal range, see below) even though these patches were connected to other suitable habitats (Appendix 1). Two isolated suitable habitat patches (i.e. patches separated from all others by unsuitable habitat) were empty even though the next suitable inhabited patch was closer than 250 m.

MARK-RECAPTURE STUDY

In total 278 butterflies were captured and marked during eight days of survey along the canal in the Reussebene (Table 3). Of 109 marked females, 45 were recaptured at least once (42 %), and so were 106 of 169 marked males (63 %). The number of males captured per day tended to decrease during the survey ($P < 0.1$) while the number of females did not change ($P > 0.5$; Table 3).

The mean daily flight distance pooled over all segments was 72 m. Female butterflies tended to fly longer distances than male butterflies (mean for females 94 m d^{-1}, $n = 30$; mean for males 61 m d^{-1}, $n = 65$), but this difference was not significant ($P = 0.42$). The maximum daily flight distances recorded were 510 m for a female and 300 m for a male.

Mean dispersal range, calculated for all individuals that were recaptured at least twice ($n = 65$), was 179 m. Again females tended to show larger dispersal ranges (mean = 251 m, $n = 17$) than males (mean = 153 m, $n = 48$; $P = 0.18$). Maximum dispersal ranges recorded were 970 m for a female and 760 m for a male.

The four canal segments where the capture-recapture study was carried out, differed in length (Table 2). Of the 278 marked individuals, 23 (7 females, 16 males) moved 30 times between two canal segments (Fig. 1). Of these 23 individuals, six moved twice, and one female even three times between the segments. The percentage of residents, immigrants and emigrants differed considerably between the four segments, the largest segment (OS) having the highest fraction of residents (Table 4).

Table 4. *Total number of captures and recaptures of* A. hyperantus *in the four canal embankment segments, and percentage of residents, emigrants and immigrants.*

Segment	OS	MS	LS	RS
Length (m)	770	170	290	270
Captures	293	142	56	50
Recaptures	152	86	29	20
Residents	85%	72%	76%	65%
Emigrants	8%	12%	14%	20%
Immigrants	7%	16%	10%	15%

The two segments OS and MS contained a higher percentage of non-shaded plots and non-shaded plots with nectar flowers compared to the other two segments LS and RS (Table 2). The absence of shading trees and the presence of nectar flowers within the non-shaded plots were associated with a higher butterfly density (Wilcoxon test, $P < 0.001$). Graminoids were present in every 10-m plot; their presence was therefore unrelated to butterfly density.

Discussion

HABITAT MAPPING AND SPECIES DISTRIBUTION

Aphantopus hyperantus strongly depends on sunny patches with high grass and scrub vegetation providing nectar flowers and oviposition sites (Dennis 1992, Sutcliffe *et al.* 1997a). In the Reussebene nearly all semi-natural embankments of the canal system are suitable and form a well-connected net of habitats. *A. hyperantus* was present in most patches of suitable habitat and occurred at high densities. It is therefore a species that is well adapted to life in the agricultural landscape.

DISPERSAL PATTERNS OF A. HYPERANTUS

Daily flight distances were rather short (72 m), and 75 % of the individuals did not fly further than 100 m (mean = 35 m). This partly explains the low migration rates found in this study and in previous studies (Sutcliffe & Thomas 1996). The small dispersal range size (mean = 179 m) also shows that individuals tend to stay in a given area. This is in accordance with the literature where *A. hyperantus* is described as a species with a closed population structure (well-defined colonies within discrete areas; Heath *et al.* 1984; Pollard & Yates 1993) with minimum breeding areas of only 1–2 ha (Thomas 1984).

It is often observed that flight distances differ for the sexes. Many butterfly species have extremely high demands on oviposition sites, which results in further dispersal of female individuals (Baguette & Nève 1994; Bergman & Landin 2001). In this study both daily flight distances and dispersal ranges tended to be higher for females, but did not significantly differ between males and females, possibly because *A. hyperantus* uses a wide range of grass species as host plants. Grasses were found in all transects along the canal which means that females do not have to search long to find suitable sites for oviposition. We assume that most females move in the search for food resources (flowering nectar plants) rather than for larval host plants.

As frequently observed in butterfly species (Wiklund & Fagerström 1977), protandry was evident. In the beginning of the MRR in the Reussebene most captures were males. This changed later in the capturing season (Table 3) and at the end of the MRR only few males were found (Table 3).

METAPOPULATION AND MIGRATION PATTERNS OF A. HYPERANTUS

According to the metapopulation concept, habitat patch area and its connection to other patches are the two main factors contributing to species persistence. Patch area influences the probability of survival (Thomas & Harrison 1992), while rates of emigration and immigration decrease with increasing patch area (Thomas & Jones 1993; Baguette *et al.* 2000). In a previous study on *A. hyperantus* the fraction of residents increased with patch area, while immigration and emigration fractions both declined (Sutcliffe *et al.* 1997a). Individuals are more likely to leave small than large patches because small patches have high perimeter to area ratios. In the habitat system of the Reussebene the four canal segments also have different areas, but due to their linear structure, perimeter-to-area ratios are similar for all segments. The residence fraction was still highest (85 %) in the largest segment (OS, 770 m), but it was also high (72 %) in the shortest segment (MS, 170 m). The most likely reason for this is habitat quality, "the missing third parameter in metapopulation dynamics" (Thomas *et al.* 2001). Of all four segments segment MS had the highest percentage (29 %) of unshaded plots with flowering nectar plants. This suggests that habitat quality is even more important than area in determining the proportion of residents. Saarinen (2002) found that the abundance of nectar plants was significantly positively correlated with the density of *A. hyperantus*, which is in accordance with our findings. Also Sutcliffe *et al.* (1997a) state that "Flowers either attracted a large number of butterflies, or that the presence of flowers resulted in the retention of most immigrants".

It is important to note that in most temperate insect species studied, it is the requirements of the immature stages that define habitat quality, and that for adults, resources are seldom limiting (Thomas 1991). However, the fact that the host plants of *A. hyperantus* (various grass species) were found in every single transect did not make their abundance a useful parameter for estimating habitat quality.

The majority of recaptured individuals were residents (88%), but some migration took place and suitable, but empty habitat patches were available. Therefore population structures for the study species in the study site could be considered as a metapopulation (sensu Hanski & Simberloff 1997).

However, different landscapes and habitat structures have different consequences on possible metapopulation dynamics. The linear, highly connected habitats in the Reussebene offer ideal conditions to migrate among patches: if the local populations become extinct due to stochastic or demographic events, empty habitat could be easily re-colonised from patches were butterflies are still present. This contrasts with results from a similar study in another Swiss agricultural landscape with more isolated habitat patches: here the patches were not sufficiently connected to enable a regular interchange of individuals (Sedivy 2002). Especially for endangered species with a closed population structure, the inherent low migration rate combined with a low connectivity of the landscape could be a threat for future persistence and recolonisation of empty habitat patches.

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Electronic Appendix

Appendix 1. Distribution map of *A. hyperantus* in the "Reussebene" study area

The Appendix can be downloaded at http://www.geobot.umnw.ethz.ch/publications/periodicals/bulletin.html (select 'Electronic Appendices', App. 2003-6).