Effect of different mowing regimes on butterflies and diurnal moths on road verges

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Abstract

Effect of different mowing regimes on butterflies and diurnal moths on road verges.— In northern and central Europe road verges offer alternative habitats for declining plant and invertebrate species of semi–natural grasslands. The quality of road verges as habitats depends on several factors, of which the mowing regime is one of the easiest to modify. In this study we compared the Lepidoptera communities on road verges that underwent three different mowing regimes regarding the timing and intensity of mowing; mowing in mid–summer, mowing in late summer, and partial mowing (a narrow strip next to the road). A total of 12,174 individuals and 107 species of Lepidoptera were recorded. The mid–summer mown verges had lower species richness and abundance of butterflies and lower species richness and diversity of diurnal moths compared to the late summer and partially mown verges. By delaying the annual mowing until late summer or promoting mosaic–like mowing regimes, such as partial mowing, the quality of road verges as habitats for butterflies and diurnal moths can be improved.

Key words: Mowing management, Road verge, Butterfly, Diurnal moth, Alternative habitat, Mowing intensity.

Resumen

Efecto de los distintos regímenes de siega de los márgenes de las carreteras sobre las polillas diurnas y las mariposas.— En Europa central y septentrional los márgenes de las carreteras constituyen hábitats alternativos para especies de invertebrados y plantas de los prados semi–naturales cuyas poblaciones se están reduciendo. La calidad de los márgenes de las carreteras como hábitats depende de diversos factores, de los cuales el régimen de siega es de los más fáciles de modificar. En este estudio se compararon las comunidades de lepidópteros de los márgenes de las carreteras que sufrieron tres regímenes distintos de siega, según el momento y la intensidad de la siega; siega a mediados del verano, siega a finales de éste, y siega parcial (una estrecha franja próxima a la carretera). Se estudiaron un total de 12.174 individuos y 107 especies de lepidópteros. Los márgenes segados a mediados de verano presentaban una menor riqueza de especies y abundancia de mariposas, y una menor riqueza de especies y diversidad de polillas diurnas, en comparación con los márgenes segados a finales de verano o segados parcialmente. Retrasando la siega anual hasta finales del verano, o promoviendo regímenes de siega en forma de mosaico, tales como la siega parcial, podría mejorarse la calidad de los márgenes de las carreteras como hábitats para las mariposas y las polillas diurnas.

Palabras clave: Gestión de la siega, Margen de la carretera, Mariposa, Polilla diurna, Hábitat alternativo, Intensidad de la siega.

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Introduction

A large number of plant and insect species living in temporal and boreal landscapes in Europe are ecologically fitted to semi–natural grasslands created by mowing or grazing regimes under traditional farming (Pykälä, 2000; Van Swaay, 2002). The agricultural intensification and abandonment of low–productive agricultural areas throughout Western Europe has, however, led to the steep decline of semi–natural grasslands and the associated fauna and flora (Thomas, 1995; Van Swaay & Warren, 1999; Poschlod & WallisDeVries, 2002). The semi–natural biotopes in Finland, for example, now cover less than 1% of the corresponding area one century ago (Vainio et al., 2001). Consequently, many ruderal areas such as road verges are recognised as important habitats for several endangered species of semi–natural biotopes (Rassi et al., 2001).

The potential of road verges is based, on one hand, on their large area, which in Finland is at least 50–fold compared to the area of remaining semi–natural grasslands on mineral soils (Valtonen & Saarinen, 2005), and on the other hand on their regular mowing management, which somewhat resembles the management of semi–natural grasslands. In general, a regular mowing regime followed by hay removal has a positive effect on vascular plant species richness on road verges (Parr & Way, 1988; Persson, 1995; Schaffers, 2000). In contrast, among invertebrates many species of Arachnida (Kajak et al., 2000), Orthoptera (Guido & Gianelle, 2001), Coleoptera (Morris & Rispin, 1988), Diptera and Lepidoptera (Völkl et al., 1993) and Hemiptera (Helden & Leather, 2004) suffer from mowing, although some species of these groups may respond favourably (Morris, 1981; Morris & Rispin, 1988). Butterflies are frequently used as indicators of changes in habitat structure and management and they are adversely affected by mowing (Erhardt, 1985; Feber et al., 1996; Gerell, 1997; New, 1997; Hogsden & Hutchinson, 2004; Valtonen & Saarinen, 2005). In the long term, however, mowing has a positive effect on meadow butterflies as it prevents the growth of bushes and trees (Erhardt, 1985). It has been observed to be a practical tool for maintaining an appropriate habitat for butterflies in savannahs in North America, for example (Swengel, 1995).

There are, however, profound differences in the management of road verges and traditional biotopes. Traditional management of meadows included either one mowing event in July or grazing, whereas road verge management in general can be divided into two categories. It can include mowing of either the whole verge, or only part of it. Totally mown verges are generally subjected to one or two mowings per year, timed in mid–summer (from June to early July) and /or late summer (from late July to September). Partially mown verges receive one or several mowings annually, covering a narrow (usually 2 m) strip next to the road; this is combined with total mowing at intervals of approximately 3 years in order to prevent the growth of trees and bushes. Partial mowings are also typical on verges mown totally every year, and can occur before or after the total mowing. Removal of cut material, inherent to the traditional management, is rare on road verges and the mowing equipment frequently includes crushing blades instead of the traditionally used cutting blades. In addition, in a large proportion of verges the soil is disturbed due to construction works on an average of once every 20–30 years (Mahosenaho & Pirinen, 1999).

If available, decision–support systems using databases on road verge flora and fauna can be used to select the best management measure for each road verge site (Siepel, 1997). However, in most cases such information is lacking and more general guidelines are needed. Ways to increase the suitability of managed grasslands for butterflies include promoting native rather than non–native vegetation (Ries et al., 2001; Valtonen et al., in press), avoiding the use of herbicides (Ries et al., 2001), removing cuttings (Schmitt, 2003), and avoiding mid–summer mowing (Feber et al., 1996; Valtonen & Saarinen, 2005). Although poorly studied, rotational (Gerell, 1997) and mosaic–like (Munguira & Thomas, 1992) mowing regimes on road verges have been recommended. However, the narrow shape of road verges, the variable topography and vegetation, the large area, and demands for improving traffic safety set limits on management. Over–intensive mowing regimes, nowadays common on many urban road verges, are both expensive and harmful to meadow insects (Saarinen et al., 2005). Mowing once a year, however, the original mowing frequency on semi–natural grasslands, may not be sufficient for verges suffering from a predominance of hay grasses or other competitive plant species (Hellström, 2004). Partial mowing of road verges is a kind of a compromise that meets the demand of sustaining traffic safety throughout the summer while also avoiding mid–summer mowing in the major part of the verge. This management regime, that includes less intensive management of the "edge"' vegetation of verges, is suggested to be beneficial to butterflies (Warren, 1985; Munguira & Thomas, 1992), but to our knowledge it has not yet been compared to other mowing regimes.

This study compared the effects of three different mowing regimes of road verges on butterfly and diurnal moth species richness, diversity, abundance, and species composition. The three regimes differed in timing and intensity of mowing. All road verges included some kind of mowing, as this measure is considered to ensure traffic safety. These three mowing regimes represent commonly applied mowing practices in Finland, thereby providing a realistic understanding of their long–term effects on Lepidoptera. The mowing regimes were: 1) total mowing in mid–summer (with possible partial mowing in late summer), 2) total mowing in late summer (with possible partial mowing in mid–summer), and 3) one or more partial mowings during the summer (leaving some undisturbed vegetation throughout the study season). Management in the last regime was the most variable, since the sites were either totally mown after the study season (September) or only once approximately every 3 years. Two hypotheses were assumed: (i) total mowing in late summer, leaving resources undisturbed during the peak flight period, is more favorable to the Lepidoptera fauna than total mowing in mid–summer and (ii) a management regime based on only partial mowing is more beneficial to Lepidoptera than the management regimes that include total mowing as some resources are always available for all life–stages of Lepidoptera. Suggestions for road verge management are given in the discussion.

Material and methods

Study sites and transect counts

The same number of study sites (N = 54) was assigned to each of the three mowing regimes: (i) mid–summer mown verges (n = 18) were mown totally before or during week 28, (ii) the late summer mown verges (n = 18) were subjected to the first total mowing after or during week 31 and (iii) the partially mown verges (n = 18) were mown at any time during the study period, but a substantial part of the verge always remained unmown. Due to the variation in the timing and intensity of mowing within the three regimes, their validity was examined by calculating a mowing index describing the total effect of mowing on the vegetation over the study period. The index was based on the mowing week, the number of times the verge was mown and the area mown. Each week was given a mowing intensity value (0 = no mowing, 1/2 = partial mowing, 1 = total mowing); the value was reduced to the lower level (from 1 to 1/2 and from 1/2 to 0) seven weeks after the mowing due to the regeneration of vegetation. The sum of weekly values, i.e. the mowing index for the site, ranged from 1 to 10.5. The index of the partially mown verges was generally the lowest, that of the late–summer mown verges was intermediate, and that of the mid–summer mown verges was the highest (fig. 1).

Located along the road network in the Imatra–Lappeenranta region, SE Finland, the sites included highway verges (n = 19), urban road verges (n = 26) and paved rural road verges (n = 9). Study sites with strong spatial dependence, i.e. located in close proximity to each other, were considered to belong to the same study areas (N = 27). Six study areas included sites belonging to several mowing regimes, while all the others included only sites belonging to one regime.

Butterflies (Hesperioidea, Papilionoidea) and other day–active Lepidoptera (Zygaenoidea, Lasiocampoidea, Bombycoidea, Geometroidea, Noctuoidea) were studied along a 250 m transect in each site. The names of the Lepidoptera species follow the checklist by Kullberg et al. (2002). All the transects were censused once a week between early June (week 23) and late August (week 35), resulting in 13 counts. All individuals

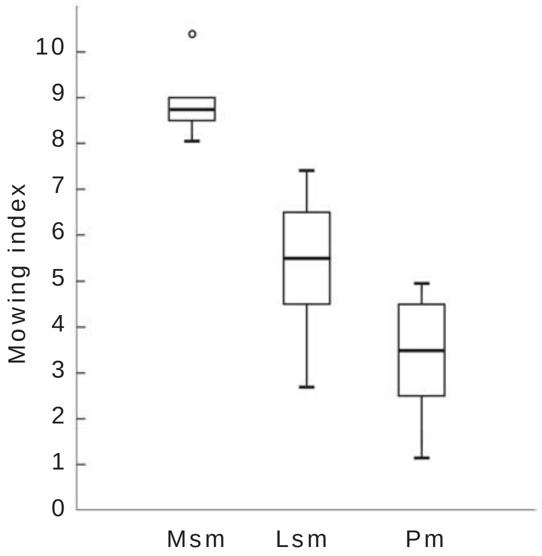

Fig. 1. Boxplot diagrams illustrating differences in mowing indices between the three mowing regimes: Intersection line. Median; Box. First and third quartiles; Whiskers. Largest and smallest observations falling within a distance of 1.5 times the box size from the nearest quartile; Circles. Outliers, observations with values between 1.5 and 3 box lengths from the upper or lower edge of the box; Msm. Mid summer mown; Lsm. Late summer mown; Pm. Partially mown.

Fig. 1. Diagramas de caja que ilustran las diferencias en los índices de siega entre los tres regímenes de siega: Línea de intersección. Mediana; Caja. Cuartiles primero y tercero; Bigotes. Observaciones mayor y menor incluidas dentro de una distancia de 1,5 veces el tamaño de la caja desde el cuartil más próximo; Círculos. Outliers, observaciones con valores entre 1,5 y 3 veces la longitud de la caja desde los bordes superior o inferior de dicha caja; Msm. Siega a mediados de verano; Lsm. Siega a finales de verano; Pm. Siega parcial.

within a 5 x 5 m square in front of the recorder were noted (Pollard & Yates, 1993). Due to the low number of individuals recorded per count (17, on average), the probability of recounting the same specimen was low. All the transect counts were conducted between 9:00 a.m. and 5:30 p.m. in satisfactory weather conditions. The minimum temperature for censuses was 12°C, and the average was 20.5°C. The wind speed on the Beaufort scale was 5 or below, with the median wind speed being 2. Estimated in percentages (0, 25, 50, 75, 100%), the sunshine percentage was 75% or above in 86% of the counts, the median of all counts being 100%. Sites were censused over a 3–year period, and each site was studied in one year only: 15 sites in 2002, nine sites in 2003, and 30 sites in 2004. According to the Finnish Meteorological Institute, the three years differed in their weather conditions. Summer 2002 was warm, with a rainy June and July but a dry August. In summer 2003 a cool June was followed by a warm July and normal August, with rainfall following the long–term average. Summer 2004 was rainy, but temperatures followed long–term averages. A total of 702 counts resulted over the three seasons.

Environmental variables

The verge width and the variables describing the vegetation and the surrounding environment were measured for each study site (*N* = 54) together with other environmental variables for each study area (*N* = 27). Road width was measured in metres, the local speed limit was used as a measure of the traffic speed (a reasonable measure in the local conditions), and the traffic density was estimated on an ordinal scale ranging from 0 (no traffic) to 4 (heavy traffic according to local scale, with up to 13,700 vehicles per day). The verge width was measured in metres and the age was evaluated as years since the last disturbance to the soil, for example for construction work. The oldest age was set at 25 years according to the average frequency of road verge construction. Soil moisture was estimated on an ordinal scale ranging from 1 (dry) to 3 (moist). The vegetation height and the plant species within the transect were recorded three times per season, i.e. in the middle of June, in July, and in August. Vegetation height was measured from the centre of the transect and in partially mown verges the average was taken from the mown and non–mown parts. Each plant species was given a value describing its abundance on the transect ranging from 1 (only a few observations) to 3 (very abundant). The information on the abundance of plant species was used when estimating the quality of the vegetation by summing the abundances of positive or negative indicator species of traditional biotopes in each site based on the classification by Pykälä (2001). Similarly, abundances of the most important larval host plants were summed for each site based on the information by Seppänen (1970). The abundance of flowering plants (other than Poaceae) and nectar plants important for adult butterflies (Mikkola & Tanner, 2001) were calculated accordingly. The surrounding environment was classified using coverage (%) of open uncultivated land (meadows, fallow or unmanaged sites), open cultivated land (fields, gardens), and forests. The evaluation was based on two zones, the inner one (< 10 m) being evaluated on the side of the road where the transect was located and the outer one (10–50 m) being evaluated on both sides of the road. The value of the inner zone had double weighting in the calculation of the average cover for each landscape class around the study sites.

Data analysis

Differences in butterfly and diurnal moth species richness, diversity and abundance between the study sites of the three mowing regimes were investigated by mixed–effects ANOVA conducted by the MIXED procedure of the SAS (SAS Institute, 1996). The mowing regime was assigned as a fixed–effect, whereas the study area and the study year were set as the random–effect variables to account for the spatial and temporal dependence (e.g. differences in the weather conditions of the three study years) in the data. Pairwise comparisons (Tukey–Kramer) were undertaken where significant differences ($P < 0.05$) were found. The square root (diurnal moth abundance, diurnal moth species richness) and logarithmic (total abundance, butterfly abundance) transformations were conducted where appropriate to improve the normality. Species diversity was calculated using the Shannon index

$$H' = -\sum_{i}^{S} p_i \ln p_i ,$$

where S = number of species and p_i = abundance of species i / total abundance.

Differences in the species composition the three mowing regimes and over the three study years were tested with a non–parametric multi–response permutation procedure (MRPP) using a Euclidean distance measure (Zimmerman et al., 1985). Indicator species analysis was used to find the most characteristic species of each regime (Dufrene & Legendre, 1997). The statistical significances of indicator values were tested using the Monte Carlo technique with 1,000 runs. The MRPP and indicator species analysis were performed by PC–ORD 4.0 (McCune & Mefford, 1999).

Differences in environmental conditions between the three mowing regimes were also compared. Variables recorded for each study area, independent of the study year, were tested with a non–parametric Kruskal–Wallis test conducted by SPSS. The verge width and variables describing the surrounding environment recorded for each study site were also tested with the Kruskal–Wallis test by taking averages within each study area. Separate averages were calculated for sites belonging to the same study area but different mowing regime. Pair–wise comparisons were calculated according to Siegel & Castellan (1988). The differences in the vegetation variables were compared with mixed–effects ANOVA, using the same procedure as described above with the Lepidoptera variables. The abundance of host plants was square root transformed and the vegetation height was logarithmically transformed.

Finally, non–parametric Spearman correlations were calculated between Lepidoptera variables and the environmental variables to investigate alternative explanatory factors for the Lepidoptera species richness and abundance. A sequential Bonferroni correction was used in all tables to lower the risk of significant differences by chance, using an error rate of 10% as suggested by Chandler (1995).

Results

A total of 12,174 individuals and 107 species of Lepidoptera were recorded in censuses and approximately half of the species (46%) and individuals (51%) were butterflies (table 1). The 49 butterfly species recorded consisted of approximately 50% of the resident butterfly fauna in Finland (Huldén et al., 2000). One threatened butterfly species, the Green–underside Blue *Glaucopsyche alexis* (VU) (Rassi et al., 2001) was recorded. Forty–one percent of the butterfly species and 79% of individuals represented species typical of meadows, 41% species and 10% of individuals represented species typical of forest edges and clearings and 16% of species and 11% of individuals represented species typical of field margins (table 1). The majority of diurnal moths belonged to either the Geometroidea (28 species / 4,134 individuals) or Noctuoidea (20 / 1,692) and 45% of species were typical of meadows, representing 94% of all moth individuals recorded (table 1).

The mid–summer mown verges had a significantly lower number of butterfly and diurnal moth species, lower butterfly abundance and lower diurnal moth diversity than the partially mown verges (table 2). In addition, the butterfly abundance of the mid–summer mown verges was lower than the late–summer mown verges. No differences were observed between the late–summer and partially mown verges. During the peak flight season of both butterflies (weeks 27–32) (figs. 2A, 2B) and diurnal moths (weeks 25–31) (figs. 3A, 3B), the weekly averages of species richness and abundance in the mid–summer mown verge were lower than the other mowing regimes. In contrast to butterflies, the partial mowing resulted in a lower abundance of diurnal moths than the late–summer mown verges during weeks 26–29. At the end of the study season (week 35), the mid–summer mown sites attracted most species and individuals.

The proportion of meadow butterflies was lower (73% of all butterfly individuals) and the proportion of butterflies typical to field margins was higher (19%) in the mid–summer mown verges as compared to both the late–summer mown verges (83% vs. 8%) and the partially–mown verges (78% vs. 10%). MRPP indicated an overall significant difference in the species' composition of the three mowing regimes in both butterflies ($P < 0.001$) and diurnal moths ($P < 0.001$). The butterfly assemblages also differed between the three years ($p = 0.031$), but such a difference was not found for the diurnal moths ($p = 0.076$). Indicator species analysis found ten significant ($P < 0.05$) indicators, comprising four butterfly species and six diurnal moth species (table 1).

Mid–summer mown sites were preferred by only one species (the Small Tortoiseshell butterfly *Nymphalis urticae)*, late–summer mown sites by three and partially–mown sites by six indicator species.

There were no significant differences between the three mowing regimes in respect to the physical environment or the surrounding environment type (table 3). A total of 197 plant species were recorded along the transects, 155 species in the mid–summer mown verges, 151 species in the late–summer mown verges and 146 species in the partially–mown verges. Altogether, 37 plant species were classified as positive indicators and 39 as negative indicators of semi–natural biotopes, 31 as important host plant species, and 35 as important nectar plant species (table 4). The three mowing regimes differed significantly in terms of variables related to mowing, i.e. flower and nectar abundance and vegetation height (table 5). In all cases the mid–summer mown verges differed either from the late–summer and/or partially–mown verges.

After the Bonferroni correction, two significant correlations between the Lepidoptera numbers and environmental variables remained, these being the negative correlation between butterfly species richness and negative indicators of traditional biotopes and the positive correlation between the butterfly species richness and the cover of adjacent forests (table 6).

Discussion

Lepidoptera abundance adversely affected by the mid–summer mowing

Mowing in the mid–summer resulted in lower abundances of Lepidoptera as compared to the other mowing regimes during the peak flight period, confirming earlier studies (Munguira & Thomas, 1992; Feber et al., 1996; Gerell, 1997). Contrary to the first hypothesis, however, only the total abundance of butterflies was significantly lower in the mid–summer mown verges than in the late–summer mown verges. According to differences in environmental variables, the decline in butterfly abundance was mainly a result of factors that are directly dependent on the mowing: the decrease in nectar (Erhardt, 1985; Gerell, 1997) and breakdown of the vegetation structure (Erhardt, 1985). The latter may lead to conversion of host plants unsuitable for egg–laying at a time when the majority of individuals reach their adult stage. In his study, Gerell (1997) observed the majority of butterflies on the wing in the mown road verge, indicating a lack of food resources. Nectar, in particular, influences the microdistribution of butterflies in their habitat (Loertscher et al., 1995) and increases their longevity and fecundity (Murphy et al., 1983). However, some butterfly species tend to return to mown sites to lay their eggs and may even benefit from the young regrowth (Erhardt, 1985; Pullin, 1987; Kuras et al., 2001). Since mid–summer mowing postpones flowering, these verges attract butterflies at the end of August, when the vegetation in the surrounding environment is already withering. Many of the attracted species overwinter as adults and then gather energy in the form of nectar during autumn.

Table 1. Butterfly and diurnal moth species and their abundance in the three mowing groups: T. Total abundance; M. Mid summer group; L. Late summer group; P. Partially mown group; I. Significant indicator according to the indicator species analysis. Preferred habitat type: [a] Meadows; [b] forest edges and clearings; [c] Field margins. The classification of butterflies mainly following Pitkänen et al. (2001) and diurnal moths by Kuussaari et al. (2003).

Tabla 1. Especies de mariposas y polillas diurnas y su abundancia en los tres grupos de siega: T. Abundancia total; M. Grupo de mediados de verano; L. Grupo de finales de verano; P. Grupo de siega parcial; I. Indicador de significación según el análisis de la especie indicadora. Tipo de hábitat preferido: [a] Praderas; [b] Lindes y claros del bosque; [c] Márgenes de los campos. La clasificación de las mariposas se ha basado principalmente en la de Pitkänen et al. (2001) y la de las polillas diurnas en la de Kuussaari et al. (2003)

	T	M	L	P	I		T	M	L	P	I
Butterflies											
Aphantopus hyperantus [a]	1,861	247	771	843	P	*Erebia ligea* [b]	16	0	11	5	L
Thymelicus lineola [a]	1,563	416	523	624		*Boloria euphrosyne* [b]	11	1	3	7	
Coenonympha glycerion [a]	343	73	148	122		*Nymphalis c–album* [b]	10	2	7	1	
Pieris napi [c]	305	75	95	135		*Aricia artaxerxes* [a]	8	3	5	0	
Polyommatus amandus [a]	275	50	116	109		*Euphydryas maturna* [b]	8	1	0	7	
Gonepteryx rhamni [b]	236	27	44	165	P	*Glaucopsyche alexis* [a]	7	0	4	3	
Nymphalis urticae [c]	222	143	17	62	M	*Vanessa cardui* [c]	7	0	4	3	
Ochlodes sylvanus [b]	186	35	75	76		*Plebeius idas* [b]	7	1	5	1	
Polyommatus semiargus [a]	181	53	84	44		*Callophrys rubi* [b]	7	1	4	2	
Brenthis ino [a]	146	16	64	66		*Albulina optilete*	6	1	2	3	
Boloria selene [a]	136	16	51	69		*Pyrgus malvae* [a]	5	0	1	4	
Nymphalis io [c]	113	13	64	36		*Anthocharis cardamines* [b]	4	1	1	2	
Polyommatus icarus [a]	88	24	31	33		*Argynnis paphia* [b]	4	0	2	2	
Lycaena virgaureae [a]	79	5	27	47		*Carterocephalus silvicola* [b]	4	0	2	2	
Argynnis aglaja [a]	67	11	19	37		*Leptidea sinapis* [b]	4	1	0	3	
Argynnis adippe [a]	64	6	13	45		*Cupido argiades* [c]	3	1	0	2	
Coenonympha pamphilus [a]	41	20	10	11		*Nymphalis antiopa* [b]	2	1	0	1	
Pieris rapae [c]	41	20	4	17		*Thecla betulae* [b]	2	0	2	0	
Lasiommata maera [b]	39	13	10	16		*Argynnis niobe* [a]	2	0	0	2	
Plebeius argus [b]	30	1	18	11		*Limenitis populi* [b]	2	0	1	1	
Melitaea athalia [b]	29	2	8	19		*Pyrgus alveus* [a]	1	0	0	1	
Lycaena hippothoe [a]	28	2	13	13		*Celastrina argiolus* [b]	1	0	1	0	
Aporia crataegi [b]	24	9	7	8		*Vanessa atalanta* [c]	1	0	1	0	
Aricia eumedon [a]	18	2	7	9		*Pieris brassicae* [c]	1	0	1	0	
Lycaena phlaeas [a]	17	6	2	9							
Diurnal moths											
Scotopteryx chenopodiata [a]	2,861	864	1245	752		*Cabera exanthemata*	4	0	3	1	
Euclidia glyphica [a]	1,159	249	585	325	L	*Aplocera praeformata* [a]	4	0	0	4	
Scopula immorata [a]	496	97	139	260	P	*Parasemia plantaginis*	4	1	1	2	
Polypogon tentacularius [a]	184	27	48	109	P	*Chersotis cuprea* [a]	4	1	0	3	
Siona lineata [a]	183	34	55	94		*Macaria brunneata*	3	0	1	2	
Cryptocala chardinyi [a]	174	10	101	63		*Angerona prunaria*	3	0	1	2	

Table 1. (Cont.)

	T	M	L	P	I		T	M	L	P	I
Odezia atrata [a]	113	14	62	37		*Autographa bractea*	3	2	1	0	
Xanthorhoe montanata	106	36	15	55		*Hyles gallii* [a]	2	1	0	1	
Idaea serpentata [a]	97	19	44	34		*Timandra griseata* [a]	2	0	0	2	
Cerapteryx graminis [a]	80	58	17	5		*Eupithecia satyrata*	2	0	1	1	
Callistege mi [a]	48	1	19	28		*Adscita statices* [a]	2	0	0	2	
Chiasmia clathrata [a]	46	20	7	19		*Caradrina morpheus*	2	2	0	0	
Ematurga atomaria	42	9	18	15		*Protodeltode pygarga*	2	0	0	2	
Diacrisia sannio	41	5	15	21		*Rivula sericealis* [a]	2	0	0	2	
Scopula immutata [a]	31	1	17	13		*Panemeria tenebrata* [a]	2	0	1	1	
Camptogramma bilineata [a]	26	5	12	9		*Aglia tau*	1	0	0	1	
Scopula ternata	21	2	15	4	L	*Idaea emarginata*	1	0	0	1	
Rheumaptera hastata	20	13	4	3		*Jodis putata*	1	0	1	0	
Epirrhoe alternata [a]	19	7	5	7		*Rheumaptera undulata*	1	0	1	0	
Lomaspilis marginata	19	2	11	6		*Chlorissa viridata*	1	0	0	1	
Eilema lutarellum	18	0	5	13	P	*Spilosoma lubricipedum*	1	1	0	0	
Autographa gamma	17	4	5	8		*Orgyia antiqua*	1	1	0	0	
Zygaena viciae [a]	14	2	8	4		*Deltode candidula*	1	0	1	0	
Idaea pallidata [a]	12	0	6	6		*Diachrysia chrysitis*	1	1	0	0	
Cybosia mesomella	9	0	2	7	P	*Mythimna conigera*	1	0	0	1	
Cabera pusaria	9	2	2	5		*Mythimna ferrago*	1	0	1	0	
Colobochyla salicalis	8	1	1	6		*Plusia festucae*	1	0	0	1	
Lythria cruentaria [a]	6	4	1	1		*Leucania impura*	1	0	1	0	
Epirrhoe tristata [a]	5	0	3	2		*Lygephila pastinum* [a]	1	0	0	1	

Besides altering the habitat characteristics of importance to adults, mowing may also destroy eggs, larvae and pupae (Courtney & Duggan, 1983; Erhardt, 1985; Feber et al., 1996). The mowing of road verges in mid–June, for example, caused complete destruction of the Orange Tip butterfly *Anthocharis cardamines* larvae during their third instar (Courtney & Duggan, 1983). In contrast, many larvae of the Karner Blue butterfly *Lycaeides melissa samuelis* were found on sites (including road verges) mown since or during the previous adult flight period, suggesting that not all butterflies or their earlier stages are vulnerable to occasional or annual mowing (Swengel, 1995). Since Lepidoptera species differ in their life cycles, there is no single time when mowing could be conducted without harming the early stages of some species. However, late summer mowing is suggested to best suit the life cycles of most invertebrates (Anderson, 1995),but more research on this matter is needed. Even if mowing destroys a large proportion of eggs, larvae and pupae, individuals may arrive in the verges from the surrounding environment after the regeneration of vegetation. Consequently, the presence of adult stages does not necessarily indicate the suitability of the area for breeding. Furthermore, different life stages may need different elements, thus requiring them to travel between patches (Dunning et al., 1992). This phenomenon is also recognized in butterflies (Ouin et al., 2004). In this study, the Brimstone butterfly *Gonepteryx rhamni* was observed in large numbers nectaring on road verges both in early spring and in late summer, while its host plant *Rhamnus frangula* grows only in forests.

The species richness of both butterflies and diurnal moths declined after the mid–summer mowing, a finding that is in keeping with the results of Feber et al. (1996). However, the differences in total butterfly species richness and diversity between the mid–summer and late–summer mown verges were small compared to the differences in abundance, suggesting that the decline concerned both abundant and rare spe-

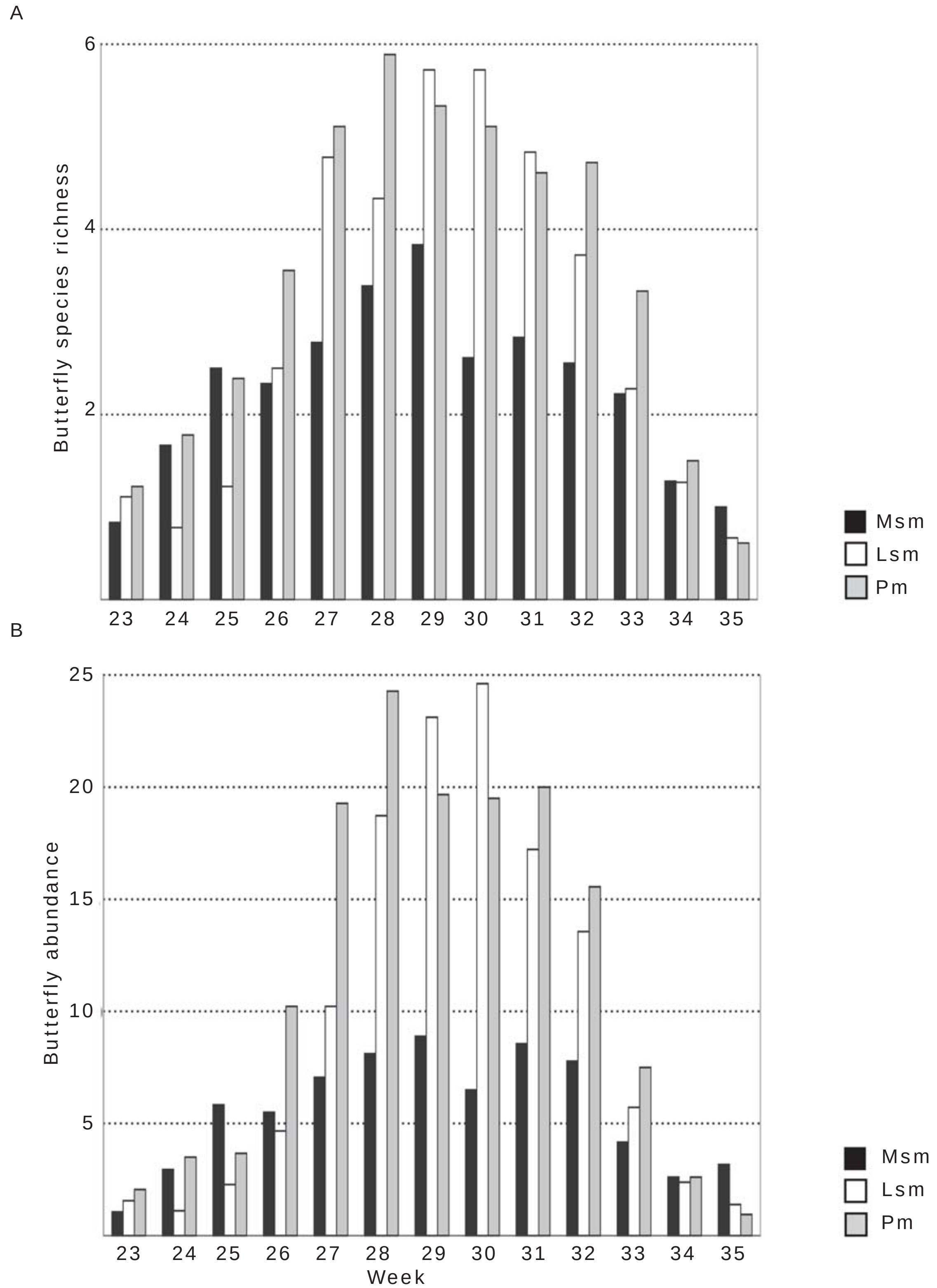

Fig. 2. Weekly averages of butterfly species richness (A) and abundance (B). (For abbreviations see fig. 1.)

Fig. 2. Promedios semanales de la riqueza de especies de mariposas (A) y de su abundancia (B). (Para las abreviaturas ver la fig. 1.)

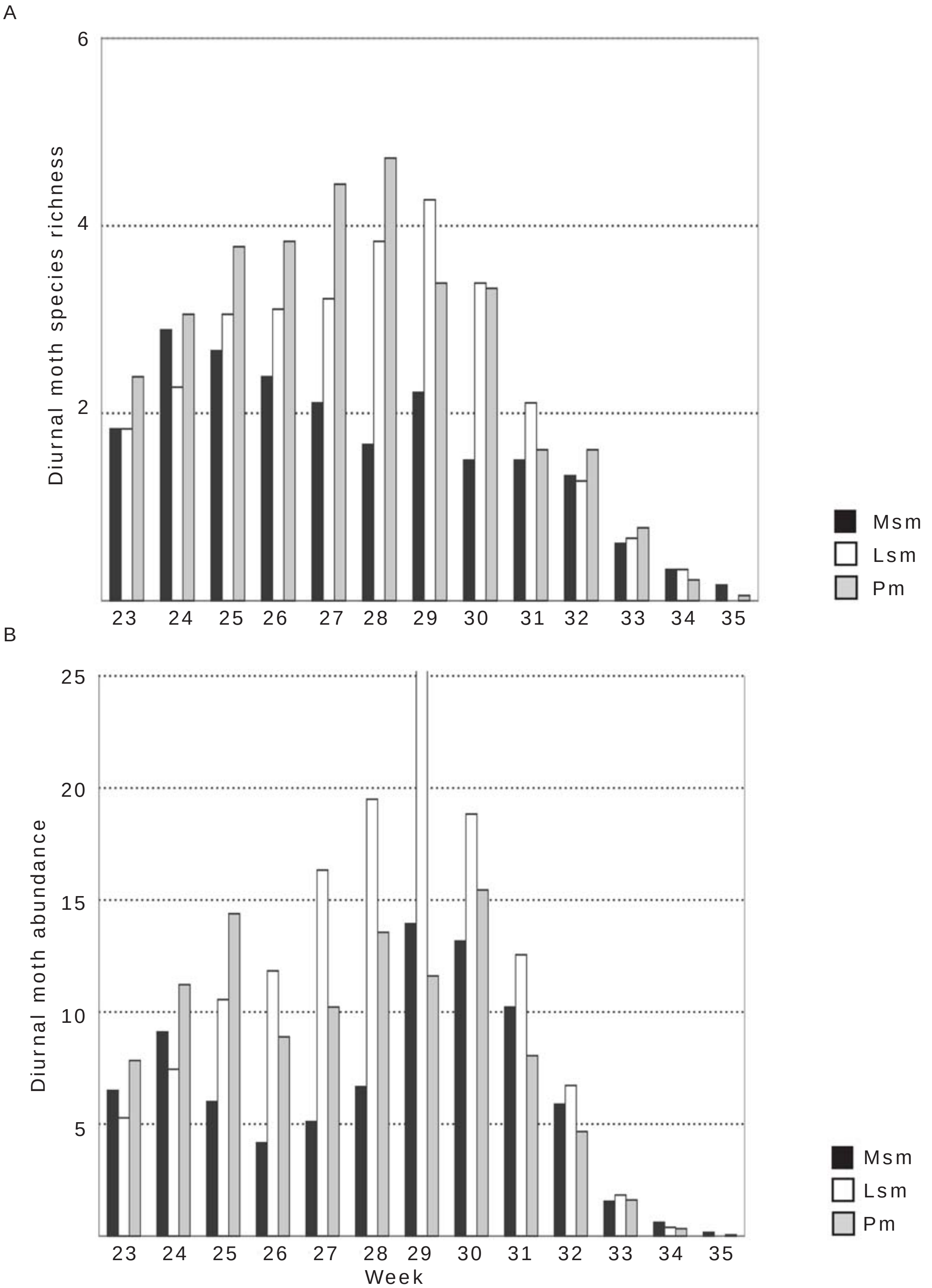

Fig. 3. Weekly averages of diurnal moth species richness (A) and abundance (B). (For abbreviations see fig. 1.)

Fig. 3. Promedios semanales de la riqueza de especies (A) y de la abundancia (B) de las polillas diurnas. (Para las abreviaturas ver la fig. 1.)

Table 2. Differences in the Lepidoptera communities between the three management regimes. Differences were tested by mixed–effects ANOVA and pair–wise comparisons by the Tukey–Kramer method: * 0.05 > *P* > 0.01; *** *P* < 0.001, significant differences after sequential Bonferroni correction are marked with *S*. Regimes with significant differences in pair–wise comparisons are indicated by separate letter *a* and *b*. (For other abbreviations see fig. 1.)

*Tabla 2. Diferencias en las comunidades de lepidópteros entre los tres regímenes de gestión. Las diferencias se comprobaron mediante un ANOVA de efectos mixtos, y las comparaciones apareadas mediante el método de Turkey–Kramer: * 0,05* > P > *0,01, **** P < *0,001; las diferencias significativas tras el ajuste secuencial de Bonferroni se indican mediante una* S. *Los regímenes con diferencias significativas en las comparaciones apareadas se indican mediante las letras separadas* a *y* b. *(Para otras abreviaturas ver fig. 1.)*

	Msm			Lsm			Pm		
	Total	Mean	Std.	Total	Mean	Std.	Total	Mean	Std.
Butterfy									
Species richness*S	36	12.4a	3.9	43	15.2ab	5.8	44	16.3b	5.4
Diversity (H')	–	1.8	0.5	–	1.9	0.4	–	1.9	0.4
Abundance***S	1,299	72.2a	30.7	2,278	126.6b	69.4	2,678	148.8b	60.4
Diurnal moth									
Species richness*S	33	9.2a	2.5	41	11.9ab	3.8	48	14.3b	4.6
Diversity (H')*S	–	1.3a	0.4	–	1.5ab	0.4	–	1.7b	0.3
Abundance	1,496	83.1	48.3	2,481	137.8	67.7	1,942	107.9	43.6

cies. The correlations indicate that factors not directly associated with mowing, such as the surrounding environment type (Gerell, 1997; Pywell et al., 2004) and the site history, have a stronger influence on species richness than mowing. Forest edges, in particular, offer shelter to butterflies and have a diversifying influence on road verge butterfly fauna (Gerell, 1997). On the other hand, the abundance of negative plant indicators, was adversely associated with butterfly species richness and may indicate both recent disturbance to the soil and high amounts of nutrients in the soil, possibly caused by imported top soil typical on road verges.

Differences in the species' composition between the mid–summer and late–summer mown verges suggest that the butterflies typical of field margins were relatively more abundant in the nectar–poor mid–summer mown verges. A closer examination of butterfly data during the week following the mowing event, however, indicated the predominance of meadow species in the verges. An alternative explanation may be that some abundant field margin species, such as the Peacock butterfly *Nymphalis io* and *Nymphalis urticae,* fly only in the spring and in the late summer and thus the adult stage avoids the adverse effect of mid–summer mowing. In urban areas in Canada both frequent and infrequent mowing events changed the structure and composition of butterfly assemblages such that only some disturbance–adaptable species returned to the mown sites (Hogsden & Hutchinson, 2004).

In contrast to butterflies, the absolute numbers of diurnal moths decreased after the mid–summer mowing but increased again after the vegetation regenerated towards the peak flight period. As a result, no significant differences resulted between the mid– and late–summer mown verges in total species richness, diversity or abundance. These trends reflect the differences between the ecology of two Lepidoptera groups. The high vegetation seems to be particularly important for the diurnal moths, many of which seek hiding or resting places during the day (Saarinen et al., 2005). The recorded diurnal moths form a continuum of species flying solely during the day to species, which fly mostly as a result of being disturbed and are more active at night. The number of individuals decreased after mowing, because hiding places are scarce in low vegetation. Furthermore, diurnal moth individuals searching new resources or habitats are observed in lower numbers during day censuses in comparison to butterflies. Later in the summer the regrowth of vegetation offers an increasing number of hiding places for diurnal moths, while for flowers important to most butterflies and only some diurnal moths it takes a longer time to regenerate. It is noteworthy, however, that the transect method conducted in tall vegetation may underestimate the numbers of diurnal moths hiding. This concerns especially large–bodied species which need longer to warm up,

Table 3. Differences in the physical and surrounding environment between the three management regimes tested by Kruskal–Wallis. Values given to study areas or averages within each study area are used (mid summer mown verges *n* = 11, late summer mown verges *n* = 10, partially mown verges *n* = 12). (For abbreviations see fig. 1.)

Tabla 3. Diferencias en el medio físico y circundante entre los tres regímenes de gestión analizadas por medio del test de Kruskal–Wallis. Se utilizan los valores dados a las áreas de estudio o los promedios dentro de cada área de estudio (márgenes segados a mediados de verano n *= 11, márgenes segados a finales de verano* n *= 10, márgenes parcialmente segados* n *= 12). (Para las abreviaturas ver la fig. 1.)*

	Msm		Lsm		Pm	
	Mean	Std.	Mean	Std.	Mean	Std.
Physical environment (%):						
Road width	13.2	8.6	13.2	6.8	10.3	6.5
Traffic speed (100/80/60/50 km/h)	2/4/4/1		2/1/5/2		2/4/4/2	
Traffic density (0/1/2/3/4)	0/0/4/3/4		0/1/5/1/3		0/2/2/2/5	
Verge width	8.2	3.7	6.9	1.7	6.0	2.0
Verge age	20.7	8.1	19.1	9.5	23.3	5.8
Soil moisture (1/2/3)	1/6/4		1/7/2		3/7/2	
Surrounding environment (%):						
Cultivated fields	17.9	21.6	17.5	20.8	32.3	34.8
Non–cultivated open	39.6	31.0	37.7	28.6	30.1	33.2
Forest	42.5	34.2	44.8	32.3	37.6	35.5

and individuals that are not on the top–layer of the vegetation or are located further from the counter, thus being less sensitive to any disturbance.

Partial mowing is most beneficial for road verge Lepidoptera

The second hypothesis was confirmed only partly, since the partially mown verges had a higher species richness, diurnal moth diversity and butterfly abundance than the two regimes with total mowing, but the differences were significant only compared to the mid–summer mown verges. Based on these results, both the late–summer and the partial–mowing regime can be recommended in road verge management. The lower species richness and abundance, but similar diversity of butterflies in mid–summer mown verges compared to partially–mown verges suggests that the abundant species, in particular, were decreased. On the other hand, the lower species richness and diversity, but similar abundance of diurnal moths suggests that the rare species in particular have suffered from total mowing in mid–summer.

The high Lepidoptera species richness, diversity and abundance in the partially–mown verges is explained by the lowest mowing intensity. A time span of approximately three years since the last total mowing on some partially–mown verges allows communities to recover from the disturbance. The partial mowing leaves untouched resources such as nectar, host plants and hiding places for adults throughout the flying season. In addition, mowing postpones the flowering and the mown part of the verge provides nectar later in the summer. However, the latter impact is likely to be small due to the low number of species and individuals in the late summer. The partial mowing also destroys fewer Lepidoptera offspring than the total mowing and leaves untouched resources in the vicinity for the larvae surviving from the mowing, if they are capable of moving on to a new host plant.

The partial mowing resembles the mosaic–like mowing regime, since it increases variety in mowing intensity and timing on different parts of the verge. The mosaic–like mowing is often suggested as benefiting Lepidoptera (Munguira & Thomas, 1992) and other invertebrates (Morris & Rispin, 1988; Bakker, 1989; Völkl et al., 1993). In the traditional mowing and grazing management, some areas such as the edges and areas around stones, trees and bushes may have remained undamaged more or less regularly, thereby serving as untouched areas for species sensitive to mowing. On the other hand, the low vegetation next to the road, created by the partial–mowing regime, can offer different resources and conditions compared to the taller vegetation further from the road.

Table 4. Plant species status: positive (Po) and negative (Ne) indicator species of semi–natural biotopes, host plant (H) and good nectar plant (N) species.

Tabla 4. Estatus de las especies vegetales: especies indicadoras positivas (Po) y negativas (Ne) de biotopos semi–naturales, especies de plantas huésped (H) y de plantas buenas suministradoras de néctar (N).

Species	Status	Species	Status
Achillea millefolium	N	*Erigeron acer*	Po
Achillea ptarmica	Ne	*Erysimum cheiranthoides*	Ne
Aegopodium podagraria	Ne	*Festuca pratensis*	Ne
Alopecurus pratensis	Ne, H	*Filipendula ulmaria*	H
Angelica sylvestris	N	*Fragaria vesca*	H, N
Antennaria dioica	Po, N	*Galeopsis bifida*	Ne
Anthoxanthum odoratum	H	*Galium album*	Ne
Anthriscus sylvestris	Ne	*Galium verum*	Po
Arctium tomentosum	Ne	*Geranium palustre*	Po
Arctostaphylos uva–ursi	Po	*Geranium sylvaticum*	H, N
Artemisia campestris	Po	*Gnaphalium uliginosum*	Ne
Artemisia vulgaris	Ne	*Heracleum sibiricum*	Po
Barbarea vulgaris	H, N	*Hieracium sp.*	N
Bistorta vivipara	Po	*Hieracium umbellatum*	N
Botrychium lunaria	Po	*Hypericum perforatum*	Po
Calamagrostis epigejos	H	*Hypochoeris maculata*	Po
Calluna vulgaris	Po, H, N	*Juncus conglomeratus*	Ne
Campanula glomerata	Po	*Knautia arvensis*	N
Capsella bursa–pastoris	Ne	*Lathyrus pratensis*	H, N
Cardamine pratensis	Po	*Lathyrus sylvestris*	Po, N
Carduus crispus	Ne, N	*Leontodon autumnalis*	N
Carex ericetorum	Po	*Leontodon hispidus*	Po, N
Centaurea jacea	N	*Leucanthemum vulgare*	N
Centaurea phrygia	N	*Linaria vulgaris*	Ne
Centaurea scabiosa	Po, N	*Lotus corniculatus*	Po
Chenopodium album	Ne	*Luzula pilosa*	Po
Cirsium arvense	Ne, N	*Lychnis viscaria*	Po, N
Cirsium helenioides	N	*Maianthemum bifolium*	Po
Cirsium oleracea	N	*Matricaria matricarioides*	Ne
Cirsium palustre	N	*Melampyrum pratense*	H
Cirsium vulgare	N	*Myosotis arvensis*	Ne
Dactylis glomerata	H	*Myosotis stricta*	Po
Deschampsia cespitosa	H	*Persicaria lapathifolia*	Ne
Deschampsia flexuosa	Po, H	*Phleum pratense*	H
Dianthus deltoides	Po	*Picris hieracioides*	Po
Elymus repens	Ne, H	*Plantago lanceolata*	Po
Epilobium adenocaulon	Ne	*Plantago major*	Ne
Epilobium angustifolium	Ne	*Poa annua*	Ne

Table 4. (Cont.)

Species	Status
Poa pratensis	H
Polygonum aviculare	Ne
Potentilla anserina	Ne, H
Ranunculus polyanthemos	Po
Rumex acetosa	H
Rumex acetosella	H
Rumex crispus	Ne, H
Rumex longifolius	Ne, H
Selinum carvifolia	Po
Solidago virgaurea	N
Sonchus arvensis	Ne, N
Spergula arvensis	Ne
Succisa pratensis	Po, N
Tanacetum vulgare	Ne, N
Taraxacum sp.	Ne, N
Thlaspi caerulescens	Ne
Thymus serpyllum	Po, N
Tragopogon pratensis	Ne
Trifolium arvense	Po
Trifolium aureum	Po
Trifolium hybridum	Ne, H, N
Trifolium medium	H, N
Trifolium pratense	H, N
Trifolium spadiceum	Po
Tripleurospermum inodorum	Ne
Tussilago farfara	Ne
Urtica dioica	Ne, H
Vaccinium vitis–idaea	Po
Verbascum nigrum	Po
Veronica chamaedrys	H
Vicia cracca	H, N
Viola canina	H
Viola palustris	H
Viola riviniana	H
Viola tricolor	Po, H

Table 5. Differences in the vegetation variables between the three mowing regimes: ** 0.01 > P > 0.001, *** P < 0.001; significant differences after sequential Bonferroni correction are marked with *S*; regimes with significant differences in pair–wise comparisons are indicated by separate letter *a* and *b*. (For other abbreviations see fig. 1.)

*Tabla 5. Diferencias en las variables de vegetación entre los tres regimenes de siega: ** 0,01 >* P *> 0,001, **** P *> 0,001, las diferencias signifiativas tras la corrección secuencial de Bonferroni se indican mediante una* S*. Los regímenes con diferencias significativas en las comparaciones pair–wise se indican mediante las letras separadas* a *y* b*. (Para otras abreviaturas ver la fig. 1.)*

	Msm		Lsm		Pm	
	Mean	Std.	Mean	Std.	Mean	Std.
Plant species richness	51.9	9.4	53.1	14.74	59.1	11.9
Positive indicator abundance	3.6	4.3	3.3	3.6	4.7	4.5
Negative indicator abundance	27.2	5.4	24.9	5.8	24.4	5.9
Host plant abundance	23.1	3.4	23.8	6.7	25.4	6.0
Flowering plant abundance**^{S}	49.2^a	15.0	65.4^{ab}	20.5	78.9^b	19.8
Nectar plant abundance***^{S}	22.6^a	7.1	34.4^b	7.1	36.1^b	8.3
Vegetation height**^{S}	25.2^a	5.9	40.6^b	13.8	38.3^b	15.6

Table 6. Correlations between the Lepidoptera numbers and environmental variables of each site: * 0.05 > P > 0.01, ** 0.01 > P > 0.001; significant correlation after sequential Bonferroni correction is marked with S.

*Tabla 6. Correlaciones entre el número de lepidópteros y las variables ambientales de cada lugar: * 0,05 >* P *> 0,01, ** 0,01 >* P *> 0,001; las correlaciones significativas tras la corrección secuencial de Bonferroni se indican mediante una* S.

	Species richness		Abundance	
	Butterflies	Diurnal moths	Butterflies	Diurnal moths
Road width	0.218	–0.222	0.070	0.199
Traffic speed	0.070	–0.254	0.101	–0.158
Traffic density	0.029	–0.296	0.001	–0.197
Verge width	0.442**	–0.024	0.120	0.328
Verge age	–0.091	0.007	–0.112	–0.084
Soil moisture	–0.190	0.051	0.007	0.070
Plant species richness	0.155	0.333	0.050	–0.041
Positive plant indicators	0.305	0.149	0.083	0.026
Negative plant indicators	–0.538**^{S}	–0.027	–0.285	–0.392*
Host plants	0.123	0.282	0.134	0.139
Flowering plants	0.096	0.334	0.322	0.028
Nectar plants	0.218	0.380*	0.482**	0.190
Vegetation height	0.085	0.400*	0.457**	0.254
Open uncultivated	–0.290	–0.285	0.045	–0.242
Open cultivated	–0.436**	–0.108	–0.122	–0.180
Forest	0.525**^{S}	0.200	0.057	0.303

Possibilities in road verge management – a case study on Finnish roads

Regular mowing as required on road verges is expensive. In Finland verge management accounts for 12% of all road management costs (Finnra, 2000) and the annual costs of mowing are approximately 6 million euros (H. Lappalainen, pers. comm.). Thus, lowering the mowing intensity may lead to substantial savings in money and energy. We have made a rough estimation of the potential area of road verges in Finland where the mowing intensity could be lowered without any threat to traffic safety. The estimation is based on the "Road Register" by the Finnish Road Administration (Finnra). It includes data on the length of public roads belonging to different management classes and guidelines for mowing management in particular classes (Finnra, 2000). If special management classes and 15% of roads for which the management data are missing are omitted, the area of annual mowings along public roads covers about 46,000 ha. Using our recommendations, i.e. that mid–summer mowing be replaced with a narrow (2 m) partial mowing, while verges are fully mown in the late summer only, the area of annual mowings would decrease to 39,500 ha. In other words, a 14% reduction in the annually mown area is achieved. This is most likely an underestimate, because the minimum observed verge widths for each management class were used and 15% of public roads for which the management class information was missing potentially make a further contribution to the reduction in the mown area. Changes in management practices for promoting biodiversity usually increase the costs, but this is not necessarily so in road verge management, as demonstrated above.

Conclusions

New methods, ideas and areas should be used to stop the ongoing decline in the biodiversity of European agricultural environments. In northern and central Europe road verges offer a large potential for restorative management and could serve as refuges or alternative habitats for species of semi–natural grasslands (Ouin & Burel, 2002). The majority of Lepidoptera individuals in this study represented meadow species. Factors influencing the quality of road verges as alternative habitats, such as the soil, verge width and topography, can be influenced only in the construction phase. Mowing management, on the other hand, is a factor that can also be readily modified in old road verges. According to our results, lowering the mowing intensity (partial mowing) or delaying the mowing to late summer may have a positive effect on Lepidoptera along road verges without increasing costs or jeopardizing traffic safety. As Lepidoptera are a sensitive indicator group of the invertebrate fauna, other insects are likely to benefit as well.

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References

Anderson, P., 1995. Ecological restoration and creation: a review. *Biological Journal of the Linnean Society*, 56 (supplement): 187–211.

Bakker, J. P., 1989. *Nature management by grazing and cutting: On the ecological significance of grazing and cutting regimes applied to restore former species–rich grassland communities in the Netherlands*. Kluwer Academic Publishers, Dordrecht.

Chandler, C. R., 1995. Practical considerations in the use of simultaneous inference for multiple tests. *Animal Behaviour*, 49: 524–527.

Courtney, S. P. & Duggan, A. E., 1983. The population biology of the Orange Tip butterfly *Anthocharis cardamines* in Britain. *Ecological Entomology*, 8: 271–281.

Dufrene, M. & Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67: 345–366.

Dunning, J. B., Danielson, B. J. & Pulliam, H. R., 1992. Ecological processes that affect populations in complex landscapes. *Oikos*, 65: 169–175.

Erhardt, A., 1985. Diurnal Lepidoptera: sensitive indicators of cultivated and abandoned grassland. *Journal of Applied Ecology*, 22: 849–861.

Feber, R. E., Smith, H. & Macdonald, D. W., 1996. The effects on butterfly abundance of the management of uncropped edges of arable fields. *Journal of Applied Ecology*, 33: 1191–1205.

Finnra, 2000. *Viherhoito tieympäristössä.* Finnish Road Administration (Finnra), Helsinki.

Gerell, R., 1997. Management of roadside vegetation: Effects on density and species diversity of butterflies in Scania, south Sweden. *Entomologisk Tidskrift*, 118: 171–176.

Guido, M. & Gianelle, D., 2001. Distribution patterns of four Orthoptera species in relation to microhabitat heterogeneity in an ecotonal area. *Acta Oecologica*, 22: 175–185.

Helden, A. J. & Leather, S. R., 2004. Biodiversity on urban roundabouts–Hemiptera, management and the species–area relationship. *Basic and Applied Ecology*, 5: 367–377.

Hellström, K., 2004. Variation in grazing tolerance and restoration of meadow plant communities. Ph. D. Thesis, Univ. of Oulu.

Hogsden, K. L. & Hutchinson, T. C., 2004. Butterfly assemblages along a human disturbance gradient in Ontario, Canada. *Canadian Journal of Zoology*, 82: 739–748.

Huldén, L. (Ed.), Albrecht, A., Itämies, J., Malinen, P. & Wettenhovi, J., 2000. *Atlas of Finnish Macrolepidoptera.* Suomen Perhostutkijain Seura, Luonnontieteellinen keskusmuseo, Helsinki.

Kajak, A., Kupryjanowicz, J. & Petrov, P., 2000. Long term changes in spider (Araneae) communities in natural and drained fens in the Biebrza River Valley. *Ekologia (Bratislava)*, 19 (Supplement): 55–64.

Kullberg, J., Albrecht, A., Kaila, L. & Varis, V., 2002. Checklist of Finnish Lepidoptera – Suomen perhosten luettelo. *Sahlbergia*, 6: 45–190.

Kuras, T., Benes, J. & Konvicka, M., 2001. Behaviour and within–habitat distribution of adult *Erebia sudetica sudetica*, endemic of the Hruby Jesenik Mts., Czech Republic (Nymphalidae, Satyrinae). *Nota Lepidopterologica*, 24: 69–83.

Kuussaari, M., Ryttäri, T., Heikkinen, R., Manninen, P., Aitolehti, M., Pöyry, J., Pykälä, J. & Ikävalko, J., 2003. *Significance of power line areas for grassland plants and butterflies.* The Finnish Environment Institute, Helsinki.

Loertscher, M., Erhardt, A. & Zettel, J., 1995. Microdistribution of butterflies in a mosaic–like habitat: The role of nectar sources. *Ecography*, 18: 15–26.

Mahosenaho, T. & Pirinen, T., 1999. *Niittykasvillisuuden perustaminen tieluiskiin. Koetuloksia ja kirjallisuusselvitys.* Tielaitoksen selvityksiä 12/1999, Helsinki.

McCune, B. & Mefford, M. J., 1999. *Multivariate analysis of ecological data, Version 4.0.* MjM software, Gleneden Beach.

Mikkola, K. & Tanner, H., 2001. *Perhospuutarha.* Tammi, Jyväskylä.

Morris, M. G., 1981. Responses of grassland invertebrates to management by cutting. IV. Positive responses of Auchenorhyncha. *Journal of Applied Ecology*, 18: 763–771.

Morris, M. G. & Rispin, W. E., 1988. A beetle fauna of oolitic limestone grassland, and the responses of species to conservation management by different cutting régimes. *Biological Conservation*, 43: 87–105.

Munguira, M. L. & Thomas, J. A., 1992. Use of road verges by butterfly and burnet populations, and

the effect of roads on adult dispersal and mortality. *Journal of Applied Ecology*, 29: 316–329.
Murphy, D. D., Launer, A. E. & Ehrlich, P. R., 1983. The role of adult feeding in egg production and population dynamics of the checkerspot butterfly *Euphydryas editha*. *Oecologia*, 56: 257–263.
New, T. R., 1997. Are Lepidoptera an effective 'umbrella group' for biodiversity conservation? *Journal of Insect Conservation*, 1: 5–12.
Ouin, A. & Burel, F., 2002. Influence of herbaceous elements on butterfly diversity in hedgerow agricultural landscapes. *Agriculture, Ecosystems and Environment*, 93: 45–53.
Ouin, A., Aviron, S., Dover, J. & Burel, F., 2004. Complementation/supplementation of resources for butterflies in agricultural landscapes. *Agriculture, Ecosystems and Environment*, 103: 473–479.
Parr, T. W. & Way, J. M., 1988. Management of roadside vegetation: the long–term effects of cutting. *Journal of Applied Ecology*, 25: 1073–1087.
Persson, T. S., 1995. *Management of roadside verges: vegetation changes and species diversity.* Ph. D. Thesis, Swedish Univ. of Agricultural Sciences, Uppsala.
Pitkänen, M., Kuussaari, M. & Pöyry, J., 2001. Butterflies. In: *Biodiversity of agricultural landscapes in Finland:* 51–68 (M. Pitkänen & J. Tiainen, Eds.). BirdLife Finland Conservation Series (No 3), Helsinki.
Pollard, E. & Yates, T. J., 1993. *Monitoring butterflies for ecology and conservation. The British butterfly monitoring scheme.* Chapman & Hall, London.
Poschlod, P. & WallisDeVries, M. F., 2002. The historical and socioeconomic perspective of calcareous grasslands – lessons from the distant and recent past. *Biological Conservation*, 104: 361–376.
Pullin, A. S., 1987. Changes in leaf quality following clipping and regrowth of *Urtica dioica*, and consequences for a specialist insect herbivore, *Aglais urticae*. *Oikos*, 49: 39–45.
Pykälä, J., 2000. Mitigating human effects on European biodiversity trough traditional animal husbandry. *Conservation Biology*, 14: 705–712.
– 2001. *Maintaining biodiversity trough traditional animal husbandry*. Finnish Environment Institute, Helsinki.
Pywell, R. F., Warman, E. A., Sparks, T. H., Greatorex–Davies, J. N., Walker, K. J., Meek, W. R., Carvell, C., Petit, S. & Firbank, L. G., 2004. Assessing habitat quality for butterflies on intensively managed arable farmland. *Biological Conservation*, 118: 313–325.
Rassi, P., Alanen, A., Kanerva, T. & Mannerkoski, I. (Eds.), 2001. *The 2000 Red List of Finnish Species*. Ministry of the Environment, Finnish Environment Institute, Helsinki.
Ries, L., Debinski, D. M. & Wieland, M. L., 2001. Conservation value of roadside prairie restoration to butterfly communities. *Conservation Biology*, 15: 401–411.
Saarinen, K., Valtonen, A., Jantunen, J. & Saarnio, S., 2005. Butterflies and diurnal moths along road verges: Does road type affect diversity and abundance? *Biological Conservation*, 123: 403–412.
SAS Institute, 1996. *SAS User's Guide: Statistics.* SAS Institute, Cary, NC, USA.
Schaffers, A. P., 2000. *Ecology of roadside plant communities.* Ph. D. Thesis, Wageningen Univ.
Schmitt, T., 2003. Influence of forest and grassland management on the diversity and conservation of butterflies and burnet moths (Lepidoptera, Papilionoidea, Hesperiidae, Zygaenidae). *Animal Biodiversity and Conservation*, 26: 51–61.
Seppänen, E. J., 1970. Suomen suurperhostoukkien ravintokasvit. *Animalia Fennica*, 14: 1–179.
Siegel, S. & Castellan, N. J., 1988. *Nonparametric statistics for the behavioral sciences.* McGraw–Hill, Singapore.
Siepel, H., 1997. Decision–support systems for nature management. *Biodiversity Letters*, 3: 157–161.
Swengel, A. B., 1995. Observations of spring larvae of *Lycaeides melissa samuelis* (Lepidoptera: Lycaenidae) in central Wisconsin. *The Great Lakes Entomologist*, 28: 155–170.
Thomas, J. A., 1995. The conservation of declining butterfly populations in Britain and Europe: priorities, problems and successes. *Biological Journal of the Linnean Society*, 56(Supplement): 55–72.
Vainio, M., Kekäläinen, H., Alanen, A. & Pykälä, J., 2001. *Traditional rural biotopes in Finland. Final report of the nationwide inventory.* Finnish Environment Institute, Helsinki.
Valtonen, A. & Saarinen, K., 2005. A highway intersection as an alternative habitat for a meadow butterfly: effect of mowing, habitat geometry and roads on the ringlet (*Aphantopus hyperantus*). *Annales Zoologici Fennici*, 42: 545–556.
Valtonen, A., Saarinen, K. & Jantunen, J. (in press). Intersection reservations as habitats for meadow butterflies and diurnal moths: Guidelines for planning and management. *Landscape and Urban Planning*.
Van Swaay, C. A. M., 2002. The importance of calcareous grasslands for butterflies in Europe. *Biological Conservation*, 104: 315–318.
Van Swaay, C. A. M. & Warren, M. S., 1999. *Red data book of European butterflies (Rhopalocera).* Nature and Environment, No. 99, Council of Europe Publishing, Strasbourg.
Völkl, W., Zwölfer, H., Romstöck–Völkl, M. & Schmelzer, C., 1993. Habitat management in calcareous grasslands: effects on the insect community developing in flower heads of Cynarea. *Journal of Applied Ecology*, 30: 307–315.
Warren, M. S., 1985. The influence of shade on butterfly numbers in woodland rides, with special reference to the Wood White *Leptidea sinapis*. *Biological Conservation*, 33: 147–164.
Zimmerman G. M., Goetz, H. & Mielke P. W., Jr., 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. *Ecology*, 66: 606–611.