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A highway intersection as an alternative habitat for a meadow butterfly: effect of mowing, habitat geometry and roads on the ringlet (*Aphantopus hyperantus*)

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The decline of semi-natural grasslands throughout Europe has given rise to the idea that road verges under mowing management could serve as alternative habitats for several meadow species. We studied the distribution and movements of the ringlet butterfly (*Aphantopus hyperantus*) at a highway intersection and its surroundings. A total of 2113 individuals were marked, and 17% of the individuals recaptured, in 2003. The population densities were generally low in the verge and in sections mown in mid-summer. Mid-summer mowing also delayed the dispersal of individuals to the area until the vegetation had regenerated. The majority of individuals were sedentary but there was more emigration from linear verges and sections with a low population density. A dense network of roads may decrease the movement of the ringlet but a single road is not an absolute barrier to the species. We conclude that intersections and road verges can provide alternative habitats for meadow species, as shown here with the ringlet, but that the quality of these habitats depends on the mowing management.

Introduction

Due to the agricultural improvements and abandonment of arable land, semi-natural grasslands have become sparse throughout Europe, causing widespread loss and fragmentation of breeding habitats for butterflies (van Swaay & Warren 1999). However, many plant and insect species typical of semi-natural biotopes have found suitable habitats in other manmade open areas, such as road verges, power line cuttings and railroad embankments (Persson 1995, Rassi *et al*. 2001, Tikka 2001, Kuussaari *et al*. 2003, Jantunen *et al*. 2004). These alternative habitats cannot replace the semi-natural biotopes, but they can offer refuges for some of their species. In Finland, road verges form the most important alternative habitats in terms of their total area. Along the public roads (78 000 km) there are approximately 85 000 hectares of regularly mown verges (Jantunen *et al*. 2004). When private road verges are included, the verge habitats cover more than 140 000 hectares of land, which is 50-fold more than the remaining semi-natural grasslands on mineral soils (Vainio *et al*. 2001).

Road verges are linear edge habitats with a wide variation in the structure and plant species composition in a small space (Way 1977).

As such they offer habitats for specialists of edge habitats and species from the surrounding environment. By contrast, intersection reservations (from here on referred to as intersections) are non-linear habitats surrounded by roads and ramps and more closely resemble semi-natural grasslands in regard to their shape. From the conservation point of view the most valuable road verges and intersections are those under management similar to that applied to semi-natural grasslands, i.e. they have been mown regularly over a long period but in other ways they have been relatively undisturbed (Way 1977). Unfortunately, only a small proportion of road verges and intersections are managed similarly to semi-natural grasslands. While the traditional management of meadows included either grazing or one mowing event in late summer, the road verges and intersections are often subject to at least two annual mowings, the first of these occurring in June when many butterfly species reach the adult stage. The mowing intensity on road verges and intersections varies from total to partial mowing, i.e. some patches of vegetation are left untouched. The traditional management also includes removal of the cut material, but this is rare on road verges or intersections. In addition a large proportion of verges in Finland are disturbed due to construction work once every 20–30 years on average (Mahosenaho & Pirinen 1999). Road verges differ from semi-natural grasslands also in the soil composition (heavy metals, pollutants and nutrients), dust, light and temperature conditions, and mechanical damage caused by snowploughing vehicles (Farmer 1993, Angold 1997, Trombulak & Frissell 2000).

The important question is how do butterflies and other meadow species cope in these alternative habitats? Previous studies have shown that many grassland butterflies use verge habitats for nectaring and breeding (Munguira & Thomas 1992). However, the question still remains open whether verges are successful breeding areas or, on the contrary, form sinks for some butterfly species due to their intensive mowing. At least for the adult stage the intensive mowing has an adverse effect (Gerell 1997, Jantunen *et al*. 2004). As a more controversial issue linear verges may also increase the connectivity in fragmented landscapes by providing corridors for butterflies moving from one habitat patch to another (Sutcliffe & Thomas 1996). Although the majority of studies have failed to demonstrate that corridors increase the rate of successful movement of animals between habitat patches (Rosenberg 1997), some studies have indicated that corridors are valuable conservation tools (Beier & Noss 1998) and can increase both interpatch movement and the population densities of certain butterflies (Haddad 1999, Haddad & Baum 1999). Range expansions along road verges have also been reported in both butterflies and moths (Dirig & Cryan 1991, Brunzel *et al*. 2004). On the other hand, roads can act as barriers and restrict butterfly movement (Dennis 1986, Munguira & Thomas 1992), individuals may die while crossing the road (Munguira & Thomas 1992, McKenna *et al*. 2001, Ries *et al*. 2001), and road construction may destroy and fragment breeding habitats (van Swaay & Warren 1999).

We studied the ringlet butterfly (*Aphantopus hyperantus*, Linnaeus 1758) in a highway intersection and its surroundings. The ringlet is a univoltine species, which in Finland has a flight period extending from the beginning of July to the beginning of August (Marttila *et al*. 1991). The larvae feed on many common grasses, such as *Phleum pratense*, *Poa* spp. and *Milium effusum* and the larval stage hibernates. The ringlet is widely distributed throughout Europe from northern Spain to the British Isles and Mid-Fennoscandia (Kudrna 2002). In southern Finland the species is very abundant (Kuussaari & Heliölä 2001) and it has been classified as a meadow species (Pitkänen *et al*. 2001). However, it may constitute the dominant species in various open habitats such as hay fields, road and field verges, and forest cuttings (Marttila *et al*. 1991). Although the ringlet is a sedentary habitat specialist, which lives in distinguishable habitat patches in Finland, it has a large "mainland" population, i.e. large areas of suitable habitat remain (Hanski & Kuussaari 1995). In Britain the population structure exhibits a mixture of patchy population and metapopulation attributes where large habitat patches act as metapopulation units with intermediate movement and small patches are aggregations of individuals with more movement between them (Sutcliffe *et al*. 1997). Unlike the majority of butterflies associated with meadow habitats, ringlet populations have not declined in Finland during the last few decades (Pitkänen *et al*. 2001). In fact the numbers have increased recently (Saarinen *et al*. 2003), a trend also observed earlier in Britain (Pollard & Yates 1993).

We studied the distribution and movements of the ringlet butterfly in an open hay dominated area mainly created by road construction. Fragmented by roads, the study area consisted of parts with different timing and intensity of mowing and differing degrees of isolation from each other. The specific questions were: how do different mowing management regimes and habitat geometry affect (i) the abundance and (ii) the movement of the ringlet butterfly and (iii) do roads form a barrier to ringlet butterfly movement?

Materials and methods

Study area

The study area of approximately 8.6 hectares was located in Joutseno, SE Finland. It comprised an intersection, highway verges and other open areas located nearby. Surrounded by forests, arable and abandoned fields, the intersection was located along a two-lane highway (width 11 m) carrying approximately 6000 vehicles per day. The 2.2-km-long and 5-m-wide line transect was composed of 13 sections (A–M) 80–280 m long (Fig. 1). Based on the management and environment, these sections represented seven different habitat types, i.e. (1) an intersection managed by late summer mowing and removing the cut material according to the recommendations for traditional biotopes (sections A, B and C), (2) an intersection under mid-summer mowing with no removal of cut material (I, K and L, mown on 24 June 2003), (3) a highway verge partially mown on 1 July 2003 (narrow 2-m strip next to the road) and the whole verge under late summer mowing with no removal of cut material (G and H), (4) a highway verge under mid-summer mowing with no removal of cut material (D and E, fully mown on 1 July 2003), (5) a non-mown abandoned field (F), (6) a partially mown abandoned field (M; two thirds of the area being mown on 21 July 2003), and (7) a non-mown ruderal area created by road construction (J). Roads representing a matrix habitat for butterflies separated the habitat patches. Four groups of sections unseparated by roads (A, B and C; D, E and F; G, H and J; K and L) were considered to represent the same habitat patch, while sections I and M were isolated habitat patches.

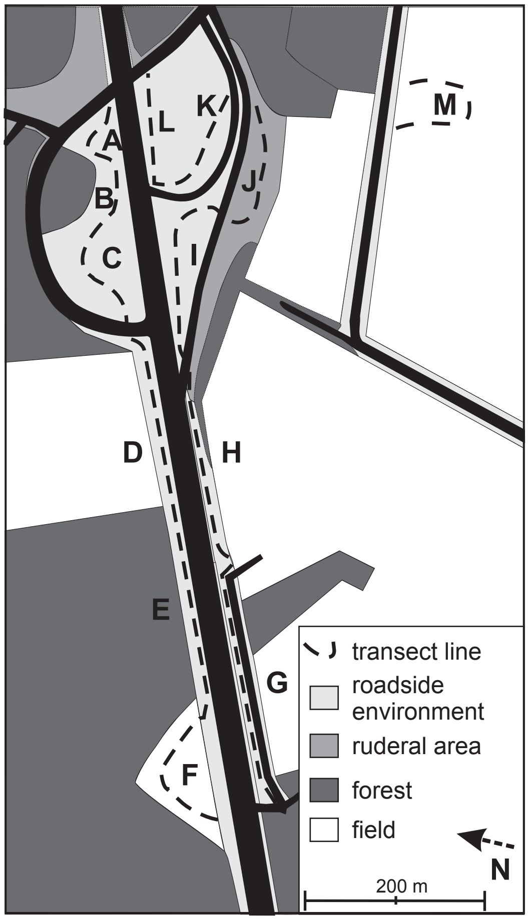

Fig. 1. The study area and the line transect, divided into 13 sections (A–M).

The population study

We collected the data using a mark-release-recapture (MRR) method. The study was conducted between 26 June and 8 August 2003, thus extending over the species' entire flight period.

Individuals were netted, marked, released and recaptured along 13 sections of the transect on each non-rainy day (30 days altogether). The duration of one census varied from one hour to seven hours, depending on the number of individuals. Each section was visited for a time period relative to its length.

Captured individuals were marked on the wings using a waterproof permanent pen. Each individual was given a unique number using the 1-2-4-7, etc., marking system of Ehrlich and Davidson (1960), modified to include 100-200-400-700-1500 notations. After the marking each specimen was immediately released at the point of capture. Individuals that were recaptured once or more provided information about movements. A recapture in the same section where the marking or previous recapture took place was regarded as representing "static" movement.

Additional information on individuals, movements and environment for the sections used in the data analysis included (1) sex, (2) distance of the movement, measured in metres between the centres of the sections of recapture and previous (re)capture, (3) time between recapture and previous (re)capture in days, (4) a road index, i.e. movement across roads as a sum of all road crossings (highway = 1, each minor road crossing = 0.5; five classes 0, 0.5, 1, 1.5 and > 1.5), (5) a verge index, i.e. either movement along the highway verge or not, (6) transect area (length of the transect multiplied by the width in hectares), (7) population density, i.e. the number of captured individuals per transect area, (8) sex ratio, (9) habitat shape (linear or non-linear), and (10) mowing (non-mown, partially mown or totally mown before the end of the study period).

Data analysis

We estimated the daily population sizes of the whole study area and each habitat type by Jolly's (1965) method using program JOLLY. The daily estimates for the whole study area were also calculated separately for males and females. The population size of each habitat type was estimated as the sum of the daily estimates multiplied by the day-specific loss rate (Watt *et al.* 1977). A mixed-effects Poisson regression was used to examine the relationship between the number of captured individuals in each section and the explanatory variables: mowing management, habitat shape and transect area. The clustered nature of sections with similar management was taken into account by specifying the habitat type as a random-effect variable. The analysis was conducted using the NLMIXED procedure (Pinheiro & Bates 1995) in the SAS statistical package (SAS Institute 1996).

A mixed-effects logistic regression was conducted to examine the reasons for the differences in frequencies of observed movements from one section (x) to another (y), the number of trials being the number of all movements from section x to any other section. Variables explaining whether the movement from one section to another was successful or not were the distance, road and verge index and the variables describing the "target" section (y), while habitat type of the "source" section (x) was set as a random-effect variable. Other variables describing the source section were not included in this regression, because they influence how many individuals left but not where the movement ended up. Thus, another mixed-effects logistic regression was conducted to study more precisely the reasons for an individual to stay in, or emigrate from, the section where it was observed. In this regression the explanatory variables were those describing the source section, the individuals and the number of days between capture and recapture, while the habitat type of the source section was set as a random-effect variable. Both mixed-effects logistic regressions were conducted with the Egret for Windows program. The analyses began with univariate regressions and the final models were constructed by adding variables one by one and comparing the extended models to the simpler models with likelihood ratio tests.

The effects of roads on the movement of individuals were further studied by comparing the number of observed movements across the highway to the predicted number of road-crossings using a calculation similar to that described by Munguira and Thomas (1992): if p is the proportion of total captures made on the north side of the road and q the proportion on the south side of the road, then $2pq$ is the probability of crossing, if the road has no effect on movement. $2pq$

multiplied by the realised frequency of movements among sections (= number of recaptures – number of static movements) gives the expected frequency of crossings, which was compared with the observed number of crossings using the χ^2-test. Thus, the method was corrected for the fact that the movements were non-random.

Results

Abundance and distribution

A total of 2113 individuals were marked; males were slightly more frequent (56%) than females (44%) (Table 1). Altogether 369 (17%) individuals (207 males and 162 females) were recaptured, the total number of recaptures being 451. The recapture percentage ranged from more than 20% of the individuals in sections A, B, C and J to less than 10% in sections E, F and M. Most of the individuals (n = 307, 83%) were recaptured only once, while 46 (13%) individuals were recaptured twice and 16 individuals (4%) at least three times. The maximum number of recaptures for one individual was 6.

The estimated population size over the whole study area was 9399 individuals. The estimated population sizes and calculated population densities were both lower at the highway verge as compared with those at the intersection, and in both groups lower in areas under mid-summer mowing (Fig. 2). According to the mixed-effects Poisson regression, the area of the section affected positively (p = 0.0005), and the total mowing (p = 0.004) as well as the linear habitat type (p = 0.021) negatively the number of captured individuals, while partial mowing had no significant effect (p = 0.211).

The flight period extended over 41 days. Males started to fly earlier than females and the peak of the male flight was on 18 July (estimated male population size 2048) and for females two days later on 20 July (estimated female population size 2392). The dispersal of ringlet butterflies to the intersection mown in mid-summer was severely delayed as compared with that to its counterpart mown in late summer (Fig. 3).

Movement

Recaptures were dominated by static movement (n = 323, 72%) (Table 2) and the majority of recaptured individuals (n = 247, 67%) were recorded in one section only. When static movement is included, the average flight distance was 58.6 ± 110.8 (mean ± S.D.) m. A total of 81 (22%) individuals moved more than 100 m and 37 (10%) more than 200 m. The longest recorded

Table 1. Recapture data on the ringlet from 13 sections. Recap. individuals = individuals marked in the section and recaptured in any section. Percentage = percentage of individuals marked in the section and recaptured in any section.

Section	Marked individuals	Marked males	Marked females	Recap. individuals	Percentage	Length (m)	Population density ha^{-1}
A	343	219	124	82	24	120	5933
B	62	34	28	13	21	80	1800
C	300	177	123	65	22	130	4908
D	79	46	33	15	19	200	870
E	25	18	7	2	8	240	225
F	182	124	58	16	9	190	1947
G	129	73	56	14	11	280	943
H	144	76	68	16	11	200	1560
I	136	57	79	23	17	200	1550
J	394	198	196	87	22	150	5520
K	73	40	33	14	19	120	1400
L	32	13	19	3	9	120	583
M	214	118	96	19	9	190	2295
Total	2113	1193	920	369	17	2220	1904

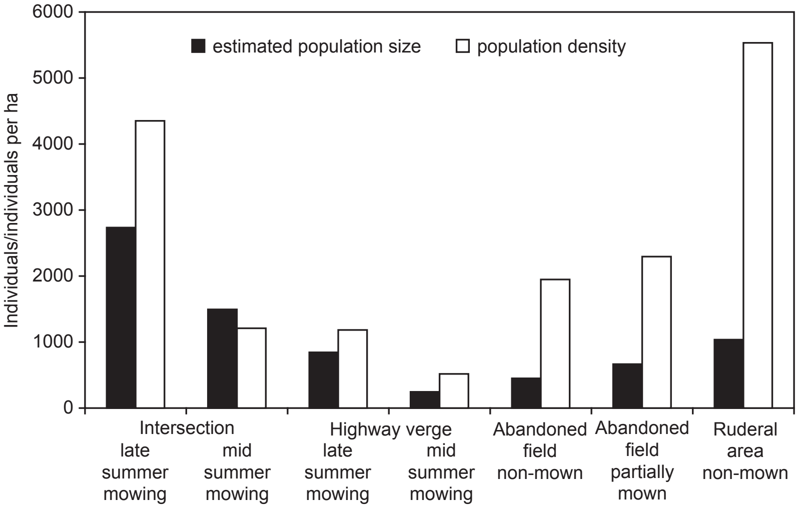

Fig. 2. Estimated population sizes and the population densities in the seven habitat types.

flight by a single individual was 760 m, the individual being recaptured twice (A–C–F). There was no difference in the flight distance between males and females, either when static movement was included in the analysis (male average 57.9 ± 114.0 m, female average 59.5 ± 107.0 m; Mann-Whitney *U*-test $p = 0.716$) or when this was excluded (males 178.7 ± 136.5 m, females 175.3 ± 116.2 m, $p = 0.818$).

The number of recaptured individuals which crossed one or more roads, i.e. moved from one habitat patch to another via a matrix habitat, was 87 (23%). There were 46 movements (10% of all recaptures) across the highway and 40 (9%) movements across the smaller roads. Of the 31 (7%) movements along the highway verge, 20 occurred exclusively either on the side of the road mown in mid summer (10 movements) or on the side mown in late summer (10). There were 8 (2%) movements across the cultivated field from any other section to M or vice versa and 2 (0.4%) movements via the verge from the intersection reservation to F or vice versa. In the verge sections, the proportion of non-migrant individuals, which stayed in the same habitat patch, was generally low and the proportion of highway crossings high (Fig. 4). The intersection mown in mid summer also had a relatively low proportion of non-migrant individuals.

The number of movements between sections

Table 2. Table of movements between sections and the number of static movements within each section.

From		A	B	C	D	E	F	G	H	I	J	K	L	M	Total
To	A	84	6	1	0	0	0	1	0	0	2	2	1	0	97
	B	2	7	7	0	0	0	0	0	0	0	0	0	0	16
	C	10	3	52	2	1	1	0	0	1	2	0	0	0	72
	D	0	0	2	6	0	0	1	3	0	2	0	0	0	14
	E	0	0	0	0	1	0	0	1	0	1	0	0	0	3
	F	0	0	1	0	0	18	1	1	0	0	0	0	0	21
	G	0	0	0	1	0	0	10	2	0	0	0	0	0	13
	H	0	0	2	4	1	0	2	8	0	3	1	0	0	21
	I	3	1	3	3	0	0	0	2	16	5	1	0	0	34
	J	3	0	3	0	0	0	0	0	6	98	4	0	4	118
	K	0	1	0	0	0	0	0	0	1	8	5	2	0	17
	L	0	0	0	0	0	0	0	0	2	0	1	1	0	4
	M	1	0	1	0	0	0	0	0	0	2	0	0	17	21
Total		103	18	72	16	3	19	15	17	26	123	14	4	21	451

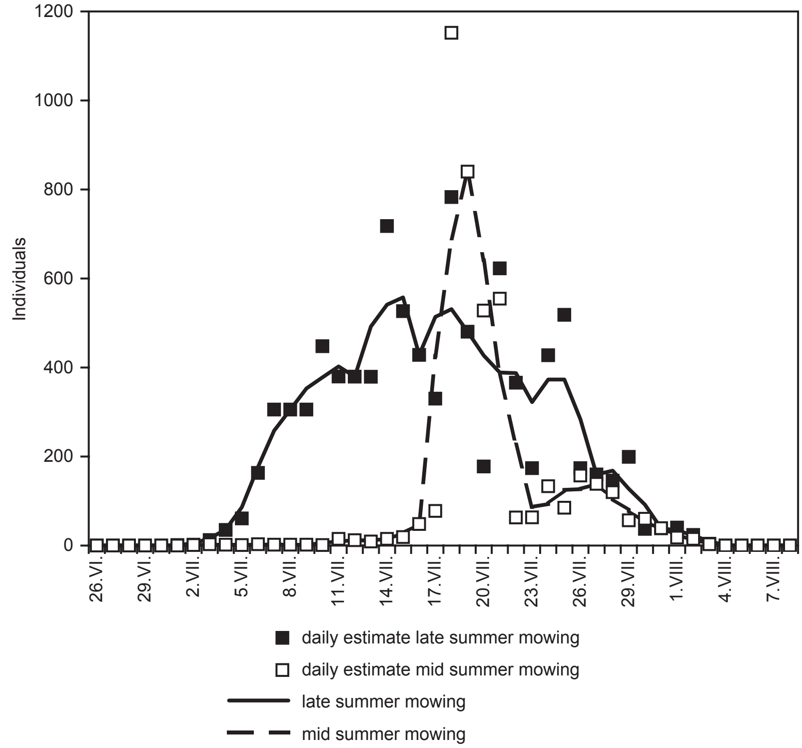

Fig. 3. Estimated daily population sizes of the ringlet in the intersection managed by late summer mowing and mid summer (24 June) mowing. The lines indicate the moving three-day averages calculated from previous, present and subsequent daily estimates.

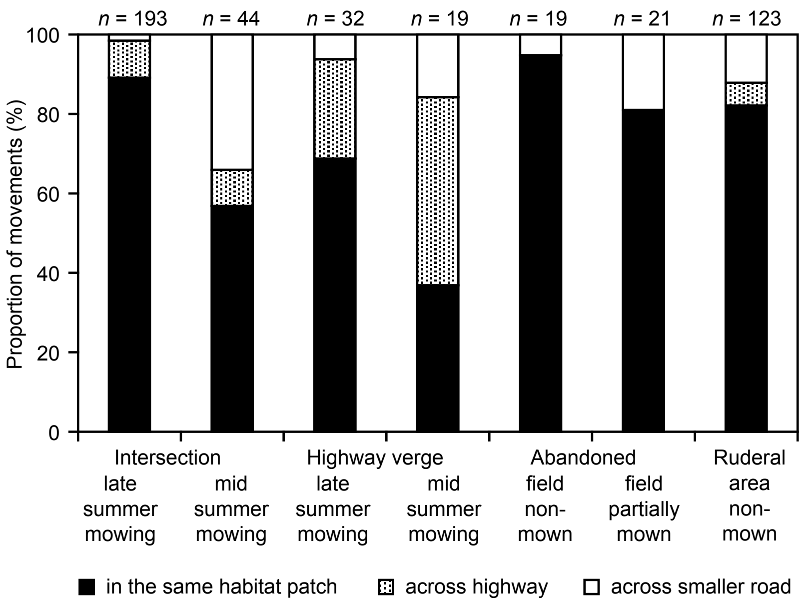

Fig. 4. Proportions of three types of movements from the seven habitat types. The total number of movements is indicated above the histograms.

was adversely affected by the distance and road index > 1, whereas the verge between sections, the population density and area of the target section had a positive influence on the ringlet's movement (Table 3). Each 100-m increase in the distance between sections more than halved the frequency of movements and more than one highway or two smaller roads between sections decreased the frequency of movements to one third. The sections connected by a verge had more than twice the number of movements compared to sections without a verge between them.

The population density and area were negatively, and the number of days between successive captures and linear habitat type positively, related to the probability that an individual left the section where it was observed (Table 4). Individuals observed in linear habitats had twice as high a probability of leaving the section than individuals observed in non-linear habitats. The mowing of the section had a non-significant influence on the probability.

The adverse effect of roads on the movement of the ringlet was further indicated by the comparison of expected and observed highway crossings. When the 46 observed highway crossings were compared to the 64 expected crossings, the highway significantly hindered the ringlet's movement ($\chi^2 = 5.90$, $p < 0.05$).

Discussion

Intensive mowing and habitat shape affect the abundance of the species

The high numbers of ringlet butterflies marked in the study area indicated that this meadow

Table 3. Variables explaining the number of movements from one section to another in the mixed-effects logistic regression. Variables excluded from the model were the road index classes 0.5 and 1, linear habitat type, total and partial mowing. Coefficient, its standard error and significance, odds ratio and its 95% confidence interval are given.

	Coefficient	S.E.	*p* value	OR	Confidence interval	
					Lower	Upper
Constant	–3.937	0.472	< 0.001	0.020	0.008	0.049
Distance	–0.009	0.001	< 0.001	0.416[a]	0.319[a]	0.543[a]
Population density	0.0004	0.00005	< 0.001	1.038[b]	1.028[b]	1.049[b]
Verge	0.909	0.313	0.004	2.481	1.342	4.585
Area	14.430	5.139	0.005	4.233[c]	1.546[c]	11.591[c]
Road index 1.5	–1.050	0.335	0.002	0.351	0.182	0.677
Road index > 1.5	–1.050	0.428	0.014	0.350	0.152	0.810
Random effect	4.8×10^{-15}	0.407				

Deviance = 158.3 (d.f. = 148).
OR and its confidence interval counted for ([a]) 100 m change in the distance, ([b]) 100 individual change in the population density and ([c]) 0.1 ha change in the area (Hosmer & Lemeshow 2000).

Table 4. Results of the mixed-effects logistic regression, explaining why an individual leaves the section where it was observed. Variables excluded from the model were the sex, partial and total mowing. Coefficient, its standard error and significance, odds ratio and its 95% confidence interval are given.

	Coefficient	S.E.	*p* value	OR	Confidence interval	
					Lower	Upper
Constant	1.583	0.710	0.026	4.871	1.212	19.570
Days	0.139	0.042	0.001	1.149	1.057	1.248
Population density	–0.0003	0.00007	< 0.001	0.967[a]	0.954[a]	0.981[a]
Area	–23.260	7.482	0.002	0.098[b]	0.023[b]	0.423[b]
Linear habitat	1.020	0.453	0.024	2.774	1.143	6.735
Random effect	3.4×10^{-17}	0.202				

Deviance = 485.8 (d.f. = 445).
OR and its confidence interval counted for a ([a]) 100 individual change in the population density, ([b]) 0.1 ha change in the area (Hosmer & Lemeshow 2000).

species is capable of thriving in different types of roadside environments, including intersections surrounded by roads. There was, however, variation in the numbers of individuals between the sections due to the different management and geometry. The highest population density was recorded in the non-linear and non-mown ruderal area created by road construction (J) and the second highest in the non-linear intersection managed by late summer mowing (A, B and C). Since 1999 the latter area has been mown after the (main) flowering period of the meadow plants, while other parts of the intersection are mown in the middle of the summer, which is the usual case in intersection management in Finland (Finnish Road Administration 2000). Besides being a good habitat for the ringlet, the meadow-like intersection was characterised by a diverse butterfly fauna. Altogether 20 species of butterflies, including a specimen of the endangered *Glaucopsyche alexis*, were observed during the data collection.

In the intersection managed by mid-summer mowing the majority of ringlets were caught on narrow edges left undisturbed, increasing the population density as compared with that in verge sections managed by mid-summer mowing, where all the vegetation was removed prior to the flight season of the species. Several meadow butterflies are adapted to low-intensity management, which leaves untouched patches of vegetation where the females can lay their eggs and larvae may feed (Erhardt 1985, Balmer & Erhardt 2000). Mowing at the beginning, or in the middle, of the flight period also delayed the emergence of individuals, which settled in the mown sections only after the renewal of the vegetation, resulting in lower estimates of the population sizes. The mowing may have an effect on the adult behaviour through the loss of host plants for egg-laying or the loss of nectar plants, which are reported to be important for the species (Henriksen & Kreutzer 1982). Mid summer mowing may also destroy early developmental stages. In June the ringlets are either full-grown larvae or pupae, the latter being suspended from a grass stalk or situated close to the ground in a fragile web under tufts of grass (Henriksen & Kreutzer 1982). It is likely that the pupae situated below the mowing height may be less vulnerable to mowing than larvae. The pupal stage takes approximately two weeks (Stoltze 1996), which means that individuals emerging in mid-July are in the larval stage until the end of June, i.e. during the mid summer mowing period. Delaying mowing to late summer (Wettstein & Schmid 1999) and leaving undisturbed patches of vegetation are likely to benefit the ringlet, and other meadow species as well, in the road verge habitats.

The adverse effect of the linear habitat type on the population density was unexpected, because in previous studies we had observed high numbers of butterflies along highway verges (Jantunen *et al.* 2004) which were assumed to concentrate individuals from the surrounding less suitable environments as demonstrated by Dover (1990). The contrast between the verge and the surrounding environment was probably less obvious than expected. Besides the adverse effect of mowing on butterflies, another explanation might be that the transect covered the whole verge and the immediate surroundings (road, forest, cultivated field) were unsuitable for the species. Hence, there were fewer individuals from the surroundings visiting the transect as compared with the non-linear habitats where the same habitat type continued on both sides of the transect. Linear and non-linear habitats may also differ in their structure, vegetation, temperature and wind conditions and the exposure to dust and pollutants, which may explain differences in the population density.

The higher the population density the higher the proportion of sedentary individuals

The majority (77%) of recaptured ringlet butterflies stayed in the same habitat patch, i.e. were non-migrant and most of their movements were short ones. In conformity with this, Sutcliffe *et al.* (1997) reported the proportion of sedentary ringlet butterflies to vary by 63%–79%. These numbers are slightly higher as compared with those for another two grassland species, *Maniola jurtina* (46%) and *Lycaena virgaureae* (59%) (Schneider *et al.* 2003). The proportion of non-migrant individuals was especially high in the non-mown abandoned field and in the meadow-like intersection. Neither were mown and both had a relatively high population density and distinct barriers surrounding them, roads around the intersection and dense forest largely surrounding the abandoned field.

The proportion of non-migrant individuals was low in both the sections mown in mid-summer and along the verges. Intensive mowing resulted in a loss of vegetation and a smaller population density, as discussed above, which in turn leads to a higher probability of individuals to take the risk to enter the matrix habitat and leave the habitat patch. Ries and Debinski (2001) reported that the individuals of a habitat specialist *Speyeria idalia* were less likely to exit habitat patches with a high density of conspecifics than from a patch with low density. In verge habitats the borders of the habitat are proportionally longer as compared with its size than in the non-linear habitats, so that individuals reach the border more frequently (Stamps *et al.* 1987). Upon reaching the edge of the road individuals may either cross the road and rarely come back (because they seem to refuse to cross several roads) or turn back to the verge and either stay there or move along the border away from the section. On the other hand, individuals in the non-linear habitats moving away from the transect are able to return without crossing the road.

Roads and verges influence the movement of the ringlet

Even if roads and intersection reservations would serve as alternative habitats to butterflies, species living in them may suffer from the fragmenting effect of roads. According to our results a dense network of roads can affect the movement of the ringlet butterfly since the number of movements between sections decreased significantly when there was more than one large road or two smaller roads between the sections. Roads have also been reported to restrict the movements of bumblebees (Bhattacharya *et al.* 2003) and some small sedentary butterfly species, while larger and more mobile butterfly species were not affected (Munguira & Thomas 1992, Fjellstad 1998, Ries & Debinski 2001). On the other hand, Dennis (1986) found that only 2% of the individuals of a relatively mobile butterfly *Anthocharis cardamines* approaching a motorway actually crossed it. Roads may form physical barriers when they are built on embankments or when they kill individuals, but this effect may be negligible as compared with that when roads are behavioural barriers, i.e. the insect refuses to cross unfavourable environments, as indicated by observations of butterflies starting to cross the road but then turning back (Dennis 1986, Munguira & Thomas 1992).

For all that, the highway was not an absolute barrier to ringlet movement. The percentage of recaptured individuals that had crossed at least one road was of the same magnitude as the 10%–32% of crossings in *Maniola jurtina*, *Melanargia galathea* and *Polyommatus icarus* in Britain (Munguira & Thomas 1992). Thus, roads are not likely to form a barrier to the gene flow of the ringlet. The proportion of movements across roads was high in the verges, where the transect was located close to the highway. Obviously individuals in the high-quality habitats were less likely to make the risky decision to enter the matrix habitat and cross the road than individuals in the low-quality habitats. In fact, the individuals observed in the highway verge mown at mid-summer had a higher probability of crossing the highway than of staying in the same habitat patch. In conformity with this, Ries *et al.* (2001) reported a relatively higher traffic-induced mortality and a higher proportion of butterflies crossing roads along an intensively managed road verge planted with non-native plant species than along a road verge with native vegetation, restricted mowing and the use of herbicides.

Movement along boundaries is common in butterflies and thus the barrier and corridor functions of a landscape element may be inseparable (Fjellstad 1998). In forested landscapes open tracks between habitat patches act as corridors and facilitate the dispersal of the ringlet butterfly (Sutcliffe & Thomas 1996) and other butterfly species (Haddad 1999). The role and effectiveness of the road verges as corridors, however, largely remains unclear (Spellerberg 2002). Due to the low number of replications, i.e. we only had one study area with only one habitat patch unconnected by verges, we could not demonstrate that the movements are more frequent between habitat patches connected by road verges than between unconnected patches. However, we found evidence that there were more movements among the sections connected by a verge than in any other type of sections and that linear habitats encouraged individuals to leave more often than non-linear habitats. It is therefore possible that intensively mown road verges, if not suitable as breeding habitats for the ringlet butterfly, may at least form corridors, but further research on this matter is needed.

Modern farming practices have led to the simplification and fragmentation of the agricultural environment, which has reduced the majority of meadow species (van Swaay & Warren 1999, Pitkänen *et al*. 2001). There exists a vast potential for road verges to serve as alternative habitats because of both the large area and obligatory management for reasons of road safety, providing a suitable environment for meadow species in the long run. To enhance the quality of these areas in the short term as well, we suggest that only one mowing in the late summer should take place. If this does not ensure adequate road safety, partial mowing in mid-summer and total mowing in the late summer can be carried out on road verges.

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