



Functional conservation units for the endangered Alcon Blue butterfly *Maculinea alcon* in Belgium (Lepidoptera: Lycaenidae)

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Received 6 June 2003; received in revised form 20 February 2004; accepted 21 February 2004

Abstract

To organize and prioritise species-specific conservation efforts, we delineate ‘functional conservation units’ for the threatened Alcon Blue butterfly *Maculinea alcon* in Belgium. We used detailed distribution data on the butterfly, its host plant and its habitat, present-day population sizes and its mobility and colonization capacity to determine functional conservation units (FCUs) on different spatial scales: FCU-1, i.e., the 12 presently occupied habitat patches plus the area within a range of 500 m surrounding them (the maximum local movement distance, based on mark-release-recapture data), FCU-2, i.e., the areas within a range of 2 km around the occupied habitat patches (the maximum observed colonization capacity) and FCU-3, i.e., potential re-introduction sites (sites where *M. alcon* went extinct recently). We suggest different management and planning measures for each type of functional conservation unit and discuss translocation and re-introduction as ‘intensive care’ conservation measures for this threatened and sedentary species.

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Keywords: Belgium; Butterflies; Functional conservation units; *Maculinea alcon*; Mobility

1. Introduction

In an era where habitat fragmentation and habitat loss are causing declines and local extinctions of many species, restoring local or regional habitat networks for target species has become an important conservation strategy throughout the world (e.g., Amato et al., 1995; Cowley et al., 2000; Poiani et al., 2000; Bergman and Landin, 2002). Both policy makers and field conservationists need to take decisions on where and how to implement species-specific conservation measures in addition to more general area- or biotope-oriented conservation. Decision-making tools based on biologically relevant – in this case species-specific knowledge can help maximizing the chances on success of these measures. For instance, the probability of a successful

colonization of restored habitat by a target species is affected by dispersal capacity, the spatial configuration of habitat and the size of source populations. Whether two populations belong to the same (future) network or should be regarded as isolated ones, depends on the mobility of the target species and on the nature of the intervening matrix (Ricketts, 2001; Keyghobadi et al., 2003). Moreover, habitat has often been treated too vaguely as vegetation types, but requires more careful definitions in terms of essential resources for the conservation of butterflies (among many other taxa) (Dennis et al., 2003).

In case of threatened species, conservation management should anticipate on species requirements at different spatial levels ranging from local habitat quality to habitat network geometry at the landscape level. In highly deteriorated landscapes, conservation efforts should not only be limited to sites where target species occur, but should also be expanded to sites with high potentials for the target species. Therefore, the recognition of clearly defined spatial conservation units with

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an associated program of measures for each level can be a useful tool in guiding the conservation process. In order to scientifically underpin such a tool, detailed knowledge on the distribution, dispersal and colonization capacities and habitat requirements of the focal species are required.

In the case of threatened species with a limited number of remnant populations in a particular focal region, spatial risk spreading strategies may contribute significantly to bridge the critical time lag between habitat restoration measures and their effects on habitat quality and quantity. Risk spreading can include: (i) translocations to suitable, unoccupied sites that have a low probability of spontaneous colonization on the short term or (ii) re-introductions into previously occupied sites (Oates, 1992). Such labour and knowledge intensive – and hence expensive – approaches have to be seen as ‘intensive care conservation’ rather than maintenance management. But, especially in countries with a high pressure on biodiversity, like in Belgium, such measures will be temporarily necessary to preserve small populations of threatened species (e.g., Maes and Van Dyck, 2001). However, conservation agencies seem to be reticent on translocation and re-introduction and often lack official policies to deal with these options. Hence, translocations and re-introductions have sometimes been executed secretly which hampers insights on the colonization capacity of species. Here, we discuss the use of re-introduction and translocation within the framework of species conservation.

Since the 1950s, butterfly diversity decreased severely in Belgium and urgent measures are needed to preserve several remaining threatened species. The most important factors for the decline in butterfly diversity are biotope loss, fragmentation of habitats in biotope remnants, and declining habitat quality, especially in wet and nutrient poor biotopes (Maes and Van Dyck, 2001). In particular, wet heathlands and bogs have strongly degraded both in area and quality. The reduction in area is estimated to be >85% in Flanders (Allemeersch et al., 1988). Biotope quality declined with 71% (estimate based on ‘completeness’ using indicator values of typical wet heathland plants – Van Landuyt, 2002). In Belgium, but also throughout Europe (cf. EU Habitat Directive), wet heathlands are of high conservation value (Rebane and Wynde, 1997; Webb, 1998). One of the most typical butterfly species of wet heathlands in Belgium is the Alcon Blue butterfly *Maculinea alcon* (Denis and Schiffermüller, 1775) that is a conservation target both in Europe (Munguira and Martín, 1999) and in Belgium (Vanreusel et al., 2000). Several authors have stated that *M. alcon* is able to survive in small habitat units (<1 ha), even with low host plant densities as long as suitable host ants are present (Tax, 1989; Bink, 1992; Wynhoff, 1996). The rationale behind this is that the butterfly’s only host plant (*Gentiana pneumonanthe*) is perennial

(up to 30 years) and responds very slowly to environmental changes (e.g., desiccation, eutrophication, etc.); therefore, adult, flowering individuals can survive for relatively long times in vegetations that no longer allow recruitment (Oostermeijer et al., 1992). This time lag between habitat deterioration and decline of the species may mislead managers who only rely on presence/absence data of the flowering host plant and of the butterfly. Small population sizes and/or small patch sizes of *G. pneumonanthe* both affect the population structure due to genetic bottlenecks and have negative effects on seed setting and rejuvenation (Oostermeijer et al., 1998). Furthermore, environmental influences that affect population structure (through negative effects on germination) have a higher impact in small areas (Vanreusel and Smets, 2002).

As it is the case elsewhere, budgets for conservation (particularly for species conservation) are limited in Belgium, and an adequate conservation relies on clear goals, programs and underpinned priorities on the one hand and on a good co-operation between ecologists, managers and policy makers on the other (Wilson and Lantz, 2000). In this article, we define functional conservation units on different spatial scales in order to help organizing and prioritising species-specific conservation efforts for *M. alcon* in Belgium. The delineation of these units are validated with data on: (i) distribution (including detailed measurements of habitat patches) and changes in distribution of the butterfly, its host plant and habitat; (ii) population sizes (based on egg counts) and (iii) mobility and colonization capacity (based on mark-release-recapture data and colonization events). These units are used to rank the priority of species-specific measures. The optimal scale and choice of conservation measures (including their intensity) differs among the units. Finally, we discuss translocation and re-introduction as ‘intensive care’ conservation measures for this threatened and very sedentary species.

2. Methods

2.1. Study species and study sites

M. alcon is an obligate ant parasite butterfly with a scattered distribution in Europe (Wynhoff, 1998b). The Marsh Gentian *G. pneumonanthe* is its single host plant in Belgium (Maes and Van Dyck, 1999) and different *Myrmica* ants are used as host ants throughout Europe (Thomas et al., 1989; Elmes et al., 1994). Apart from some doubtful records in western and southern Belgium, *M. alcon* has always been restricted to wet heathlands with *Erica tetralix*, bogs and nutrient poor hay meadows in the Campine region (North East Belgium, Fig. 1; Maes and Van Dyck, 1999; Goffart and De Bast, 2000). Its host plant declined in distribution area by at least

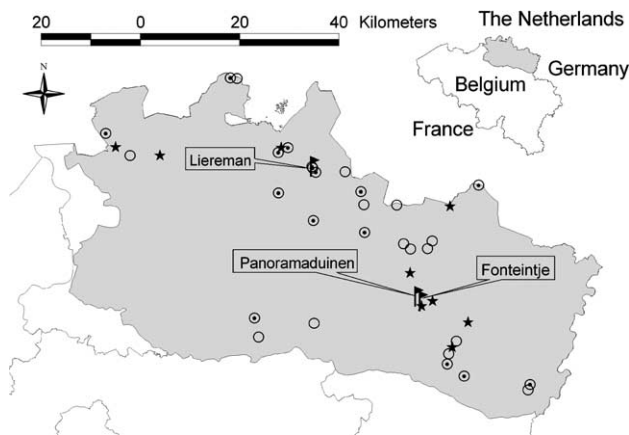


Fig. 1. Location of the investigated sites; sites with present-day populations of *M. alcon* are marked with black stars (sites where the MRR-study was performed are marked with flags); sites where *M. alcon* went extinct are marked with dotted circles and wet heathlands where *M. alcon* has never been documented are marked with an empty circle. The Campine region is shown in grey.

64% in the last 30 years (Biesbrouck et al., 2001). The three potential host ant species *Myrmica ruginodis*, *M. rubra* and *M. scabrinodis* (Elmes et al., 1994) are, however, rather common in Flanders (Schoeters and Vankerkhoven, 2001). Detailed historical distribution data are not available for ants in Belgium, making estimates of changes in distribution of the host ants impossible.

In 1999 and 2000 we investigated 39 wet heathland sites in the Campine region where both wet *E. tetralix* heathland (data from Biological Valuation Map; De Blust et al., 1994) and *G. pneumonanthe* were present (data from Florabank; Biesbrouck et al., 2001). These included all present and formerly known sites of *M. alcon* in Belgium. Table 1 gives the conservation status and the area of wet heathlands in the investigated sites. Typical dominant plant species in the study sites were Purple Moor-grass (*Molinia caerulea*, average coverage 42%), Cross-leaved Heath (*E. tetralix*, 24%), Heather (*Calluna vulgaris*, 9%) and Deer grass (*Scirpus cespitosus* subsp. *germanicus*, 4%).

2.2. Mark-release-recapture (MRR) and colonization events

In 1997, we carried out MRR-studies in the nature reserves of Liereman (Oud-Turnhout, N 51°20' E 5°05') and Zwarte Beek (Koersel-Beringen, N 51°05' E 5°20'), where we studied two different populations (Panoramaduinen and Fonteintje) that are separated by about 1 km of woodland and meadows (Fig. 1). *M. alcon* individuals were caught by hand net, marked with a unique number on the ventral left hind wing with a permanent marker and released on the spot of capture. Distances between consecutive capture points were measured by theodolite in Liereman and by hand meter

in Zwarte Beek. Maximal distances between the outer boundaries in each of the three populations were 650, 275 and 410 m in Liereman, Panoramaduinen en Fonteintje, respectively.

We estimated the colonization ability of *M. alcon* from: (i) occasional observations of adult butterflies away from permanently occupied habitat patches and (ii) observations of *M. alcon* eggs on *G. pneumonanthe* in habitat patches that were previously unoccupied and hence colonized during the year of observation. In addition, we observed the behaviour of a small subsample of *M. alcon* males released in non-habitat (a woodland ride and an improved grassland).

2.3. Distribution and habitat use

Potential habitat patches for *M. alcon* were determined as wet *E. tetralix* heathlands with *G. pneumonanthe* populations and with *Myrmica* spp. ant nests. The size of the patches was determined by the outer limits of *G. pneumonanthe* populations. The habitat patches were localized and measured with a global positioning system (GPS) corrected by a base station (precision 1 m). In all sites, we counted the number of *G. pneumonanthe* plants and, if the butterfly was present, all *M. alcon* eggs, except for one site (Fonteintje) where, due to the very large number of plants, only about 1/3 of the *G. pneumonanthe* plants was counted. The white eggs are very conspicuous on the green flower buds of *G. pneumonanthe*; caterpillars hatch through the basal side of the egg (Thomas et al., 1991) and most of the (empty) egg shells remain on the host plant until about two weeks after the flight season (Ebert and Rennwald, 1993). We estimated the number of adult butterflies in each population by assuming that every female lays on average 50–100 eggs and that the sex ratio is 1, based on other *Maculinea* species (Hochberg et al., 1992; Hochberg et al., 1994; Meyer-Hozak, 2000; Griebeler and Seitz, 2002). We searched host ant nests by inspecting all possible nest substrates in 62 plots of 10 × 10 m² in 24 of the 39 investigated sites (Maes et al., 2003). In order to test for differences in plant species cover (especially *Molinia caerulea* cover; Berendse and Aerts, 1984) between present-day populations and sites where populations went extinct, we estimated plant species cover in all sites in four subplots of 2 × 2 m² within a plot of 10 × 10 m² using the Londo scale (Londo, 1976).

2.4. Statistical analyses

We analysed the spatial patterns of occupied and vacant flight areas with a logistic regression with presence/absence as dependent variable and flight area and distance to the nearest population (both log₁₀-transformed to obtain normality) as independent variable. For the calculation of distances between two consecutive

Table 1
Status of present-day and extinct populations of *M. alcon* in Belgium

Site	Status	WH (ha)	FA (#P) (ha)	#GP	Dens.HA			#eggs	EPS	
					rug	rub	sca			
Current populations (site code in Fig. 2)										
1.	Groot Schietveld (GRS)	M	401.6	>10.3 (>7)	>1646 ^a	0.2	0.3	2.3	>2975	Small
2.	Hageven (HAG)	N	15.3	3.0 (8)	1662	3.0	2.4	3.3	4431	Small
3.	Liereman (LIE)	N	53.1	4.4 (6)	515	3.9	2.4	2.0	5506	Small
4.	Sonnisheide (HHH)	M	?	1.3 (1)	871	5.5	1.0	0.5	4611	Small
5.	Teut (TEU)	G	48.9	4.8 (1)	242	6.0	0.5	4.5	5472	Small
6.	Visbedden (VIS)	M	136.3	1.3 (1?)	–	–	–	–	–	?
7.	Withoefse heide (WIT) ^b	G	16.1	2.7 (1)	44	3.5	2.0	0.3	456	Very small
8.	Zwarte Beek		133.9							
	8a. Mathiashoeven (ZWB-1)	M		1.8 (1)	172	4.5	4.0	11.5	4873	Small
	8b. Fonteintje (ZWB-2)	M		5.3 (2)	>426 ^a	2.5	1.6	1.8	>12798	Large
	8c. Panoramaduinen (ZWB-3)	M		3.0 (1)	114	3.8	2.8	5.8	3510	Small
	8d. Katershoeve (ZWB-4)	M		1.3 (6)	380	4.5	1.5	7.5	1843	Very small
9.	Zwart Water (ZWW)	N	16.4	3.3 (2)	491	2.0	0.5	1.0	2287	Very small
Extinct populations (year of extinction)										
10.	Buitengoor (1998) (BUI-MEE)	N	42.9	1.4	10–20	–	1.7	2.0	–	–
11.	Goor (1998) (GOO)	N	0	0.1	1–5	–	–	–	–	–
12.	Wolfsven (1998) (WOL)	G	2.1	0.03	1–5	–	–	–	–	–
13.	Ziepbeek (1998) (ZIE)	G	92.3	2.1	50–100	2.3	0.3	15.2	–	–
14.	Tielenhei (1997) (TIE)	M	0	0.2	10–20	2.0	–	–	–	–
15.	's Gravendel (1995) (GRA)	P	0	0.3	1–5	–	–	–	–	–
16.	Zwarte heide (1995) (ZWH)	N	1.2	0.6	50–100	–	–	–	–	–
17.	Kauwbosstraat (1994) (KAU)	C	0	0.2	10–20	3.5	4.0	2.0	–	–
18.	Korhaan (1994) (KOR)	N	2.1	0.2	1–5	1.0	–	1.0	–	–
19.	Kalmthoutse heide (1993) (KAL)	G	281.5	0.3	50–100	6.0	–	0.7	–	–
20.	De Maten (1973) (MAT)	N	22.9	0.9	10–20	–	2.5	–	–	–
21.	Ronde Put (1973) (RON)	G	9.7	1.3	1–5	–	–	–	–	–
22.	Hei van Van Damme (1970–79) (DAM)	N	0	0.1	1–5	–	–	–	–	–
23.	Hoge Mierdse Hei (1970–79) (HMH)	N	0	0.02	1–5	–	–	–	–	–
24.	Koeiven (<1970) (KOE)	P	2.0	1.4	–	12.0	2.0	–	–	–
25.	Meerseldreef (1947) (DRE)	N	0	0.9	1–5	–	–	–	–	–
Wet heathland sites with <i>G. pneumonanthe</i> where <i>M. alcon</i> has never been documented										
26.	Elsakker	G	3.2	–	1–5	–	–	–	–	–
27.	Gerhagen	G	3.8	–	1–5	–	–	–	–	–
28.	Goorken	P	2.8	–	10–20	–	–	–	–	–
29.	Kattenbosserheide	N	0	–	–	–	–	–	–	–
30.	Klein Schietveld	M	73.5	–	1–5	4.0	2.0	4.0	–	–
31.	Koemook	P	0	–	1–5	–	–	–	–	–
32.	Langdonken	N	0	–	10–20	–	–	–	–	–
33.	Moensweyer	G	1.2	–	–	–	–	–	–	–
34.	Neerharenheide	G	33.5	–	10–20	1.0	–	2.0	–	–
35.	Plat-Holven	N	4.3	–	–	–	–	–	–	–
36.	Riebos	N	1.7	–	10–20	–	–	–	–	–
37.	Slangebeekbron	N	8.7	–	10–20	1.0	–	–	–	–
38.	Tenhaagdoornheide	G	59.8	–	10–20	–	2.0	–	–	–
39.	Vriesput	M	0	–	1–5	–	–	–	–	–

With information on the ownership (M, Military area; N, non-governmental nature reserve; G, Flemish nature reserve; P, private property; C, city property); the area of wet heathland according to the Biological Valuation Map (WH), the total area of the patch and the number of separate habitat patches (FA (#P)), the number of *G. pneumonanthe* in the habitat patch (#GP), the density of the three potential host ant nests per 100 m² (Dens.HA): rug, *Myrmica ruginodis*; rub, *Myrmica rubra*; sca, *Myrmica scabrinodis*. EPS = population size based on the number of eggs: very small, <100 adults; small, 100–400 adults; large, >400 adults; ?, unknown.

^a Only part of the total population was counted.

^b The population went extinct in 2001.

captures, we only used the recaptures with at least one day time interval. Differences in distances moved were analysed by means of a 2-way ANOVA with site and sex as independent variables and distance (log₁₀-trans-

formed to obtain normality) as dependent variable. We used a logistic regression to detect differences in plant cover between sites with and without *M. alcon*. Subplots were grouped per 10 × 10m² plot. All analyses were

done with the Statistica software package (StatSoft Inc., 2001).

3. Results

3.1. Mobility, colonization and behaviour

Table 2 gives an overview of the results of the MRR-study. In total, we caught 576 individuals in the three populations. In Liereman, the recapture ratio did not differ between males and females. In both populations of Zwarte Beek the recapture ratio was significantly higher for males. The overall recapture ratio (34%) however did not differ significantly between sexes (Table 2). The overall mean movement of males and females differed among sites resulting in a significant two-way interaction (Table 2); both in Fonteintje and in Panoramaduinen males moved longer distances than females, while in Liereman the opposite was true. The maximum recorded distance moved was larger in females than in males in Liereman and in Panoramaduinen, but shorter in Fonteintje (Table 2). The majority of the individuals was very sedentary: 63% of the males and 71% of the females moved less than 50 m between two consecutive captures; only a small proportion of all recaptured individuals covered distances larger than 150 m (7% for both males and females, Fig. 2). In Zwarte Beek, we did not observe movements of individuals between the two investigated populations.

The data on colonization events of empty habitat patches indicate that dispersal distances can be much

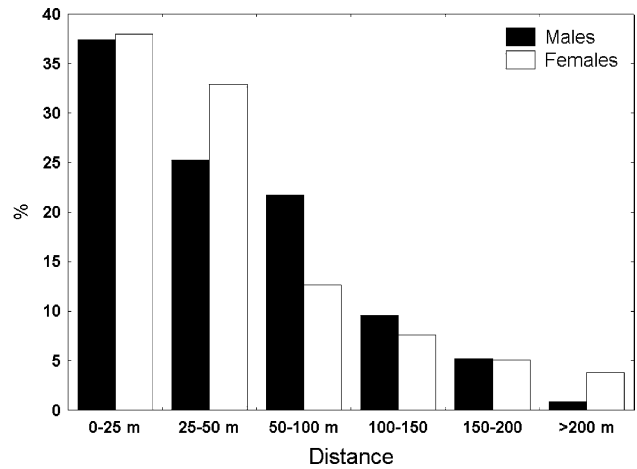


Fig. 2. Frequency distribution of distances moved by males and females of *M. alcon*.

longer than the maximum distances recorded in MRR-studies (Table 3). The observation of 100 *M. alcon* eggs (probably coming from one or two females) at almost 7 km from the nearest known population, is most probably the result of a 'secret' re-introduction (Ghis Palmans, personal communication). This re-introduction was unsuccessful since no more eggs were found in the following years.

Observations of behaviour at edges of habitat patches indicated that *M. alcon* mostly returns to the patch when it encounters woodland edges. The few release experiments in a potential corridor (large woodland ride nearby a flight area on wet heathland, $n = 5$) showed that individuals flew straight upwards, leaving the ride

Table 2
Movement statistics from the MRR-study of *M. alcon* in three study sites in North East Belgium

	<i>N</i> marked	<i>N</i> recaptured	<i>N</i> recapture events	Mean distance (m)	Longest single move (m)	Longest cumulative move (m)
<i>Liereman</i>						
Males	125	36	45	33 ± 32	114	235
Females	116	38	42	68 ± 108	500	509
<i>Panoramaduinen</i>						
Males	51	23	22	46 ± 35	149	263
Females	37	11	11	36 ± 52	190	206
<i>Fonteintje</i>						
Males	148	60	48	76 ± 57	221	409
Females	97	30	25	55 ± 56	193	229
<i>Overall</i>						
Males	324	119	115	53 ± 49	221	409
Females	252	79	78	59 ± 88	500	509
	$p = 0.033$	$p = 0.23$		$F(\text{sex}) = 1.418; p = 0.24$		
				$F(\text{site}) = 2.775; p = 0.07$		
				$F(\text{interaction}) = 4.868;$		
				$p = 0.009$		

Differences between sexes in the numbers marked and recaptures were tested using χ^2 test; overall differences between sexes and sites in moved distances were tested using a two-way ANOVA.

Table 3

Minimal distances between newly colonized habitat patches and the nearest known population of *M. alcon* in Belgium observed between 1999 and 2001

Site	Distance (m)
Fonteintje	165
Katershoeve	595
Teut	650
Plateaux (NL)	700
Liereman	835
Teut	940
Plateaux (NL)	1700
Riebos ^a	7000

A colonization event was determined by observing adult butterflies or eggs in a site that was unoccupied in the previous years.

^aMost probably the result of a secret re-introduction instead of natural colonization.

by flying over the trees (c. 8 m height) instead of flying along the ride as we originally expected; the released males in non-habitat (improved meadow) showed a zigzag searching flight behaviour before alighting on available nectar sources that are absent on typical heathlands (*Taraxacum* sp. and *Trifolium* sp.); afterwards, they left the meadow by flying straight over the adjacent woodland. Although adults mostly fly close to the vegetation at low speed, one adult in Fonteintje was seen passing a dense *Molinia caerulea* vegetation at a height of 3–4 m in a straight line at high speed. Although based on small sample sizes, these observations clearly indicate different behavioural patterns in habitat and non-habitat conditions.

3.2. Distribution and population sizes

M. alcon declined in distribution area from 39 Universal Transverse Mercator (UTM) grid squares (5×5 km) in the period 1901–1950, over 24 grid squares between 1951–1970 and 18 grid squares between 1971–1990 to 12 grid squares in 1999–2000. One of the present-day populations concerns a private re-introduction after extinction in 1995 (Vanreusel et al., 2000). Using grid squares as units for the trend calculation, *M. alcon* showed a decline in distribution area of 70% in Belgium in the 20th century (Maes and Van Dyck, 2001) which is most probably an underestimate (Thomas and Abery, 1995; León-Cortés et al., 1999; León-Cortés et al., 2000). Using sites instead of grid cells, present-day populations of *M. alcon* can be found in nine sites. Since 1991 the species went extinct in at least ten sites. Most of the present-day sites have one or a few habitat patches with one (meta)population. Considering flight areas separated by at least 500 m of non-habitat as populations, the actual number of *M. alcon* populations in Belgium is reduced to 12 (Fig. 1).

The total area of *M. alcon* sites in Belgium in the period 1999–2000 was 42.4 ha (i.e., 0.02% of all wet heathlands in Belgium). The spatial pattern of vacant ($N=17$) and occupied sites ($N=11$, the re-introduced population was considered extinct) showed that the probability of a patch being occupied increased with habitat patch size and decreased with distance to the nearest occupied patch (Fig. 3). Populations that went extinct in the last decade were mainly located in small

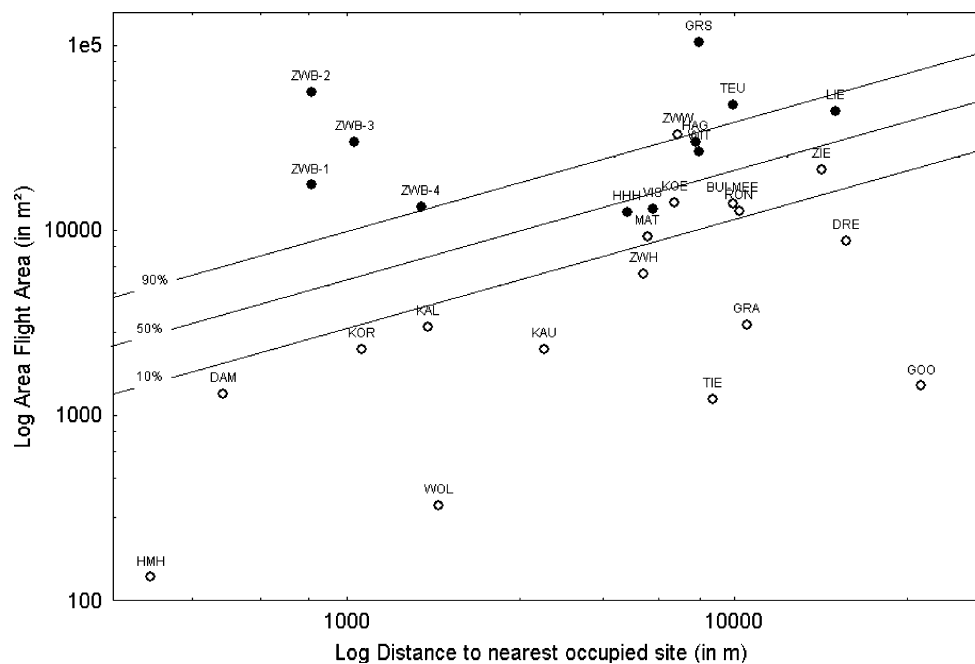


Fig. 3. Distribution of occupied and extinct sites in relation to flight area and distance to the nearest population. Lines indicate the probability (90%, 50% and 10%) of the presence of *Maculinea alcon*. Logistic regression: $\chi^2 = 25.842$, $df = 2$, $p < 0.001$; parameter estimate for \log_{10} area (m^2) = 10.366 and for \log_{10} distance (m) = -7.260 . Abbreviations of sites correspond with those in Table 1.

Table 4
Management measures in the current *M. alcon* populations in Belgium

Site	Gr	Co	Exc	SC	Mw	Bu	Ch	Manager
1. Groot Schietveld (GRS)	–	–	–	–	–	+	–	FPD/ND
2. Hageven (HAG)	HC	+	+	+	+	–	+	NGNO
3. Liereman (LIE)	H	–	–	+	–	–	–	NGNO
4. Sonnisheide (HHH)	–	–	–	–	–	–	–	MA
5. Teut (TEU)	–	–	–	–	–	–	–	ND
6. Visbedden (VIS)	–	–	–	–	–	–	–	MA
7. Withoefse heide (WIT) ^b	–	–	–	+	–	–	–	ND
8. Zwarte Beek								
8a. Mathiashoeven (ZWB-1)	C	–	–	+	–	–	–	NGNO/ND
8b. Fonteintje (ZWB-2)	S	–	–	+	–	–	–	NGNO/ND
8c. Panoramaduinen (ZWB-3)	S	–	–	+	+	–	–	NGNO/ND
8d. Katershoeve (ZWB-4)	S	–	–	+	–	(+)	–	NGNO/ND
9. Zwart Water (ZWW)	C	–	–	+	–	–	–	NGNO

Gr, Grazing; H, horses; C, cattle; S, sheep; Co, combing (removing decaying litter from *Molinia caerulea* tussocks); Exc, enclosure; (excluding grazers from dense *G. pneumonanthe* patches). SC, sod-cutting; Mw, mowing; Bu, burning; Ch, chopping (creating open ground by mowing into the ground with a brush cutter); Manager: ND, Nature Department; FPD, Forest and Parks Department; NGNO, non-governmental nature organization; MA, military authorities.

habitat patches and the few larger sites where the species went extinct (e.g., Ziepbeek, Buitengoor) were isolated ones (≥ 10 km away from the nearest population – Fig. 3). The mean nearest neighbour distance for all present-day populations is 6.2 km (range = 0.8–18.3 km).

The estimated population sizes are given in Table 1: only one population can be considered as large in Belgium (>400 adult butterflies), while all others are very small to small (<400 adult butterflies).

3.3. Description of present-day *M. alcon* populations

Table 1 indicates that most of the current Belgian *M. alcon* populations are located on a very limited area. Although the number of eggs may seem fairly high in some populations (e.g., Fonteintje), the actual number of butterflies does not exceed 1000 individuals in 11 out of 12 populations. A logistic regression analysis did not detect a significant difference in plant cover between present-day and former *M. alcon* sites ($\chi^2(15) = 22.44$; $p > 0.10$). Differences between present-day populations and extinct ones were the larger area of wet heathland in which the habitat patch was situated, larger habitat patch areas and a higher *G. pneumonanthe* cover (cf. Wallis de Vries, in press). Host ant densities did not differ between present and former populations.

Seven of the current Belgian *M. alcon* populations are located in military areas (Table 1) and all present-day populations are in areas under protection of the European Habitat Directive and/or Bird Directive. Most of the populations are either managed by the Nature Department or the Forest and Parks Department of the Flemish Community (including some of the military areas) or by non-governmental nature conservation organizations.

Management measures applied in the current populations are summed up in Table 4. Seven sites are grazed by either horses, cattle, or sheep (or a combination of these grazers). In the majority of the sites, sod-cutting is used as a management measure to create suitable germination sites for the host plant *G. pneumonanthe*. At present, enclosures are used at only one site to reduce grazing pressure in dense host plant areas.

4. Discussion

Despite the alarming state of biodiversity in Belgium (e.g., Maes and Van Dyck, 2001), the use of detailed species-specific knowledge and appropriate, often small-scaled management measures to ensure the survival of threatened species, is still in one's infancy in Belgium (Van Dyck et al., 1999). The data collected on *M. alcon*'s distribution and changes therein, its host plant and habitat, population sizes and on mobility and colonization capacity, allows us to define functional conservation units (FCU) to organize and prioritize the conservation of this threatened butterfly in Belgium. In this sense, conservation units as defined here are pragmatic tools based on scientific species-specific evidence. Although we have not verified it at the population genetic level, the FCU-approach is likely to resemble the concept of evolutionary significant units (ESU; Rucelshaus et al., 2003). An ESU is a population that is reproductively isolated from other non-specific population units, and which represents an important component in the evolutionary legacy of the species (Meffe and Carroll, 1997). Before we discuss the different FCUs and the associated conservation measure programs, we firstly interpret our results on the state of the Belgian

populations of *M. alcon* and results on mobility and colonization capacity.

4.1. The critical state of the Belgian *M. alcon* populations

Although most of the former *M. alcon* populations were located in areas with a protected status, a large number of local extinctions occurred. Table 1 shows that the Belgian populations of *M. alcon* are actually small to very small, often located in small habitat patches, with a limited number of host plants and host ants. According to Thomas (1991), *Maculinea arion* populations with fewer than 400 adults are likely to experience periodic extinctions and populations with 400–1000 adult butterflies can be regarded as 'safe'. Apart from one population (Fonteintje), Belgian *M. alcon* populations are all below this threshold (Elmes and Thomas, 1987; Hanski and Thomas, 1994).

The main factors associated with the presence of *M. alcon* in Belgium are wet heathland area and the number of *G. pneumonanthe* plants (cf. Wallis de Vries, in press). Large heathland areas have a larger habitat heterogeneity which makes them more resilient to environmental dynamics. For example, in small areas, *G. pneumonanthe* and host ant nests tend to be spatially concentrated in the lowest depressions of a site which makes them vulnerable since prolonged rainfall can drown a large proportion of the ants and caterpillars (e.g., 177 mm rain in July 2000 compared to 41–76 mm in the five previous years). Furthermore, Maes et al. (2003) have shown that larger wet heathlands have higher ant nest densities, which probably increases the necessary spatial overlap between host plants and host ant nests (Van Dyck et al., 2000). The absence of a correlation between vegetation cover and the presence of *M. alcon* is probably due to the fact that populations of *M. alcon* can persist for a relatively long time after habitat degradation due to the longevity of the Marsh gentians and the time lag between changes in vegetation structure and changes in ant species composition.

4.2. Mobility, colonization and behaviour

As in most *Maculinea* spp. (Stettmer et al., 2001), but also in other specialized butterflies (e.g., Thomas, 1985; Nève et al., 1996; Bergman and Landin, 2002; Betzholtz, 2002), a large proportion of *M. alcon* butterflies is very sedentary. Although mean distances moved did not differ between males and females, in both populations of Zwarte Beek males covered larger distances than females, contrary to Liereman. These differences can probably be explained by differences in the configuration of both sites: Liereman consists of a cluster of nearby habitat patches with many edge situations (resulting in a area/perimeter ratio of 15.8) with a prominent tree row splitting the site in two discrete flight areas (Talloen and

Van Dyck, unpublished data) while the Zwarte Beek populations have a more continuous habitat (with area/perimeter ratios of 31.5 and 21.3 for Fonteintje and Panoramaduinen, respectively). Host plant distribution also differs between both sites: in Liereman *G. pneumonanthe* are clustered in patches while in Zwarte Beek they are uniformly spread over the flight area. Therefore, females have to move longer distances between host plant patches in Liereman than in Zwarte Beek. This result indicates that one should be careful to interpret sexual differences in movements when based on data from one site, or even from a single year (e.g., Baguette, 2003). Host ant nest distributions were only surveyed in plots of 100 m² (Maes et al., 2003) and it may be difficult to extrapolate these densities to entire flight areas. The role of host ant nests on the female's choice of ovipositing on host plants and thus on the daily movements is still under debate (Thomas and Elmes, 2001; Van Dyck et al., 2000; Van Dyck and Regniers, unpublished data).

MRR-studies usually underestimate dispersal distances because the chance of recapturing marked butterflies decreases with distance and the distance covered by butterflies leaving the population is usually unknown (Turchin et al., 1991; Shreeve, 1992, 1995). Colonization data give more relevant figures for feasible dispersal distances (cf. Baguette, 2003). The limited mobility and colonization capacity of *M. alcon* observed here are not only a species-specific trait, but also depend on the size of potential source populations and on the availability of suitable habitat patches within a certain distance of other populations (Thomas et al., 1998).

The behaviour of species at the edge or even outside the habitat has become an important research topic, especially in highly fragmented landscapes (Merckx et al., 2003; Schtickzelle and Baguette, 2003). Behavioural responses can have important implications for the optimal design of habitat edges, stepping stones or corridors (Schultz, 1998; Haddad, 1999; Ricketts, 2001; Ries and Debinski, 2001; Schultz and Crone, 2001). For example, the Fender's blue butterfly (*Icaricia icarioides fenderi* – Schultz, 1998; Schultz and Crone, 2001) and the Black-veined White *Aporia crataegi* (Watanabe, 1978) dispersed 2–3 times faster, and also further, outside than within suitable habitat. Recent observations in other butterfly species by Schultz (1998), Ries and Debinski (2001) and Schultz and Crone (2001) are in line with our observations in *M. alcon* of high returning probabilities of butterflies approaching the edge of their habitat: the higher the trees at the edge of the habitat, the more likely the species was to return. This knowledge can be used to manipulate the design of (or to create) physical edges to temporarily prevent individuals from leaking from a small local population (e.g., by planting tree rows around isolated patches), certainly when suitable habitat is unavailable within colonization

capacity (Kuussaari et al., 1996; Thomas et al., 1998; Thomas and Hanski, 1999; Betzholtz, 2002). Further experiments on behaviour at habitat boundaries and movements through the landscape matrix are required to understand the mechanisms behind particular movement patterns among different landscapes (Merckx et al., 2003).

4.3. Functional conservation units for *M. alcon* in Belgium

Traditional but non-specific management regimes have low chances of being beneficial for small relict populations of habitat specialists like *M. alcon*. The scale at which species-specific conservation measures are taken, has to be in accordance with the target species' ecology. We defined 'functional conservation units' (FCU) by combining data on: (i) detailed distribution of the butterfly, its host plant and wet heathland; (ii) population sizes; (iii) mobility and colonization capacity. A FCU is a spatial entity in which actual or potential habitat for the study species is available and in which specific management and restoration measures should be concentrated. In the case of *M. alcon*, we assume FCUs separated by >10 km as completely isolated (Fig. 4). FCUs have to be regarded as dynamic instruments that can change both in time and in space when conditions change (e.g., absence/presence, habitat quality).

4.3.1. Functional conservation unit-1

Because 500 m was the maximum observed distance moved during our MRR study, it can be used as an upper limit for relatively frequent, daily movements within habitat. Within this range, habitat will be used almost immediately after it becomes suitable. Objectives in functional conservation unit-1 (FCU-1) are to in-

crease the butterfly population size by optimizing actual habitat conditions (cf. Thomas et al., 2001), enlarging habitat patches and restoring all potential habitat. Management measures should be small-scaled and with a close attention for remaining resources. In addition to a conventional maintenance management such as low intensity grazing (1 grazer/3–10 ha – Londo, 1997), small-scale burning and sod-cutting, intensive care management will be necessary in FCU-1 to increase both the densities of *G. pneumonanthe* plants and *Myrmica* ant nests (Van Dyck et al., 2000). Such labour-intensive measures cannot be maintained on the long term, and should be regarded as a temporal investment to increase the number of butterflies to a safer and sustainable level. Spatial spreading and increasing densities of *G. pneumonanthe* is achieved by very small-scaled sod-cutting (m²) and/or 'chopping' in un-grazed sites and 'combing' in grazed situations. Seeds of *G. pneumonanthe* are absent from seed banks and are poor dispersers (<1 m – Oostermeijer et al., 1992). Therefore, sod-cutting needs to be executed in the immediate vicinity of existing *G. pneumonanthe* plants (within a radius of 20–100 cm), should not be too deep (to maintain suitable abiotic conditions for the germination of *G. pneumonanthe* seeds) and should leave the microrelief intact to enable *Myrmica* ants to rapidly colonize the sod-cut patches. However, due to atmospheric deposition, conditions at the sod-cut soil surface can be far too acid for the germination of *G. pneumonanthe* (Vanreusel and Smets, 2002). In some experimental plots, germination could, therefore, be stimulated considerably by treating the soil with lime, which is in our opinion only acceptable if it is regarded as a temporary measure. 'Chopping' (i.e., creating scattered bits of open ground by mowing into the ground with a brush cutter) imitates the trampling of cattle and creates germination sites for *G. pneumonanthe*. Finally, 'combing' (i.e., the removal of decaying litter from *Molinia caerulea* tussocks) makes young leaves of *Molinia caerulea* more accessible for grazers and therefore increases the actually grazed area by guiding grazers into formerly un-grazed patches. The newly grazed areas can become more suitable for germination, while grazing pressure will be relaxed in areas where *G. pneumonanthe* has a good chance to germinate, but only little chance to reach the flowering, adult stage due to overgrazing.

Some of the nature reserves with actual *M. alcon* populations are grazed by cattle, horses or sheep, which is an appropriate management strategy to maintain or create well-structured wet heathland. So far, managers in most reserves have only little experience in fine-tuning effects of grazing, and the pressure on particular habitat patches can be far too great for this butterfly-plant-ant system because of an underestimate of the actual grazing pressure. The exclusion of grazers between 15 July and 30 September from the *G. pneumonanthe* patches with

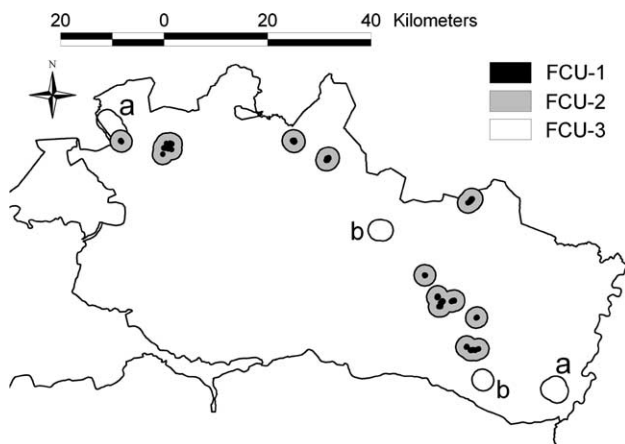


Fig. 4. Functional conservation units for *M. alcon* in Belgium. FCU-1, presently occupied habitat patches plus the area within a range of 500 m; FCU-2, the areas within a range of 2 km around the occupied habitat patches; FCU-3, potential re-introduction sites (a), actually suitable and (b), potentially suitable after restoration.

the highest numbers of *M. alcon* eggs is an appropriate additional intensive care measure that resulted in a threefold increase of the number of eggs in one of the populations between 2001 and 2002 (Hageven; Ghis Palmans, personal communication).

4.3.2. Functional conservation unit-2

The functional conservation unit-2 (FCU-2) determines the scale at which has to be looked for potentially new habitat. Heathland patches within 2 km around occupied patches, as derived from the colonization data, have a reasonable chance to be colonized naturally when they become suitable. Within this area, habitat restoration or creation on a larger spatial scale can help develop local or regional networks of patches in a metapopulation structure (Thomas and Jones, 1993). In this respect, stepping stones seem to be better for *M. alcon*, in 'connecting' occupied habitat with other suitable patches than supposed corridors like woodland rides (Webb and Thomas, 1994; Schultz, 1998; own observations). Emphasis should therefore be on restoring habitat and creating new habitat between existing populations, in order to increase network connectedness.

4.3.3. Functional conservation unit-3

The third type of functional conservation unit are networks of potential habitat in which the species is actually absent. Functional conservation unit-3 (FCU-3) sites are candidates for re-introduction programmes. These units can be divided into sites that are actually suitable (FCU-3a) and sites where the habitat can become suitable after a restoration program (FCU-3b). All FCU-3s that meet the criteria are sites where *M. alcon* went extinct in the 1990s. Only two sites (Ziepsbeek and Kalmthout) appear immediately suitable for *M. alcon* (FCU-3a: large area of wet heathland, large number of host plants, high densities of *Myrmica* ants; *M. alcon* can be considered a target species in the management schemes, etc.). Two other sites (Buitengoor and Maten) have a large area of wet heathland but the densities of both the host plant and *Myrmica* ant nests should be increased before considering a possible re-introduction (FCU-3b).

In both FCU-2 (where patches have a reasonable chance to be colonized in a spontaneous way) and FCU-3 (where local introductions are required), restoration management should be executed to restore presently unsuitable wet heathland patches. Since the butterfly is absent from FCU-2 and FCU-3, management measures can be executed more intensively than in actual *M. alcon* populations. Large-scale sod-cutting (100–1000 m²) and a more intensive grazing regime can help to achieve a suitable starting point for wet heathland restoration. Prior to any large-scaled sod-cutting, a census on the presence of *Myrmica* ants is highly relevant. *Myrmica*

ants can be present in deteriorated heathlands (Maes et al., 2003) and although they are relatively rapid colonizers of suitable areas, it may take a long time before a restored site provides suitable nesting and foraging habitat. Therefore, there is a considerable gain in terms of time when in inevitable large-scaled sod-cutting practice, micro-topography and some vegetation strips are spared (Brian et al., 1976; Mabelis, 1976; Maes et al., 2003). Long, relatively small strips of sod-cutting and of spared vegetation are predicted to have the best potential in this respect. Additional measures in the spared vegetation stripes like particular mowing regimes can further contribute to heathland restoration without a dramatic temporal loss of local ant diversity. Further research on responses of ants to restoration measurements are required to refine these guidelines.

Re-introduction should, in our opinion, be considered as an emergency measure, but one that should be considered together with the several other strategies discussed above to deal with the precarious situation of *M. alcon* in Belgium. However, this measure has not yet been included in the regional nature conservation legislation and policy of conservation agencies. It therefore remains largely unexploited (Van Den Berge et al., 1995). Scientifically underpinned re-introductions of other *Maculinea* spp. elsewhere in Europe have shown their potential to speed up spatial risk spreading in a successful way (e.g., *M. arion* in England; Thomas, 1995; and *M. teleius* and *M. nausithous* in the Netherlands; Wynhoff, 1998a). At present, the re-introduction of *M. alcon* in one of the former populations (Ziepsbeek), is under investigation (Vanreusel et al., 2002). In some of the present-day *M. alcon* sites, especially in large military areas such as Sonnisheide and Groot Schietveld, suitable habitat patches are too far apart to have a reasonable chance of colonization on the short term. Here, translocation could be considered to spread the risks on local extinctions among an increased number of patches. It is evident that such a measure has to be accompanied by restoration measures in and among suitable patches to re-create a sustainable population network on the long term.

Two major gaps remain in the ecological knowledge of *M. alcon* in Belgium but also elsewhere: host ant use and genetic differences between populations. Both information sources are important to determine the best 'matching' source population for a translocation or re-introduction. It recently became clear that much more efforts are needed to study host ant use of *M. alcon* in Belgium. The Belgian populations are probably on the transition zone between *Myrmica ruginodis* and *Myrmica scabrinodis* as optimal host ant (Elmes et al., 1994; Karsten Schönrogge, personal communication). Our own preliminary observations indicate that *Myrmica ruginodis* is used in the majority of the populations, but other *Myrmica* ants were observed as host ant as well

(*Myrmica rubra*, *Myrmica scabrinodis* and probably even *M. schencki*). Host ant-use, genetic differentiation and patterns of pheromone profiles of caterpillars and candidate host ants (cf. Akino et al., 1999; Elmes et al., 2002) are currently under investigation within an extended European research program.

5. Conclusion

The species action plan for *M. alcon* (Vanreusel et al., 2000) was the first action plan for an invertebrate species in Flanders (north Belgium). This pilot project points at a more widely important issue that needs to be tackled by conservation policy: site-based conservation strategies that deny species-specific aspects are only seldomly able to preserve threatened habitat specialists. Additionally, labour-intensive and expensive species-specific measures need to be temporarily incorporated into current management schemes. The implementation of this species action plan in the field aims at both increasing the viability of the existing populations and creating new suitable sites. Although the Flemish government has invested in a species action plan for *M. alcon*, we ascertain that there is, so far, only little effort and virtually no budget to monitor and imply the proposed measures. It remains a typical and highly relevant bottleneck for conservation that policy makers are less willing to invest in constructive feed-back and implementation programs than in plans. We consider the approach of functional conservation units a useful tool to organize species-specific measures at different spatial scales in Belgium (or elsewhere) that can be similarly applied for other threatened species.

Acknowledgements

We thank Joeri Cortens, Sofie Regniers, Hans Matheve and Inge Brichau for field assistance and Willy Vanlook, Dirk Geysels and the military authorities for research permissions (MRR-studies). We kindly acknowledge Andrew Pullin, Marc Dufrière, Maurice Hoffmann, Irma Wynhoff, Dirk Bauwens and an anonymous referee for their critical remarks on the manuscript. This research was funded by the Flemish Ministry of Nature Conservation (project no. MINA/120/98/SB01 and MINA/121/99/01 to the University of Antwerp) who also granted us the licenses to study this legally protected species. Hans Van Dyck has a postdoctoral fellowship from the Fund of Scientific Research in Flanders – Belgium (FWO). Dirk Maes (Institute of Nature Conservation) and Hans Van Dyck (University of Antwerp) are associated partners of the MacMan research project within the 5th framework of the EU (Contract No. EVK2-CT-2001-00126 – www.macman-project.de).

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