

# **Arthropods in linear elements**

**Occurrence, behaviour and conservation management**

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# **Arthropods in linear elements**

## **Occurrence, behaviour and conservation management**

**Jinze Noordijk**

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C'est une prairie au petit jour, quelque part sur la Terre. Caché sous cette prairie s'étend un monde démesuré, grand comme une planète. Les herbes folles s'y transforment en jungles impénétrables, les cailloux deviennent montagnes et le plus modeste trou d'eau prend les dimensions d'un océan.

Nuridsany C & Pérennou M 1996. *Microcosmos, Le peuple de l'herbe*. Galatée Film – France 2 Cinéma.

'De natuur biedt toch altijd een aangename verkwikking,' sprak Erik, opgewekt rondziend, 'en stelt zelden teleur.' [...] 'Zeer juist,' sprak de mier, die naast hem liep, hem enigszins schichtig aankijkend, 'u slaat daar den spijker wel op den kop.'

Bomans G 1941. *Erik of het klein insectenboek*. Het Spectrum, Utrecht.



## ABSTRACT

Intensification of agriculture and urbanisation have caused large-scale destruction and fragmentation of natural and semi-natural areas in the Netherlands, with a considerable loss of biodiversity. As a consequence, the conservation of the biodiversity in the remaining small landscape elements has become increasingly urgent. This thesis presents the results of our study of arthropods in (mainly) roadside verges. The diversity of species proved to be considerable, with several rare and threatened, as well as many specialised species. These arthropod assemblages should be taken into account during the management of roadside verges. Our research aimed at a better understanding of the distribution and ecology of these species, which enables us to recommend appropriate measures for their conservation.

Roadside verges are often covered by grassland vegetation and need to be mown in order to retain a high biodiversity. We studied ground beetles, weevils, ants and epigeic spiders in experimental plots with five different mowing regimes: no mowing; mowing once a year in autumn with or without removal of the cuttings; mowing twice a year, in early summer and autumn, with and without removal of the cuttings. Plots were located on three different verges which represented a plant productivity gradient, ranging from low-productive, through medium-productive to high-productive grassland. The different mowing regimes had hardly any effect on the biodiversity at the low-productive site, whereas at the medium-productive and high-productive sites, mowing twice a year with removal of the cuttings resulted in the highest arthropod species-richness and abundance. A second experiment carried out on the medium-productive verge showed that mowing twice a year with removal of the cuttings also gave the highest values for flower richness, flower diversity and abundance of flower-visiting insects. Therefore such verges also had the highest number of visits to flowers by insects. On low-productive verges, yearly mowing is not necessary. However, to ensure a high diversity of arthropods on medium-productive to high-productive grassland verges, a regime of mowing twice a year with removal of cuttings is recommended for the largest part of the verge. Small patches of vegetation should be left intact to provide a refuge for arthropods in the period just after mowing when their resources are otherwise almost absent. This type of rotational management will probably improve their chance of survival.

Sandy verges can be important to xerophilic and thermophilic arthropods. These species are in decline due to the fragmentation and decreasing quality of heathland nature reserves. In the past, habitats for these species were numerous in the roadside verges in the Veluwe area. However, now vegetation succession is causing them to disappear and restoration management is urgently needed. We sampled arthropods in patches of grey hair-grass (*Corynephorus canescens*) vegetation on the verges, and found that there were fewer stenotopic ground beetles and spiders than in similar vegetation patches in nature reserves. This seems attributable to

differences in 'habitat quality', namely a denser cover of grass in the verges, as well as more herbaceous plants and tree seedlings. Moreover, any suitable vegetation patches are smaller. In addition, we sampled ground-dwelling and flying ground beetles in open sandy roadside verges and newly-created linear forest clearings. The occurrence of teneral individuals and flightless species indicate that verges may function as 'habitat corridors'. In the forest clearings, teneral individuals were rare, but flying beetles were very abundant: more than twice as many individuals were caught here than in nature reserves and on roadside verges. This indicates that the clearings are used particularly by dispersing ground beetles, and thus function mainly as 'movement corridors'. To make conditions more suitable for xerophilic and thermophilic species in roadside verges, we recommend restoring nutrient-poor zones and recreating pioneer conditions. Subsequently, a regular management of selectively removing encroaching vegetation should be installed. If this is done over large distances, roadside verges can act as habitat corridors. Linear clearings in forests, situated between separate heathland habitat areas can help species bridge short distances between them. In this way, ecological networks can be created in highly fragmented heathland landscapes.

Being relatively straight and narrow, roadside verges have an enormous distance of edge biotopes. We therefore studied edge effects on insect species to obtain more insight into how a verge functions as a habitat. We looked at the effects of the border between the vegetation and asphalt of the road on the direction of movement of two ground beetle species. The road appeared to be a barrier for these species and its presence caused movement patterns parallel to the asphalt. In another study, the number of flying ground beetles increased in linear forest clearings, probably because they are directed by forest edges when dispersing. Both studies provide extra evidence that roadside verges may act as ecological corridors. In addition, we found that flying ants used forest edges to find each other for mating, while their nests were located elsewhere. All these results indicate a substantial effect of edges on insect behaviour and their occurrence. This knowledge can be applied in conservation management.

Roadside verges are distinctive biotopes with anthropogenic disturbances and edge effects that may negatively influence arthropods. However, as roads are an inherent, inevitable part of the densely populated Netherlands landscape, we choose here to emphasise the positive aspects of these linear habitats. Our investigations show that arthropod communities of high conservation interest occur in roadside verges, that verges can be used to create ecological networks, that abrupt biotope edges in verges act as a guide for dispersing insects and are sometimes favoured as a mating site, and that a regular applied mowing scheme provides valuable conditions for arthropods of hay-meadows.



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# 1



## GENERAL INTRODUCTION

### **Arthropod conservation**

The global decline in species concerns all life forms. Arthropods comprise the absolute majority of organisms (May 1992), so it can be concluded that also the majority of the extinctions concerns this group (Dunn 2005). In addition, there are indications that insects, a major group within the arthropods, are more vulnerable and have a higher rate of extinction compared to other groups, so probably they suffer disproportionately from the biodiversity crisis (Thomas & Morris 1994; Thomas *et al.* 2004). Numerous examples can be given of places where local or even complete extinctions of insects have been recorded (e.g., Rents 1977; Lockwood & DeBrey 1990; McCafferty 2001; Cartagena & Galante 2002; Wenzel *et al.* 2006). Unfortunately, the main focus – both of scientist and policy makers – is still on vertebrates and plants (New 1999; Clark & May 2002). Conservation of insects and other arthropods is difficult because of the enormous amount of species, insufficient specialised scientists and little public support (New 1993; Skerl 1999).

Much more awareness should be created on arthropod diversity, the ecosystem functions they provide, and the beauty of species (Fig. 1). Although a slight increase in attention is noticeable, the conservation of the “*little things that run the world*” (Wilson 1987) remains a major challenge (Lewis *et al.* 2007; Leather *et al.* 2008). With this thesis, I intend to stimulate this awareness and to contribute to a more elaborate conservation of arthropods. Our studies mainly concentrate on an omnipresent landscape feature: roadside verges. We studied the influence of management, environmental site conditions and surrounding landscape on the occurrence of spiders and insects in these linear biotopes. In highly populated countries like the Netherlands, nature conservation cannot be restricted to the remaining small and isolated nature reserves. Conservation strategies should aim at ecological improvement of all landscape elements, including highly anthropogenic structures (Novacek & Cleland 2001).



**Figure 1.** Arthropods come in many forms (e.g., the harvestman *Trogulus tricarinatus* (L.) and the bug *Pentatoma rufipes* (L.)), are often very beautiful (e.g., the thread-waisted wasp *Ammophila sabulosa* (L.)), and provide essential ecosystem functions (e.g., the bumblebee *Bombus lucorum* (L.) pollinating Devil's bit scabious).

### Roads in the Netherlands

The Netherlands has the highest density of roads in the world: all roads together extent to almost 135.500 km (CBS 2008). Negative ecological effects of roads on the fauna are numerous and range from direct effects like traffic casualties, to indirect effects resulting from the associated habitat destruction, landscape fragmentation, and changes in habitat quality due to the chemical, noise and light pollution caused by vehicles (for reviews see Forman & Alexander 1998 and Spellerberg 2002 and references therein). Extensive natural areas are essential to preserve our biodiversity, and the absence of roads is one way to keep areas as natural as possible (Gelbard & Harrison 2003). However, in the Netherlands the omnipresence of roads is a fact we have to deal with.

Most roads are bordered by verges; particularly regional roads and highways (Fig. 2) have broad verges where relatively species-rich situations exist or can be realized. Roadside verges outside urban areas cover almost 2% of the total land surface of the Netherlands (Schaffers 2000). With the right management and construction they can be used to increase biodiversity both locally and nationally.



**Figure 2.** Highways and regional roads in the Netherlands. Line thickness reflects traffic intensity.

After the sixties and seventies of the twentieth century, when verges were mown up to seven times a year and herbicides were commonly applied, management practices changed considerably. Since the early eighties, both the construction and management of roadside verges were based more on ecological principles (Sýkora *et al.* 1993). Since then, verges were preferably constructed with nutrient-poor soil, mowing frequency was strongly reduced, and it was recommended to remove the cuttings. The positive effect of this management on the development of valuable vegetation types was later confirmed (e.g., Zonderwijk 1979; Sýkora *et al.* 1993; Schaffers 2000). While initial research at the Wageningen University provided information on the botanical aspects of verges, the knowledge on faunistic aspects of verges remained very limited. Consequently, the main attention at the chair of 'Ecological Construction and Management of Infrastructure' shifted to studies on the importance of verges as habitat for arthropods, the relation between vegetation types and arthropod communities, and the influence of vegetation management and connectivity on arthropod presence and migration. The current thesis was written within this framework.

To increase knowledge on the actual conservation value of road verges, in CHAPTER 2 arthropod species diversity is described and summarized based on ecological studies in roadside verges in the previous ten years. Having done this, management effects on these arthropods is discussed in the following chapters, both for grassland and for heathland verges.



**Figure 3.** Roads are detrimental to ecosystems in many ways; on the other hand their accompanying verges are often the only non-fertilized grasslands in the landscape.

### **Vegetation management in grassy verges**

Most roadside verges are covered by grassland (Fig. 3). As they are never fertilized and are regularly mown with removal of the cuttings, these verges may contain well-developed hay meadows. In the Netherlands, non-fertilized grasslands are at present very scarce, as a result hay meadows in roadside verges currently play an important ecological role for many plant and arthropod species. In intensive agricultural landscapes these verges act (together with e.g., ditches and dike verges) as refuges for many plants and small animals (de Bonte *et al.* 1997; Hoffmann 2005). Way (1977) already stated: *“Whilst all the habitats represented by roadsides are potentially valuable for some species of plants or animals, probably the most valuable contribution that verges make to wildlife conservation is that they include herb-rich grassland”*.

For one of the studies, covering three roadside verges, we installed experimental plots with five different management treatments. These treatments were selected so they would reflect two mowing practises common in roadside verges; hay making once and twice per year, and three forms of ‘neglect’; no management and mowing once or twice per year but without removal of the cuttings (Sýkora *et al.* 2002). In CHAPTER 3, we explore the diversity and abundance of several ground-dwelling arthropod groups – spiders, ants, ground beetles and weevils – in these experimental plots. Relations between management practise, vegetation characteristics and the ground-dwelling fauna were analysed after four years of treatment. In CHAPTER 4, we discuss the effects of the five treatments after three years of application on the diversity and total number of flowers and on the flower-visiting insects. With both studies we aimed to find guidelines for roadside management promoting high arthropod abundance and diversity.

### **Open sandy verges in the Landscape**

Some highway verges on inland sandy soils contain open vegetation characteristic of nutrient-poor soil (Fig. 4). These verges mainly occur in the eastern part of the country, for example in the Veluwe region in the province of Gelderland. In contrast to most grassy verges the soil is more acid and dry and, due to the low fertility,



productivity is low (Schaffers 2002a; 2002b). In addition – and in contrast to many grassy verges – vegetation in these sandy verges is often similar to that of the surroundings: heathland and drift sand nature reserves delimited by forests. This landscape context partly explains the ecological value as expressed by the presence of many rare or threatened species.

Management is very different from that in grassy verges, which are visited yearly by mowing machines. As a consequence of the low productivity of the sandy verges, even with extensive management the vegetation remains open for a long time. In fact, ever since the construction of the four highways on the Veluwe, between 1953 and 1977, management of these verges simply consisted of the occasional removal of some encroaching trees or the occasional mowing of heather at a few selected sites. Only since approximately twenty years, vegetation succession has started to have a negative influence on the thermo- and xerophilic habitats in these verges. These observations suggest that management intervention is necessary to preserve the rare and characteristic species assemblages.

We studied several of these sandy highway verges in the Veluwe region. In CHAPTER 5, we focus on the stenotopic ground beetle and spider species in these verges, and we compared their species richness and composition with that of nearby nature reserves. We focussed on the differences in vegetation characteristics between the verges and the nature reserves, in order to optimise future restoration works aiming at the conservation of characteristic arthropods.

In CHAPTER 6 we discuss the possibilities to increase landscape connectivity for characteristic xero- and thermophilic ground beetle species using linear forest clearings and roadside verges to enlarge the available habitat and to create corridors between suitable areas.



**Figure 4.** A highway verge in the Veluwe region, containing dry, open and warm situations.

## Insect behaviour in linear elements

Roadside habitats can often be classified as edge habitats and as such they experience many so-called edge effects, i.e., deviations in ecological processes and patterns as compared to large stretches of habitat due to the influence of other biotopes in the vicinity. Many edge effects are described in the literature and include deviations in diversity, individual behaviour, ecological interactions, etc. (e.g., McGeoch & Gaston 2000; Ewers & Didham 2008; Larivée *et al.* 2008). As anthropogenic landscapes frequently have a high proportion of edges (often quite 'hard' and straight), the consequences of edge effects on organisms are of high importance, especially in the discipline of road ecology.

To gain more insight into edge effects on insects, we experimentally studied the behaviour of several species. We discuss flight occurrence of ground beetles in small linear forest clearings in the context of ecological corridor construction in CHAPTER 6. Secondly, CHAPTER 7 deals with an experiment on walking directions of the ground beetle species *Agonum sexpunctatum* and *Poecilus versicolor* when confronted with the asphalt of a provincial road at the edge of the bordering vegetation. Likewise, in CHAPTER 8 we studied the behaviour of ant sexuals, winged males and females, in relation to a sharp forest edge and the locations of their nests. These studies provided useful insights for insect conservation in linear elements.

Finally, in CHAPTER 9 various links between the results presented in the previous chapters are discussed. Implications of the results are given and recommendations with a focus on how to integrate arthropods into nature conservation management are presented.

## References

- Cartagena MC & Galante E 2002. Loss of Iberian island tenebrionid beetles and conservation management recommendations. *Journal of Insect Conservation* 6: 73-81.
- CBS 2008. Centraal Bureau voor de Statistiek – Cijfers. Available at [www.cbs.nl](http://www.cbs.nl). [accessed on 8.viii.2008]
- Clark JA & May RM 2002. Taxonomic Bias in Conservation Research. *Science* 297: 191-192.
- de Bonte AJ, Hazebroek E, van den Hengel LC, Keizer P-J, Sýkora KV & Schaminée JHJ 1997. *Botanische kwaliteit van bermen in het agrarische landschap*. Rapport nr. W-DWW-97-092. Rijkswaterstaat, DWW, Delft, the Netherlands.
- Dunn RR 2005. Modern insect extinctions, the neglected majority. *Conservation Biology* 19: 1030-1036.
- Ewers RM & Didham RK 2008. Pervasive impact of large-scale edge effects on a beetle community. *Proceedings of the National Academy of Sciences* 105: 5426-5429.
- Forman RTT & Alexander LE 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29: 207-231.
- Gelbard JL & Harrison S 2003. Roadless habitats as refuges for native grasslands: interactions with soil, aspect, and grazing. *Ecological Applications* 13: 404-415.

- Hoffmann F **2005**. *Biodiversity and pollination – flowering plants and flower-visiting insects in agricultural and semi-natural landscapes*. PhD-thesis, University of Groningen, the Netherlands.
- Larivière M, Drapeau P & Fahrig L **2008**. Edge effects created by wildfire and clear-cutting on boreal forest ground-dwelling spiders. *Forest Ecology and Management* 255: 1434-1445.
- Leather SR, Basset Y, Hawkins BA **2008**. Insect conservation: finding the way forward. *Insect Conservation and Diversity* 1: 67-69.
- Lewis OT, New TR & Stewart AJA **2007**. Insect conservation: progress and prospects. In: *Insect conservation biology* (Stewart AJA, New TR & Lewis OT eds.): 431-436. The Royal Entomological Society / CABI, Wallingford, United Kingdom.
- Lockwood JA & DeBrey LD **1990**. A solution for the sudden and unexplained extinction of the Rocky Mountain grasshopper (Orthoptera: Acrididae). *Environmental Entomology* 19: 1194-1205.
- Losey JE & Vaughan M **2007**. The economic value of ecological services provided by insects. *BioScience* 56: 311-323.
- May RM **1992**. How many species inhabit the earth? *Scientific American* 267: 18-24.
- McCafferty WP **2001**. Status of some historically unfamiliar American mayflies (Ephemeroptera). *Pan-Pacific Entomologist* 77: 210-218.
- McGeoch MA & Gaston KJ **2000**. Edge effects on the prevalence and mortality factors of *Phytomyza ilicis* (Diptera, Agromyzidae) in a suburban woodland. *Ecology Letters* 3: 23-29.
- New TR **1993**. Angels on a pin: Dimensions of the crisis in invertebrate conservation. *American Zoologist* 33: 623-630.
- Novacek MJ & Cleland EE **2001**. The current biodiversity extinction event: scenarios for mitigating and recovery. *Proceedings of the National Academy of Sciences of the United States of America* 98: 5466-5470.
- Rentz DCF **1977**. A new and apparently extinct katydid from Antioch sand dunes. *Entomological News* 88: 241-245.
- Schaffers AP **2000**. *Ecology of roadside plant communities*. PhD-thesis, Wageningen University, the Netherlands.
- Schaffers AP **2002a**. Soil, biomass, and management of semi-natural vegetation I. Interrelationships. *Plant Ecology* 158: 229-246.
- Schaffers AP **2002b**. Soil, biomass, and management of semi-natural vegetation II. Factors controlling species diversity. *Plant Ecology* 158: 247-258.
- Skerl KL **1999**. Spiders in conservation planning: a survey of US natural heritage programs. *Journal of Insect Conservation* 3: 341-347.
- Spellerberg IF **2002**. *Ecological effects of roads*. The land reconstruction and management series, vol. 2. Science Publishers, Enfield, USA.
- Sýkora KV, de Nijs LJ & Pelsma TAHM **1993**. *Plantengemeenschappen van Nederlandse wegbermen*. Stichting Uitgeverij KNNV, Utrecht, the Netherlands.
- Sýkora KV, Kalwij JM & Keizer P-J **2002**. A phytosociological and floristic evaluation of 15-year ecological management of roadside verges in the Netherlands. *Preslia* 74: 421-436.
- Thomas JA & Morris MG **1994**. Patterns, mechanisms and rates of extinction among invertebrates in the United Kingdom. *Philosophical transactions of the Royal society of London, Series B* 344: 47-54.

- Thomas JA, Telfer MG, Roy DB, Preston CD, Greenwood JJD, Asher J, Fox R, Clarke RT & Lawton JH **2004**. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* 303: 1879-1881.
- Way JM **1977**. Roadside verges and conservation in Britain: a review. *Biological Conservation* 12: 65-74.
- Wenzel M, Schmitt T, Weitzel M & Seitz A **2006**. The severe decline of butterflies on western German calcareous grasslands during the last 30 years: a conservation problem. *Biological Conservation* 128: 542-552.
- Wilson EO **1987**. The little things that run the world (The importance and conservation of invertebrates). *Conservation Biology* 1: 344-346.
- Zonderwijk P **1979**. *De bonte berm*. Zomer en Keuning, Ede, the Netherlands.



# 2



# ARTHROPOD RICHNESS IN ROADSIDE VERGES IN THE NETHERLANDS

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**Summary.** Urbanisation and intensification of agriculture have caused large scale destruction of natural and semi-natural areas in Western Europe. Consequentially, the conservation of biodiversity in small landscape units has become a matter of increasing urgency. In this paper, we inventoried the arthropod diversity in roadside verges in the Netherlands and studied the relative importance of these linear elements. In addition, the occurrence of arthropods in roadside verges in other countries was studied by literature research. In the period 1998-2008, we sampled 57 roadside verges. This was mainly done by pitfall trapping, using sweeping nets and insect nets, and by sight observations. For several arthropod groups the majority of the Dutch indigenous species was sampled: ants (56% of the indigenous species), grasshoppers (53%), harvestmen (67%) and two spider families (52 and 68%). For ground beetles, weevils, butterflies, bees, hoverflies and three other spider families, values between 18–41% were found. Considering that only a minute fraction of the vast network of roadsides was sampled, these figures are remarkably high. Roadside verges are occasionally reported to act as dispersal corridors for exotic species, but this could not be confirmed for arthropods in the Netherlands. Several of the arthropod species inventoried in the Dutch verges are classified as threatened: five grasshopper and eleven bee species appear on national Red Lists and six ant species on the IUCN Red List. Also in several other countries roadside verges in intensively used landscapes appear to offer opportunities for arthropod conservation. We conclude that, if rightly managed, roadside verges can serve as an important and valuable arthropod habitat. We therefore strongly recommend taking always into account the conservation of these arthropod assemblages during planning and actual management of roadside verges.

**Key words.** anthropogenic habitats, species diversity, conservation, linear landscape elements

## Introduction

Many Western European countries are densely populated, generally resulting in a large proportion of the country being covered by agricultural lands, urban areas and an extensive network of transportation infrastructure. The increasing human influence on the landscape and the reduction, degradation and fragmentation of more natural areas, have resulted in a rapid decrease of arthropod diversity (e.g., Maes & Van Dyck 2001; Groenendijk & van der Meulen 2004; Thomas & Morris 1994; Brandmayr *et al.* 2008). As these processes continue, all sorts of extensively used landscape elements are becoming increasingly important for the survival of arthropods; e.g., hedges, urban parks, gardens, brownfields, colliery spoil heaps, quarries, power line corridors, roadside and railway verges (e.g., Dover *et al.* 2000; Schwerk & Abs 2002; Beneš *et al.* 2003; Eyre *et al.* 2003; Wats & Larivière 2004; Carpaneto *et al.* 2005; Hollmen *et al.* 2008). However, as small areas are usually not ideal for the conservation of arthropod species that are specialized, have poor dispersal abilities, show high population fluctuations or occupy a high trophic level (Tschamntke *et al.* 2002 and references therein), they can never replace nature reserves.

Roadside verges might well be the most abundant anthropogenic habitat where more or less native plant and animal communities can persist (Bennet 1991; Spellerberg 2002). Several studies in the Netherlands pointed out that a high number of plants (Sýkora *et al.* 1993; Schaffers 2000), reptiles (Zuiderwijk 1989) and small mammals (van der Reest 1989) can be found there. Roadside verges also appear to provide habitat functions for a number of arthropod groups, for instance butterflies (Bink *et al.* 1996) and ground beetles (Vermeulen 1993). The arthropod fauna in roadside verges may include rare and specialized species. For example, in the Netherlands only two populations of the highly threatened butterfly *Maculinea nausithous* (Bergsträsser) exist, and the habitat of both populations comprises large stretches of roadside, channel and railway verges. As a consequence, these particular verges will be incorporated in the Natura 2000 ecological network under the European Habitats Directive and a fine-tuned vegetation management aiming at the survival of these populations is applied (Wynhoff *et al.* 2005, 2007; Ministry of Agriculture, Nature and Food Quality, without date).

During the last decade (1998-2008), we have conducted several ecological studies on arthropods in roadside verges in the Netherlands covering the following topics (among others): the relation between arthropod assemblages and plant species composition (Schaffers *et al.* 2008), overwintering of arthropods in verges (Raemakers *et al.* in prep.), the presence of protected species (Noordijk & Boer, 2007), comparisons with nature reserves (CHAPTER 5 & 6), and effects of vegetation management (CHAPTER 3 & 4).

In this paper, we present an overview of the number of species sampled in verges in comparison to the total species list of the Netherlands, in order to show the relative importance of roadside verges for the conservation of the national arthropod fauna. The presence of threatened (Red List) and exotic species is examined as well.



To put our results in a broader perspective, we discuss some published results on arthropods in roadside verges from other countries.

### Sampling sites and methods

The studies were performed at 57 sites scattered throughout the Netherlands, with an emphasis on the central part of the country (Fig. 1). The sites comprise a gradient in soil moisture content, nutrient richness, degree of ruderalization and species richness. The range consists of various well-developed hay-meadow communities (*Calthion*, *Molinietalia*, *Arrhenatheretalia*), tall-herb communities and ruderalized grasslands (*Valeriano-Filipenduletea*, *Galio-Urticetea*, *Artemisietea*) as well as early and late-stage pioneer and heath communities on dry, nutrient-poor and acid sandy soils (*Corynephorion*, *Thero-Airion* and *Calluno-Genistion*). At all sites pitfall traps were used to catch ground-dwelling arthropods. The number of pitfall traps ranged from 5 to 50 per site and they sampled from spring to autumn in one, two or four consecutive years. Spiders, ground beetles, weevils and grasshoppers were identified to species level. From some sites the ants and harvestmen were identified as well. At most locations sweeping-nets and insect nets were used to sample bees, hoverflies and weevils. Some further species could be added by sight observations during field work, e.g., some grasshoppers and all butterflies were noted this way. More detailed descriptions of the methods used to collect specimens can be found in Raemakers *et al.* (2001), Noordijk (2005, 2006, 2008), Noordijk & Boer (2007), Schaffers *et al.* (2008) and this thesis.



**Figure 1.** Sampling locations in road-side verges from 1998-2008. At all locations pitfall traps were installed to collect arthropods. At most locations additional sweeping net samples were collected (circles), and only for some sites ants and harvestmen were also identified (triangles).

We compared the number of species found in the roadside verges with the total number of indigenous species in the Netherlands, after removing species with only one recorded individual from our dataset. Data on native species was obtained from van Helsdingen (2008) for spiders, H. Wijnhoven (in prep.) for harvestmen, P. Boer (in prep.) for ants, Th. Heijerman (pers. comm.) for weevils, Peeters and Reemer (2003) for bees, the database of the 'Carabid Foundation' for ground beetles, Reemer (2000) for hoverflies, Bos *et al.* (2006) for butterflies, and Kleukers and Krekels (2004) for grasshoppers.

**Table 1.** The numbers of arthropod species found in 57 roadside verges between 1998 and 2008 and the proportion of the total number of species of the respective group in the Netherlands (species lists can be obtained from the authors).

Order	Arthropod group	Family	# species in verges	% of the Dutch fauna
ARANEAE				
		Lycosidae – wolf spiders	22 species	52 %
		Gnaphosidae – ground spiders	21 species	68 %
		Clubionidae – foliage spiders	7 species	30 %
		Thomisidae – crab spiders	14 species	41 %
		Salticidae – jumping spiders	10 species	26 %
		Several spider families <sup>1)</sup>	41 species	26 %
OPILIONES				
		All Harvestmen <sup>2)</sup>	20 species	67 %
HYMENOPTERA				
		Apidae s.l. – bees	63 species	19 %
		Formicidae – ants	35 species	56 %
DIPTERA				
		Syrphidae – hoverflies	61 species	18 %
COLEOPTERA				
		Carabidae – ground beetles	151 species	40 %
		Curculionidae s.l. – weevils <sup>3)</sup>	145 species	24 %
ORTHOPTERA				
		All grasshoppers and crickets <sup>4)</sup>	23 species	53 %
LEPIDOPTERA				
		All butterflies <sup>5)</sup>	25 species	35 %

<sup>1)</sup> Agelenidae, Amaurobiidae, Anyphaenidae, Atypidae, Corinnidae, Dictynidae, Dysderidae, Eresidae, Hahnidae, Liocranidae, Mimetidae, Miturgidae, Philodrominae, Pisauridae, Tetragnathidae, Theridiidae and Zoridae.

<sup>2)</sup> Nemastomatidae, Trogulidae, Ischyropsalididae and Phalangiidae.

<sup>3)</sup> Apionidae, Curculionidae, Dryophthoridae, Eirrhinidae, Nanophyidae, Rhynchitidae

<sup>4)</sup> Tettigoniidae, Gryllidae, Gryllotalpidae, Tetrigidae and Acrididae.

<sup>5)</sup> Hesperidae, Papilionidae, Lycaenidae, Nymphalidae and Pieridae.



**Figure 2.** Roadside verges can be rich in arthropods; common species are (clockwise from upper left): the butterfly *Polyommatus icarus* (Rottemburg), the spider *Clubiona terrestris* Westring, the ground beetle *Carabus monilis* Fabricius, and the weevil *Curculio glandium* (Marsham).

## Results

Altogether, we found 638 species, divided over fourteen recognised groups (Table 1, Fig. 2). In the roadside verges we sampled more than half of the indigenous ground spiders and wolf spiders, grasshoppers, ants and harvestmen species. For ground beetles, weevils, butterflies, bees, hoverflies and three other spider families, values between 18–41% were found.

Some of the observed arthropods are classified as threatened according to policy documents (Table 2, Fig. 3). Six ant species are mentioned on the IUCN Red List (IUCN 2008). In addition, *Formica pratensis* Retzius, *F. rufa* L., *F. polycтена* Förster and *F. truncorum* Fabricius (the last one not being an IUCN Red List species) are protected under the national Flora and Fauna legislation. Five grasshopper and eleven bee species found appear on national Red Lists (Ministry of Agriculture, Nature and Food Quality, 2004). Some bee species from the national Red List were caught with one individual only and are therefore not included in Table 1 and 2. However, as the inventory effort for bees was limited, it seems worthwhile to mention them: *Lasioglossum quadrinotatum* (Kirby) [threatened], *Megachile centuncularis* (L.) [vulnerable], *Nomada fulvicornis* Fabricius [threatened], *Nomada leucophthalma* (Kirby) [vulnerable], *Osmia cornuta* (Latreille) [vulnerable] and *Sphecodes ephippius* (L.)

**Table 2.** Red List insect species encountered with more than one individual during several studies in 57 roadside verges in the Netherlands between 1998 and 2008. The Red List status is given in square brackets (Ministry of Agriculture, Nature and Food Quality 2004 for grasshoppers and bees; IUCN 2008 for ants).

Grasshoppers (Orthoptera)
<i>Chorthippus montanus</i> (Charpentier) [vulnerable]
<i>Gryllotalpa gryllotalpa</i> (L.) [vulnerable]
<i>Oedipoda caerulescens</i> (L.) [vulnerable]
<i>Phaneroptera falcata</i> (Poda) [near threatened]
<i>Stenobothrus lineatus</i> (Panzer) [near threatened]
Ants (Formicidae)
<i>Formica rufa</i> L. [lower risk/near threatened]
<i>Formica polyctena</i> Förster [lower risk/near threatened]
<i>Formica pratensis</i> Retzius [lower risk/near threatened]
<i>Anergates atratulus</i> (Schenck) [vulnerable]
<i>Myrmica hirsuta</i> Elmes [vulnerable]
<i>Formicoxenus nitidulus</i> (Nylander) [vulnerable]
Bees (Apidae s.l.)
<i>Andrena bimaculata</i> (Kirby) [threatened]
<i>Andrena fuscipes</i> (Kirby) [vulnerable]
<i>Andrena gravis</i> Imhoff [threatened]
<i>Andrena humilis</i> Imhoff [vulnerable]
<i>Andrena nigriceps</i> (Kirby) [vulnerable]
<i>Andrena ovatula</i> (Kirby) [vulnerable]
<i>Lasioglossum malachurum</i> (Kirby) [vulnerable]
<i>Nomada bifasciata</i> Olivier [vulnerable]
<i>Nomada fuscicornis</i> Nylander [threatened]
<i>Nomada lathburiana</i> (Kirby) [vulnerable]
<i>Nomada similis</i> Morawitz [vulnerable]



**Figure 3.** Example of two Red List species observed in roadside verges in the Netherlands: the ant *Formica rufa* L. (above) appears on the IUCN Red List, and the grasshopper *Oedipoda caerulescens* (L.) (below) is listed on the national Red List.

[vulnerable]. Undoubtedly, species with similar or higher conservation concern are present among the other sampled groups, but inconspicuousness and lack of knowledge on their status prevents these species from appearing in conservation policies.

Apart from the Red List species, many other interesting arthropods were found. For example, the spider samples from sandy highway verges in the Veluwe region rendered thirteen species previously unreported for the province of Gelderland (Noordijk 2005). The spider wasp *Eoferreola rhombica* (Christ) was discovered for the first time in the Netherlands and the ground spider *Callilepis nocturna* (L.) was found for the first time in more than one hundred years, both in samples from roadside verges (Raemakers & van Helsdingen 2000; Noordijk 2006). Moreover, a socially-parasitic ant species, which was new for science, was discovered in a highway verge and named *Myrmica schenckioides* Boer & Noordijk, 2005. In general, many additional distribution data were obtained for uncommon and rare species.

Not a single exotic species was sampled from the roadside verges. However a few thermophilic species, which have recently reached the Netherlands from more southern countries, were found: the spider *Argiope bruennichi* (Scopoli) (first record in 1980 in the Netherlands) and two harvestmen *Dicranopalpus ramosus* (Simon) (first record in 1993) and *Opilio canestrinii* (Thorel) (first record in 1991). However, with only one sampling site for each species, they were far from abundant in the verges.

## Discussion

Roadside verges in the Netherlands appear to harbour a diverse and species-rich arthropod fauna, including threatened and protected species. For some groups even the majority of the total species list for the Netherlands was present. Considering that only a minute fraction of the vast network of roadside verges was covered by our inventories and that we did not include some major regions of the Netherlands (e.g., five provinces, the dune area along the coast, see Fig. 1), these figures are remarkably high. In addition, the number of recorded species strongly depends on the insect's behaviour in relation to the sampling method. Non-epigeic arthropod species have a lower chance of ending up in pitfall traps, while sweeping-nets and insect nets were not employed everywhere and only part of the arthropod groups under study were collected from these samples. Further targeted sampling in roadside verges would therefore surely have rendered many more species.

So far, roadside verges in the Netherlands had never systematically been checked on the presence of exotic arthropod species. The often reported occurrence and spread of exotic species via roadside verges (e.g., Forsys *et al.* 2002; Gelbard & Belnap 2003; Cameron *et al.* 2007; Lelong *et al.* 2007) could not be affirmed during our studies (see also Tshiguvho *et al.* 1999). In the Netherlands, quite a few exotic arthropod species are found indoors or close to buildings. Yet, our study corroborates the general impression that the number of exotic arthropod species that is capable to survive in (semi-)natural circumstances is very limited. Even the few

'new' thermophilic species that have currently been found in the Netherlands have only been sampled from very few locations and no indication exists that these species particularly use road verges as dispersal corridors. There is little doubt that in more natural areas, the construction of roads and their verges, through disturbance and soil modification, negatively affects the original characteristic biodiversity and might promote the spread of exotic species (Greenberg *et al.* 1997; Johnston & Johnston 2004; Cameron *et al.* 2007; Farji-Brener & Ghermandi 2008). In contrast, we would argue that roadside verges in densely populated and intensively used areas, like most parts of the Netherlands, actually constitute the more 'natural' areas of the landscape. Therefore, they can play an important role as habitat for *indigenous* species (see also Vermeulen 1994).

Besides, we have strong indications that for many species (beetles belonging to numerous families, ants, bees, flies, spiders, etc.), roadside verges truly act as habitats during the entire life-cycle and not just as sinks for populations in the surrounding areas. During several studies we found many species to overwinter and reproduce in these verges (Raemakers *et al.* in prep.; Noordijk & Boer 2007; Noordijk 2008).

### **Studies from other countries**

Dekoninck and Grootaert (2001) made an inventory of a highway verge in the north-eastern part of Flanders in Belgium and found many spiders, ants, flies, butterflies, grasshoppers, ground beetles and bees, including Red List species for many of these groups. They concluded that the studied verge was a true refuge area for arthropod species and of similar conservation value as two nearby nature reserves. Lambrechts *et al.* (2000) and Desender *et al.* (2004) provide species lists for other roadside verges in Belgium; they found several Red List species as well. Le Viol *et al.* (2008), studying a French highway verge stretch of 50 km near Paris, found no less than 123 epigeic spider species. Sayer (2002) investigated the effects of vegetation management on three highway verge sites in Germany and identified species belonging to many invertebrate groups dwelling in the soil, on the ground and in the vegetation. For all groups many species were found and he concluded that the studied sites harbour diverse and typically structured ecological communities. Way (1977) mentioned 25 of the 60 British species of butterflies (42%) and 8 of the 17 species of bumblebees (47%) for roadside verges in Britain. Munguira and Thomas (1992) found 27 butterfly and burnet species in their survey of twelve verges in southern Britain (47% of the indigenous species) including several scarce species. One particular site even harboured 23 species. Helden and Leather (2004) found a species-rich Hemiptera assemblage on eighteen roundabouts in an urban area in Britain. Eversham and Telfer (1994) conclude, after a survey in a roadside in England that many rare and characteristic ground beetles occur and reproduce there, thus providing a true refuge area for these animals. Koivula *et al.* (2005) discuss the conservation potential of road median strips, after finding several rare beetles alongside roads in Helsinki, Finland. Saarinen *et al.* (2005) conclude that roadside verges should be considered important

reserves for butterfly and diurnal moths of semi-natural grasslands, as they found many species of these groups at 51 sites in Finland.

Studies on roadside verges are somewhat less abundant outside Western Europe. Keals and Majer (1991) compared remnants of native vegetation with roadside verges in Australia, and found a similar ant fauna when the verges were relatively wide and covered with native vegetation. Major *et al.* (1999) found that beetle and ant richness and abundance did not differ between roadside verges covered with forests and large forests patches in Australia, although they did find a difference in species composition. Samways *et al.* (1997) and Tshiguvho *et al.* (1999) found that roadside verges carried highest ant diversity in comparison to surrounding urban and agricultural landscape in South-Africa. Both studies stress the conservation value of roadside verges with rich and heterogeneous native vegetation. Ries *et al.* (2001) give insight in the way butterflies use roadside verges in Ohio, USA and conclude that verges with restored prairie vegetation provide habitat for at least some characteristic species. Hopwood (2008) found valuable bee communities in similar roadside verges with restored native prairie vegetation.

## **Conclusion**

Many arthropod species can be found in roadside verges in the Netherlands and in other European countries. Outside Europe it is reported that characteristic arthropod communities in verges covered with native vegetation, can be important complimentary areas next to nature reserves (see also Vermeulen 1993 for the Netherlands). The ecological value of roadside verges and other anthropogenic habitats will however never meet the standard of natural areas or nature reserves and it can not be sufficiently stressed that roads have many detrimental effects on plants and animals (for reviews see Forman & Alexander 1998; Spellerberg 2002). However, due to the dramatic decline in area and quality of more natural landscape units in the Netherlands, it has become urgent to protect species everywhere possible. In our modern landscape, conservation strategies should not be confined to nature reserves but should be applied just as much in areas created and managed for human use (Novacek & Cleland 2001; Bengtsson *et al.* 2003).

Up till now, the conservation of arthropods in roadside verges is hardly ever considered. Given the high number of species present here, this neglect is undeserved. Therefore, we strongly recommend taking into account the conservation of these arthropod assemblages during planning and actual management of roadside verges.

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## References

- Beneš J, Kepka P & Konvička M **2003**. Limestone quarries as refuges for European xerophilous butterflies. *Conservation Biology* 17: 1058-1069.
- Bengtsson J, Angelstam P, Elmquist T, Emanuelsson U, Forbes C, Ihse M, Moberg F & Nyström M **2003**. Reserves, resilience and dynamic landscapes. *Ambio* 32: 389-396.
- Bennett AF **1991**. Roads, roadsides and wildlife conservation: a review. In: *Nature Conservation 2: the Role of corridors* (Saunders DA & Hobbs RJ eds.): 99-117. Surrey Beatty & Sons, Chipping Norton, NSW, Australia.
- Bink FA, Maaskamp FIM & Siepel H **1996**. *Betekenis van wegbermen voor dagvlinders*. Report P-DWW-96024. Rijkswaterstaat, Dienst Weg- en Waterbouwkunde. Delft, the Netherlands.
- Boer P & Noordijk J **2005**. *Myrmica schenckioides* nov. sp., a new socially parasitic ant species (Hymenoptera, Formicidae). *Entomologische Berichten* 65: 120-123.
- Bos F, Bosveld M, Groenendijk D, van Swaay C & Wynhoff I **2006**. *De dagvlinders van Nederland, verspreiding en bescherming (Lepidoptera: Hesperioidea, Papilionoidea)* – Nederlandse Fauna 7. NNM Naturalis, Leiden; KNNV Uitgeverij, Utrecht; EIS-Nederland, Leiden, the Netherlands.
- Brandmayr P, Pizzolotto R, Colombetta G & Zetto T **2008**. In situ extinction of carabid beetles and community changes in a protected suburban forest during the past century: the “Bosco Farneto” near Trieste (Italy). *Journal of Insect Conservation* 13: 231-243.
- Cameron EK, Bayne EM & Clapperton MJ **2007**. Human-facilitated invasion of exotic earthworms into northern boreal forests. *Ecoscience* 14: 482-490.
- Carpaneto G-M, Mazziotta A & Plattella E **2005**. Changes in food resources and conservation of scarab beetles: from sheep to dog dung in a green urban area of Rome (Coleoptera, Scarabaeoidea). *Biological Conservation* 123: 547-556.
- Dekoninck W & Grootaert P **2001**. *Onderzoek naar de faunistische waarde van de autosnelweg te Waasmunster*. Koninklijk Belgisch Instituut voor Natuurwetenschappen. Report ENT.2001.02, Belgium.
- Desender K, Grootaert P, Dekoninck W, Baert L, de Bakker D, Pauly A & Maelfait J-P **2004**. Evaluatie van de natuurwaarden en het graslandbeheer van de bermen langs de noordelijke ring rond Brussel. *Bulletin van de Koninklijke Belgische Vereniging voor Entomologie* 140: 126-139.
- Dover J, Sparks T, Clarke S, Gobbet K & Glossop S **2000**. Linear features and butterflies: the importance of green lanes. *Agriculture, Ecosystems and Environment* 80: 227-242.
- Eversham BC & Telfer MG **1994**. Conservation value of roadside verges for stenotopic heathland Carabidae: corridors or refugia? *Biodiversity and Conservation* 3: 538-545.
- Eyre M, Luff M & Woodward J **2003**. Beetles (Coleoptera) on brownfield sites in England: an important conservation resource? *Journal of Insect Conservation* 7: 223-231.
- Farji-Brener AG & Ghermandi L **2008**. Leaf-cutting ant nests near roads increase fitness of exotic plant species in natural protected areas. *Proceedings of the Royal Society Biological Sciences Series B* 275: 1431-1440.
- Forman RTT & Alexander LE **1998**. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29: 207-231.
- Forys EA, Allen CR & Wojcik DP **2002**. Influence of the proximity and amount of human development and roads on the occurrence of the red imported fire ant in the lower Florida Keys. *Biological Conservation* 108: 27-33.



- Gelbard J & Belnap J **2003**. Roads as conduits for exotic plant invasions in a semiarid landscape. *Conservation Biology* 17: 420-432.
- Greenberg CH, Crownover SH & Gordon DR **1997**. Roadside soils: a corridor for invasion of xeric scrub by nonindigenous plants. *Natural Areas Journal* 17: 99-109.
- Groenendijk D & van der Meulen J **2004**. Conservation of moths in The Netherlands: population trends, distribution patterns and monitoring techniques of day-flying moths. *Journal of Insect Conservation* 8: 109-118.
- Helden AJ & Leather SR **2004**. Biodiversity on urban roundabouts – Hemiptera, management and the species-area relationship. *Basic and Applied Ecology* 5: 367-377.
- Hollmen A, Välimäki P, Itämies J & Oksanen J **2008**. The value of open power line habitat in conservation of ground beetles (Coleoptera: Carabidae) associated with mires. *Journal of Insect Conservation* 12: 163-177.
- Hopwood JL **2008**. The contribution of roadside grassland restorations to native bee conservation. *Biological Conservation* 141: 2632-2640.
- IUCN **2008**. *The IUCN red list of threatened species 2008*. Published on [www.iucnredlist.org](http://www.iucnredlist.org). [accessed on 12.iii.2009]
- Johnston FM & Johnston SW **2004**. Impacts of road disturbance on soil properties and on exotic plant occurrence in subalpine areas of the Australian Alps. *Arctic, Antarctic and Alpine Research* 36: 201-207.
- Keals N & Majer JD **1991**. The conservation status of ant communities along the Wubin-Perenjori corridor. In: *Nature Conservation 2: the role of corridors* (Saunders DA & Hobbs RJ eds.): 387-393. Surrey Beatty & Sons, Chipping Norton, NSW, Australia.
- Koivula MJ, Kotze DJ & Salokannel J **2005**. Beetles (Coleoptera) in central reservations of three highway roads around the city of Helsinki, Finland. *Annales Zoologici Fennici* 42: 615-626.
- Kleukers R & Krekels R **2004**. *Veldgids sprinkhanen en krekels*. KNNV Uitgeverij, Utrecht, he Netherlands.
- Lambrechts J, Verheijen W, Gorssen J & Rutten J **2000**. *Fauna-elementen op de wegbermen langsheen de autosnelweg E314. Eindverslag*. AEOLUS in opdracht van AMINAL afdeling Natuur (Limburg), Belgium
- Lelong B, Lavoie C, Jodoin Y & Belzile F **2007**. Expansion pathways of the exotic common reed (*Phragmites australis*): a historical and genetic analysis. *Diversity and Distributions* 13: 430-437.
- Le Viol I, Julliard R, Kerbiriou C, de Redon L, Carnino N, Machon N & Porcher E **2008**. Plant and spider communities benefit differently from the presence of planted hedgerows in highway verges. *Biological Conservation* 101: 1581-1590.
- Maes D & Van Dyck H **2001**. Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario? *Biological Conservation* 99: 263-276.
- Major RE, Smith D, Cassis G, Gray M & Colgan DJ **1999**. Are roadside strips important reservoirs of invertebrate diversity? A comparison of the ant and beetle faunas of roadside strips and large remnant woodlands. *Australian Journal of Zoology* 47: 611-624.
- Ministry of Agriculture, Nature and Food Quality **2004**. TRCJZ/2004/5727, *houdende vaststelling van rode lijsten flora en fauna*. Published on [www.minlnv.nl](http://www.minlnv.nl). [accessed on 12.iii.2009]
- Ministry of Agriculture, Nature and Food Quality **without date**. <http://www.minlnv.nl/natura2000>. [accessed on 12.iii.2009]

- Munguira ML & Thomas JA **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.
- Noordijk J **2005**. Spinnen van bermen op de Veluwe (Arachnida, Araneae). *Nieuwsbrief Spined* 20: 29-34.
- Noordijk J **2006**. *Callilepis nocturna* (Linnaeus, 1758), *Xysticus acerbus* Thorell, 1872 en *Pardosa proxima* (C.L. Koch, 1874) gevonden bij Heerlen (Araneae, Gnaphosidae, Thomisidae, Lycosidae). *Nieuwsbrief Spined* 22: 20-22.
- Noordijk J **2008**. De fenologie van *Arctosa perita* (Araneae, Lycosidae). *Nieuwsbrief Spined* 25: 30-33.
- Noordijk J & Boer P **2007**. Mieren in Veluwebermen: soortenrijkdom en aanbevelingen voor beheer (Hymenoptera: Formicidae). *Nederlandse Faunistische Mededelingen* 27: 23- 50.
- Noordijk J, Sýkora KV & Schaffers AP **2008**. Conservation value of sandy roadside verges for arthropods – implications for management. *Proceedings of the Netherlands Entomological Society Meeting* 19: 75-93.
- Novacek MJ & Cleland EE **2001**. The current biodiversity extinction event: scenarios for mitigating and recovery. *Proceedings of the National Academy of Sciences of the United States of America* 98: 5466-5470.
- Peeters TMJ & Reemer M **2003**. *Bedreigde en verdwenen bijen in Nederland (Apidae s.l.). Basisrapport met voorstel voor de Rode Lijst*. Stichting European Invertebrate Survey - Nederland, Leiden, the Netherlands.
- Raemakers IP, Schaffers AP, Sýkora KV & Heijerman Th **2001**. The importance of plant communities in road verges as a habitat for insects. *Proceedings of the Section Experimental and Applied Entomology of the Netherlands Entomological Society* 12: 101-106.
- Raemakers IP & van Helsdingen PJ **2000**. De vuurspindoder *Eoferreola rhombica*, een voor Nederland nieuwe spinnendoder, en haar bijzondere waard: de lentevuurspin *Eresus sandaliatus* (Hymenoptera: Pompilidae; Araneae: Eresidae). *Nederlandse Faunistische Mededelingen* 9: 1-6.
- Reemer M **2000**. *Zweefvliegen veldgids*. Jeugdbondsuitgeverij, 's Gravenland, the Netherlands.
- Ries L, Debinski DM & Wieland ML **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.
- Samways MJ, Osborn R & Carliel F **1997**. Effect of a highway on ant (Hymenoptera: Formicidae) species composition and abundance, with a recommendation for roadside verge width. *Biodiversity and Conservation* 6: 903-913.
- Sayer M **2002**. *Einfluss von Pflegemaßnahmen auf die Entwicklung der Tierwelt in Straßenbegleitflächen*. Bundesministerium für Verkehr, Bau- und Wohnungswese, Abteilung Straßenbau, Straßenverkehr, Bonn, Germany.
- Schaffers AP **2000**. *Ecology of roadside plant communities*. PhD-thesis, Wageningen University, the Netherlands.
- Schaffers AP, Raemakers IP, Sýkora KV & ter Braak CJF **2008**. Arthropod assemblages are best predicted by plant species composition. *Ecology* 89: 782-794.
- Schwerk A & Abs M **2002**. The carabid fauna (Coleoptera: Carabidae) of forest stands on colliery spoil heaps. *Baltic Journal of Coleopterology* 2: 15-24.

- Spellerberg IF **2002**. *Ecological effects of roads*. The land reconstruction and management series, vol. 2. Science Publishers, Enfield, USA.
- Sýkora KV, de Nijs LJ & Pelsma TAHM **1993**. *Plantengemeenschappen van Nederlandse wegbermen*. Stichting Uitgeverij KNNV, Utrecht, the Netherlands.
- Thomas JA & Morris MG **1994**. Patterns, mechanisms and rates of extinction among invertebrates in the United Kingdom. *Philosophical Transactions of the Royal society of London, Series B* 344: 47-54.
- Tscharntke T, Steffan-Dewenter I, Kruess A & Thies C **2002**. Characteristics of insect populations on habitat fragments: A mini review. *Ecological Research* 17: 229-239.
- Tshiguvho TE, Dean WRJ & Robertson HG **1999**. Conservation value of road verges in the semi-arid Karoo, South Africa: ants (Hymenoptera: Formicidae) as bio-indicators. *Biodiversity and Conservation* 8: 1683-1695.
- van der Reest PJ **1989**. *Kleine zoogdieren in wegbermen*. Vereniging voor Zoogdierkunde en Zoogdierbescherming, mededeling 1. The Netherlands.
- van Helsdingen PJ **2008**. *Catalogus van de Nederlandse spinnen*. Versie 2008.1. Published on [www.naturalis.nl/spinnen](http://www.naturalis.nl/spinnen). [accessed on 8.viii.2008]
- Vermeulen HJW **1993**. The composition of the carabid fauna on poor sandy road-side verges in relation with comparable open areas. *Biodiversity and Conservation* 2: 331-350.
- Vermeulen HJW **1994**. Corridor function of a road verge for dispersal of stenotopic heathland ground beetles (Carabidae). *Biological Conservation* 69: 339-349.
- Wats CH & Larivière M-C **2004**. The importance of urban reserves for conserving beetle communities: a case study from New Zealand. *Journal of Insect Conservation* 8: 47-58.
- Way JM **1977**. Roadside verges and conservation in Britain: a review. *Biological Conservation* 12: 65-74.
- Wynhoff I, van Swaay C & Boeren J **2005**. Overleven in de wegberm: het Donker Pimpernelblauwtje in Limburg. *Natuurhistorisch Maandblad* 94: 145-149.
- Wynhoff I, Jansen S, Peet N & Vennix H **2007**. *De pimpernelblauwtjes in en rondom de Moerputten 2007*. VS2007.047, De Vlinderstichting, Wageningen, the Netherlands.
- Zuiderwijk A **1989**. *Reptielen in wegbermen: een analyse van 106 locaties*. Instituut Taxonomische Zoologie, UvA / Rijkswaterstaat DWW, Delft, the Netherlands.





3



# EFFECTS OF VEGETATION MANAGEMENT BY MOWING ON EPIGEIC ARTHROPODS

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**Summary.** Species-rich grasslands are rare in the Netherlands and need consistent management to retain their characteristic biodiversity. Roadside verges are important refuges for grassland plants since the mowing management no longer aims at traffic safety only but also strives for botanical diversity. Although arthropods are highly abundant in roadside verges the effect of different mowing practices on this group is largely unknown. During four years we studied ground beetles, weevils, ants and epigeic spiders with pitfall traps in experimental plots in roadside verges with five mowing treatments: no management, and mowing once a year with and without hay removal, and mowing twice a year with and without hay removal. This was done in a plant productivity gradient; the experiment was repeated in a low, medium and high-productive verge. In the low-productive site the effect of management on the arthropods only existed of a higher abundance in plots mown twice per year with hay removal. In the medium and high-productive site, mowing twice a year with hay removal not only resulted in highest abundances but also in highest arthropod species richness. Mowing twice without hay removal and mowing once with removal showed intermediate values, while mowing once per year without removal and particularly the absence of management resulted in low diversity and low abundance. To promote epigeic arthropods in medium to high-productive grassland verges, we recommend a management of mowing twice a year with the removal of hay. It is reasoned that some form of rotational management, aiming at leaving some vegetation refuges intact after mowing events, may further promote arthropod survival. However, caution should be taken that these refuges are not too large, as overall suitability for epigeic arthropods decreases rapidly in such patches. Out of several studied vegetation characteristics, plant inflorescences – number of flowering species in the medium-productive verge and total flower abundance in the high-productive verge – appeared to represent suitable and easily monitored proxies that significantly mirror arthropod diversity.

**Key words.** Araneae, Carabidae, conservation, Curculionidae, diversity, Formicidae, roadside verges, vegetation management

## Introduction

Grasslands can be species-rich ecosystems harbouring plant and animal communities of considerable nature conservation interest. Since in the Netherlands grassland consists of plagic climax vegetation, it must be managed to preserve its specific character and species composition (e.g., Bakker 1989; Dolek & Geyer 2002; Bauer *et al.* 2007; Dekoninck *et al.* 2007; Kampmann *et al.* 2008; Rudmann-Maurera *et al.* 2008). In Western Europe, semi-natural grassland vegetation almost exclusively originates from forms of agricultural land-use, i.e., grazing or hay production. These grasslands are rapidly degrading in ecological quality as traditional land-use is replaced by more intensive forms of agricultural practices (Robinson & Sutherland 2002; Schmitt & Rákossy 2007; Dostálek & Frantík 2008) or as these lands are abandoned resulting in succession to vegetation types with shrub and tree dominance (Delescaille 2005; Schneider & Fry 2005; Öckinger *et al.* 2006; Wenzel *et al.* 2006; Marini *et al.* 2008).

In the Netherlands the biodiversity situation is critical; about two-thirds of the land surface is covered with intensive agricultural areas. In these areas, species-richness is low and many species are restricted to river dikes and verges of roads, railways and water courses, provided these are properly managed (Sýkora *et al.* 1993; CHAPTER 2). Roadside verges occupy a vast area and, together with dikes, comprise the largest area of species-rich grasslands. Sýkora *et al.* (1993, 2002) and Schaffers (2000) provide detailed overviews of the grassland plant communities occurring in Dutch roadside verges. These verges not only act as refuges for many grassland species, but due to their linear outline they may also function as corridors in the highly fragmented landscape of the Netherlands (see also Vermeulen 1994; Tikka *et al.* 2001; CHAPTER 6).

Grassy roadside verges are generally managed by mowing, not only to secure traffic safety, but also to maintain high plant diversity. A lack of biomass removal rapidly leads to a change in plant composition and generally a decrease in species-richness (Bobbink *et al.* 1998; Schaffers *et al.* 1998). This is mainly caused by the high atmospheric nitrogen deposition. Although the effects of mowing management are well studied for plant species composition and diversity, effects on arthropods are insufficiently known (WallisDeVries *et al.* 2002; Dennis *et al.* 2007). More insight is urgently needed to be able to formulate guidelines for conservation and management of arthropods, also since there are indications that they are more vulnerable and have a higher rate of extinction compared to other groups of organisms (Thomas & Morris 1994; Thomas *et al.* 2004).

It is impossible to study all arthropod groups in one research project as arthropods are very rich in species, with a myriad of different life strategies and niches (Morris 1981; New 1995; Di Giulio *et al.* 2001; Samways 2005). In this paper, we study the effects of mowing management on the diversity and abundance of four arthropod groups often inhabiting the ground-level of the vegetation: spiders, ground beetles, ants and weevils. These groups are rich in species, and involve different feeding guilds and life-history traits. During four years we studied the



effects of five grassland mowing treatments in experimental plots on the arthropod groups mentioned, as well as on changes in vegetation characteristics.

## Material & Methods

### *Study sites and experimental design*

The experiment was conducted in three highway verges, reflecting a gradient in nutrient-richness of the soil (Fig. 1). The three sites will be referred to in this paper as 'low-productive', 'medium-productive', and 'high-productive'. The low-productive site is located on a sand and gravel body next to highway A15 in the east of the Netherlands (Province of Gelderland close to the town Bemmelen, 51°54'N - 5°54'E). The sand-body is intended for future widening of the road and this location harbours scarce vegetation of the *Festuca ovina* subsp. *cinerea* type [*Trifolio-Festucetalia ovinae*]. Plant biomass production is very low: around 80 g/m<sup>2</sup> per year (measured in mid-September). The medium-productive verge is located on a lime-rich soil alongside highway A76 in the most southern region of the Netherlands (Province of Limburg, close to the city Heerlen, 50°51'N - 5°57'E). The vegetation consists of a species-rich hay-meadow *Arrhenatheretum elatioris*, with a plant biomass production of around 670 g/m<sup>2</sup> per year (measured in mid-September). The high-productive verge is situated on dense river-clay soil, alongside highway A15 in the east of the Netherlands (Province of Gelderland close to the town Valburg, 51°54'N - 5°48'E). This verge is covered with a *Arrhenatheretum elatioris* hay-meadow and plant biomass production is around 780 g/m<sup>2</sup> per year (measured in mid-September).

In the years before the start of the experiment, both the low-productive and the high-productive site were mown for hay twice a year. The medium-productive site was not mown in the four years before the start of our experiment but had been under a regular mowing regime before that. In each site, a 300 m long stretch of initially homogenous vegetation was subdivided into 25 contiguous plots of 12 by 15 m for the application of five different management treatments, each replicated five times in a randomised-block design. Treatments were: no management (0), mowing once a year in early autumn with or without hay removal (1M+ or 1M), and mowing twice a year in early summer and early autumn with or without hay removal (2M+ or 2M). These treatments reflect common management practises in Dutch roadside verges (1M+, 2M+) and forms of neglect or irregular management (0, 1M, 2M) (Sýkora *et al.* 2002). Management treatments started in 2004 and the last measurements were carried out in 2007 (the fourth year of the treatments). During the entire experiment, the vegetation surrounding the plots was uniformly managed by hay-making once (for the medium-productive) or twice a year (for the low- and high-productive sites).



**Figure 1.** The three roadside verge locations: the low-productive (above left), the medium-productive (above right) and the high-productive (below left). Mowing of the plots was done with small machinery (below right).

#### *Arthropod sampling*

We sampled arthropods with pitfall traps; both in 2003 (the year before the start of the different mowing regimes) and in 2005 and 2007 (while the plots were managed for the second and fourth year). The pitfall traps had a diameter of 8.5 cm, were partly filled with a 3% formol solution and had a plastic cover approximately 2 cm above them to keep out the rain. In the middle of each plot two traps were placed separated by 4 m; the contents of which were bulked to make one sample. Each of the sampling years, the traps were opened during four periods of fourteen days: from the end of March to the beginning of April, from the end of May to the beginning of June, in mid-August and from the end of September to the beginning of October. All ants (Hymenoptera: Formicidae), ground beetles (Coleoptera: Carabidae), weevils (Coleoptera: Curculionidae) and epigeic spiders (Araneae; see Table 1 in CHAPTER 2 for the spider families concerned) were identified to species-level and counted. The catches from the different periods in one year were pooled for each plot. The diversity analysis was run with the four groups pooled; while for the analysis on the arthropod abundances, we omitted the ant abundances, since these numbers mainly reflect distances to nests and not abundance in the plots.

*Vegetation characterisation*

We studied several variables in order to find easily measurable/observable vegetation characteristics that would reflect arthropod richness. During the three years in which arthropods were sampled, we made vegetation relevés of 4 by 6 m in the middle of each plot. For this, the locations were visited twice in those years. Plant species occurrence was noted. In 2007 several additional characteristics were noted both in June and September. We counted flowers and flowering species in the whole plot. To determine standing biomass the vegetation was clipped at ground level in four 1 by 1 m areas in the plots (not in the middle 4 by 6 m where vegetation relevés were made), after which the biomass was dried for 72 h at 80 °C and weighted. Vegetation height was measured at fifty points in each plot with a 10 cm diameter, 6.9 g polystyrene ring (drop-disk) that was dropped down over a wooden rule and the height at which it came to rest in the vegetation was recorded. We used the standard deviation of these height measurements as an indication of local heterogeneity.

*Analysis*

We used GLM models and LSD post-hoc tests to analyse differences in arthropod species diversity and abundance, and vegetation characteristics, in relation to management treatments. Furthermore, multiple stepwise regression was used to detect vegetation variables significantly correlated with arthropod diversity. All analyses were performed in SPSS 15.0. Data of arthropod diversity and abundance, and of most vegetation characteristics, were ln transformed to meet statistical requirements. Block was always incorporated as random factor in the models when analysing means per location.

**Table 1.** Average number of species caught in the plots at the three locations under the studied management treatments. Means are based on the back-transformed values of the estimated marginal means of the GLM tests. Values not sharing the same letter are different for that year ( $P < 0.05$ ). Test statistics for the significant GLM tests (in bold in this table) are given in the text.

Location & year		0	1M	2M	1M+	2M+
<b>low-productive verge</b>						
2003	# species	23.755	19.959	21.576	20.262	20.537
2005	# species	22.340	23.321	23.670	21.770	22.966
2007	# species	22.886	21.612	25.149	22.259	22.358
<b>medium-productive verge</b>						
2003	# species	30.110	31.187	32.553	27.052	36.448
2005	# species	<b>33.459<sup>ab</sup></b>	<b>31.116<sup>a</sup></b>	<b>35.895<sup>b</sup></b>	<b>35.687<sup>b</sup></b>	<b>40.367<sup>c</sup></b>
2007	# species	<b>29.140<sup>a</sup></b>	<b>35.146<sup>ab</sup></b>	<b>39.390<sup>b</sup></b>	<b>38.394<sup>b</sup></b>	<b>42.301<sup>b</sup></b>
<b>high-productive verge</b>						
2003	# species	27.217	28.404	26.502	25.089	28.724
2005	# species	<b>18.518<sup>a</sup></b>	<b>20.613<sup>ab</sup></b>	<b>21.988<sup>ab</sup></b>	<b>20.921<sup>ab</sup></b>	<b>25.396<sup>b</sup></b>
2007	# species	<b>12.038<sup>a</sup></b>	<b>12.855<sup>a</sup></b>	<b>16.550<sup>ab</sup></b>	<b>16.244<sup>ab</sup></b>	<b>20.658<sup>b</sup></b>

## Results

### *Arthropod diversity in the experimental plots*

During the entire experiment, we found 50 spider, 93 ground beetle, 62 weevil, and 19 ant species. Diversity results and possible differences between management treatments for the separate groups are given in Appendix A. Before application of the treatments (data on 2003), no differences could be found in overall arthropod diversity between the plots that would later receive a different management ( $F_{4,8} = 1.76$ ,  $P = 0.230$ ). However, a strong location effect was found ( $F_{2,8} = 37.12$ ,  $P < 0.001$ ); the medium-productive verge was richest in species; followed by the high-productive site and the low-productive site (see also Table 1). No interacting effects between the two was found (management  $\times$  location  $F_{8,60} = 1.28$ ,  $P = 0.269$ ).

During the second year of applying the mowing regimes (data on 2005), effects of management became visible, but not significantly so ( $F_{4,8} = 3.24$ ,  $P = 0.074$ ). Location effects were much stronger ( $F_{2,8} = 81.31$ ,  $P < 0.001$ ). A significant interacting effect between the two was found (management  $\times$  location  $F_{8,60} = 2.16$ ,  $P = 0.043$ ), asking for separate within-location analyses. At the low-productive site no management effects were found ( $F_{4,16} = 0.95$ ,  $P = 0.463$ ), while at the medium and the high-productive site effects on arthropod diversity were significant (respectively  $F_{4,16} = 6.38$ ,  $P = 0.003$  and  $F_{4,16} = 3.86$ ,  $P = 0.022$ ) (Table 1).

During the last year of the experiment (2007; representing the fourth year of treatment application) management effects on arthropod diversity were also clearly visible, but not significant at the 5% level ( $F_{4,8} = 3.44$ ,  $P = 0.064$ ). Location effects were strong again ( $F_{2,8} = 72.35$ ,  $P < 0.001$ ). No significant interaction effect between the two was found (management  $\times$  location  $F_{8,60} = 1.57$ ,  $P = 0.152$ ). However, when analysing the three locations separately, the medium-productive site again showed significant management effects ( $F_{4,16} = 4.42$ ,  $P = 0.014$ ), the high-productive site showed a weak effect ( $F_{4,16} = 2.83$ ,  $P = 0.060$ ), while no effects of management could again be detected for the low-productive verge ( $F_{4,16} = 1.86$ ,  $P = 0.167$ ) (Table 1). Effects of management on arthropod diversity therefore depend strongly on site productivity. In both the high- and medium-productive verge diversity was highest under a 2M+ management and decreased in the order 2M, 1M+, 1M to 0.

In the low-productive verge, overall species richness increased with time when comparing 2003 and 2007 ( $F_{1,44} = 6.06$ ,  $P = 0.017$ ). In the medium-productive verge, overall species diversity increased over the course of the experiment ( $F_{1,44} = 7.28$ ,  $P = 0.010$ ). In the high-productive verge, diversity decreased in all plots ( $F_{1,44} = 64.98$ ,  $P < 0.001$ ), including the ones with a 2M+ management, the same management that the entire verge received prior to the experiment (Table 1).

**Table 2.** Average abundance (activity-density) of ground beetles, weevils and spiders caught in the plots at the three locations under the studied management treatments. Means are based on the back-transformed values of the estimated marginal means of the GLM tests. Values not sharing the same letter are different for that year ( $P < 0.05$ ). Test statistics for the significant GLM tests (in bold in this table) are given in the text.

Location & year		0	1M	2M	1M+	2M+
<b>Low-productive verge</b>						
2003	abundance	185.082	153.239	158.001	147.791	165.075
2005	abundance	316.841	292.598	318.557	289.108	320.025
2007	abundance	<b>163.924<sup>a</sup></b>	<b>164.317<sup>a</sup></b>	<b>182.363<sup>a</sup></b>	<b>168.410<sup>a</sup></b>	<b>252.144<sup>b</sup></b>
<b>Medium-productive</b>						
2003	abundance	236.465	199.737	235.851	219.510	252.346
2005	abundance	<b>151.079<sup>a</sup></b>	<b>179.684<sup>a</sup></b>	<b>268.003<sup>b</sup></b>	<b>260.656<sup>b</sup></b>	<b>348.487<sup>b</sup></b>
2007	abundance	<b>104.606<sup>a</sup></b>	<b>178.145<sup>b</sup></b>	<b>241.918<sup>c</sup></b>	<b>323.694<sup>d</sup></b>	<b>394.414<sup>d</sup></b>
<b>High-productive</b>						
2003	abundance	234.534	220.434	239.559	233.038	288.011
2005	abundance	<b>276.165<sup>a</sup></b>	<b>209.726<sup>ab</sup></b>	<b>186.569<sup>b</sup></b>	<b>175.00<sup>b</sup></b>	<b>384.522<sup>ac</sup></b>
2007	abundance	<b>72.952<sup>a</sup></b>	<b>72.690<sup>a</sup></b>	<b>108.051<sup>ab</sup></b>	<b>141.119<sup>bc</sup></b>	<b>209.893<sup>c</sup></b>

#### *Arthropod abundance in the experimental plots*

In the initially homogenous roadside verges (data on 2003), some differences could nevertheless be found in arthropod abundance between the plots that would later receive different management treatments ( $F_{4,8} = 4.37$ ,  $P = 0.036$ ). However, post-hoc tests could not significantly reveal differences between any treatment pair (Table 2). In addition, a strong location effect was found ( $F_{2,8} = 59.18$ ,  $P < 0.001$ ); the high-productive verge harboured greatest epigeic arthropod abundance; followed by the medium-productive site and the low-productive site (see also Table 2). No interaction effect between management and location was found (management  $\times$  location  $F_{8,60} = 0.28$ ,  $P = 0.970$ ).

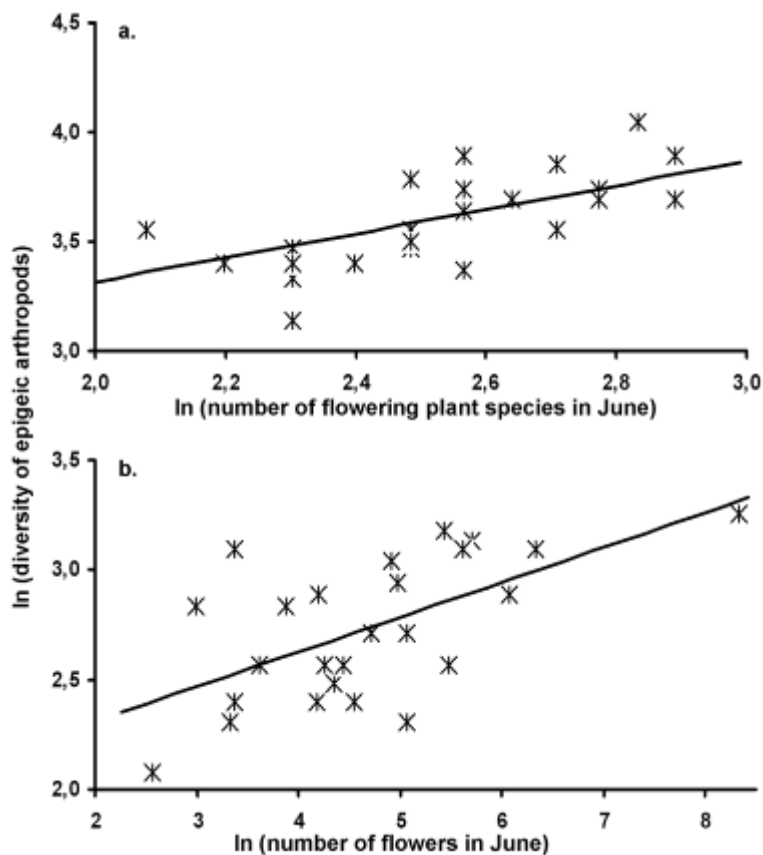
During application of the five mowing regimens for the second year, differences in arthropod abundance were not visible ( $F_{4,8} = 1.60$ ,  $P = 0.265$ ). Overall location effects disappeared ( $F_{2,8} = 2.06$ ,  $P < 0.190$ ) but management effects differed between locations (management  $\times$  location  $F_{8,60} = 3.61$ ,  $P = 0.002$ ), asking for within-location analyses. At the low-productive site no management effects were found ( $F_{4,16} = 0.41$ ,  $P = 0.799$ ), while at the medium- and high-productive site effects on arthropod abundance were significant (respectively  $F_{4,16} = 7.48$ ,  $P = 0.001$  and  $F_{4,16} = 7.21$ ,  $P = 0.002$ ) (Table 2).

In 2007, arthropod abundance was clearly affected by both management ( $F_{4,8} = 7.47$ ,  $P = 0.008$ ) and location ( $F_{2,8} = 12.18$ ,  $P = 0.004$ ) while also the interaction between these two proved significant ( $F_{8,60} = 3.02$ ,  $P = 0.007$ ). When analysing the locations separately an effect of management could be found at each of them: the low-productive ( $F_{4,16} = 6.32$ ,  $P = 0.003$ ), medium-productive ( $F_{4,16} = 35.30$ ,  $P < 0.001$ ), and high-productive site ( $F_{4,16} = 7.64$ ,  $P = 0.001$ ) (Table 1). At all three locations arthropod abundance was highest under a 2M+ management and for the medium and high-productive sites decreased in the following order: 1M+, 2M, and 1M or 0 (Table 2).

### Correlations between arthropods and vegetation characteristics

Many vegetation characteristics in the verges showed differences related to management in 2007 (Appendix B). For the low-productive verge the patterns herein seemed not very clear. However, for the medium and high-productive verge similar patterns appear. When comparing only the extreme treatments 0 and 2M+ respectively, plant species richness, flowering plant species richness and flower abundance increased, while standing biomass, vegetation height and local heterogeneity decreased. The other treatments took intermediate positions, in orders varying between the different vegetation characteristics (Appendix B; CHAPTER 4; Sýkora *et al.* in prep).

When using these variables in stepwise linear regression per location, to find the variables most related to arthropod diversity, two significant correlations were found. For the low-productive verge none of the measured variables appeared to show a relationship with arthropod diversity; this is not surprising since arthropod diversity (and most vegetation characteristics) did not differ between treatments. For the medium-productive site, the number of flowering species in June alone ( $t = 4.03$ ,  $P = 0.001$ ) gave the best regression model with diversity ( $R^2 = 0.43$ ,  $P = 0.001$ ) (Fig. 2a). For the high-productive verge, the number of flowers in June alone ( $t = 3.62$ ,  $P = 0.001$ ), gave the best model ( $R^2 = 0.36$ ,  $P = 0.001$ ) (Fig. 2b).



**Figure 2.** The relationship between two vegetation characteristics and epigeic arthropod diversity for a.) the medium-productive verge and b.) the high-productive verge.

## **Discussion**

### *Epigeic arthropods and grassland management*

Roadside verges can be important arthropod habitats as illustrated again by the many species found during this study. Several (very) rare spiders and insects were sampled (CHAPTER 9) indicating that roadside verges not only harbour common species, but arthropods with high conservation concern as well. Also for grassland roadside verges in other studies, the presence of important insect communities has been proven (Way 1977; Munguira & Thomas 1992; Ries *et al.* 2001; Hopwood 2008).

Except in the low-productive site, the management type that rendered highest epigeic arthropod diversity was the most intensive one: hay-making twice a year (see also Chambers & Samways 1998; Marini *et al.* 2008). Most probably this can be explained by the fact that the epigeic poikilothermic animals studied prefer situations where much sunlight can reach the ground (e.g., van Wingerden *et al.* 1991; Bell *et al.* 2001; Schwab *et al.* 2002). In plots with a 2M+ management plant standing-biomass is lowest and light penetration is consequently highest (Schaffers 2002). The 1M+ treatment also gives 'thin' vegetation, while in the 2M+ treatment plants are cut twice, allowing for the sun to reach ground-level during a substantial part of the year. So both mowing regimes resulted in relatively high arthropod numbers. In addition to the arthropod results, the 2M+ management also rendered highest plant diversity (see also Parr & Way 1988, Sýkora *et al.* 2002). High plant species richness indicates that many micro-scale differences are present at ground level to allow diverse communities, which in turn might apply to arthropods as well. Open sward vegetation often contain many herb species and fewer grasses, likely explaining why arthropod diversity was most correlated with flower diversity or abundance (the latter two are often interrelated - CHAPTER 4). Thus, with mowing and removal of the cuttings, roadside verges retain their hay-meadow characteristics with both high epigeic arthropod species richness and plant diversity. When no reductions in atmospheric nitrogen depositions can be realised, such an intensive management remains necessary (Terry *et al.* 2004; Wamelink *et al.* 2007). Long-term vegetation studies in the Netherlands have shown that in some verges productivity can still increase under a 2M+ management (van de Haterd *et al.* 2009), so to retain or decrease productivity levels an even more intensive management might occasionally be desired. Under low-productive conditions the need for frequent management is not imperative; the vegetation does not change quickly, allowing for species diversity to persist longer without management (see also Noordijk *et al.* 2008; CHAPTER 5). The thresholds in productivity that allow a 2M+ management to be replaced by a 1M+ regime or a more extensive form of management without diversity loss requires further research.

Pitfall trap catches should be interpreted with some caution. Vegetation density at ground-level might affect the activity of invertebrates and therefore the number of individuals caught (Greenslade 1964; Thomas *et al.* 2006). However, this would affect only the abundance data and will hardly affect our diversity analyses as

these are based only on the presence or absence of species. Moreover, at the medium-productive site we performed an additional experiment on weevils, where we did not measure activity-density but actual abundance as revealed by sweeping net samples. These data are clearly in accordance with the pitfall trap results presented in this paper: the 2M+ plots harboured most weevil species as well as highest abundance, probably caused by the highest plant diversity in these plots (CHAPTER 9; Heijerman & Noordijk in prep).

#### *Arthropods and mowing*

Mowing can have substantial direct effects on arthropods (Morris 2000 and references therein). Obvious examples are casualties of the mowing machines, damage to constructions like spider webs or ant nests, removal of nectar and pollen food sources for flower-visiting insects, changes in micro-climate affecting arthropods that can not seek another suitable site like less-mobile larva and pupa, homogenisation of the vegetation with loss of many micro-habitats, etc. (e.g., Gibson *et al.* 1992; Caittin *et al.* 2003; Morris *et al.* 2005; Gardiner & Hill 2006). Consequently, we can assume that some form of rotational management might be needed to secure hiding places, food resources and survival of sufficient individuals.

Generally, rotational management schemes exclude a part of the area from mowing each year; a small strip or just patches that may provide refuge (e.g., Munguira & Thomas 1992; Thorens 1993; Valtonen & Saarinen 2005; Humbert *et al.* 2009). Although low vegetation with an open sward is most beneficial to epigeic arthropod diversity, tall grassland is preferred by various other species (Morris & Lakhani 1979; Morris & Plant 1983; Brown *et al.* 1992; Gibson *et al.* 1992; Sayer 2002). Leaving some parts of the verges occasionally un-mown, would therefore not only increase the survival of many arthropods, but would allow other (non-epigeic) species to persist as well. Nevertheless, also arthropods living high in the vegetation could suffer from stress when typical open sward vegetation is lost (van Wingerden *et al.* 1992).

In our experiment, overall diversity increments were observed in the low-productive site, possibly caused by the 'rotational' mowing scheme created by the experimental plots. In the medium-productive verge, before the first year of sampling (reference year) the vegetation had been left un-mown for four years. It can be clearly seen that all treatments except 'no management', can be considered as a form of restoration management, resulting in increasing species richness. In the high-productive site diversity decreased significantly during the course of the experiment, even in the plots still receiving the original 2M+ management. Probably the plots that did not receive 2M+ management had a significant negative effect on the neighbouring plots that did receive this management, warranting that patches with less intensive forms of mowing should not be too large. Our results demonstrate that a lack of management rapidly results in a decrease in hay-meadow species in medium and high-productive verges; hay-making twice a year should therefore be common practise in the largest part of the verge. The apparent devil's dilemma



between inducing mortality by cutting and maintaining habitat quality on the one hand and reducing the intensity of management on the other hand appears not difficult to solve under the high atmospheric nitrogen stress in the Netherlands. The indirect benefits of hay-making clearly outweigh the direct negative aspects for epigeic arthropods, at least in medium to high-productive grasslands. Less intensive management regimes lead to a decrease in epigeic arthropod (and plant) richness already within the few years this experiment lasted.

#### *Management recommendations*

In medium to high-productive roadside verges, hay-making in early summer and autumn appears necessary to retain valuable species-rich hay-meadows not only from a floristic point of view, but also where epigeic arthropods are concerned. Management effects strongly depend on the nutrient-richness of the site (see also Kondoh 2001); e.g., a more extensive management may be acceptable in low-productive vegetation, whereas a management of neglect is very harmful at high-productive sites. Rotational management will undoubtedly provide additional opportunities for arthropods to survive in roadside verges, but care should be taken that the largest parts of the verges receive hay-making management twice a year. An easy solution might be offered by the many ditches running parallel to roadside verges. These ditches are managed by water boards, and if mown in a different period or with a different intensity as the roadside verge, a rotational scheme is already in practice. Flower richness and abundance in June appears a very suitable proxy for epigeic arthropod richness. This is important information for roadside management organisations aiming at high arthropod diversity. Differences in flower abundance and composition are much easier to quantify than arthropod presence. In grassy verges, management for botanical diversity largely coincides with management for epigeic arthropod diversity.

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#### **References**

- Bakker JP **1989**. *Nature management by grazing and cutting*. Geobotany 14. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Baur B, Cremene C, Groza G, Schileiko AA, Baur A & Erhardt A **2007**. Intensified grazing affects endemic plant and gastropod diversity in alpine grasslands of the Southern Carpathian mountains (Romania). *Biologia, Bratislava* 62: 438-455.
- Bell JR, Wheeler CP & Cullen WR **2001**. The implications of grassland and heathland management for the conservation of spider communities: A review. *Journal of Zoology* 255: 377-387.

- Blake S, Foster GN, Eyre MD & Luff ML **1994**. Effects of habitat type and grassland management practises on the body size distribution of carabid beetles. *Pedobiologia* 38: 502-512.
- Bobbink R, Hornung M & Roelofs JGM **1998**. The effects of airborne pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology* 86: 717–738.
- Brook AJ, Woodcock BA, Sinka M & Vanbergen AJ **2008**. Experimental verification of suction sampler capture efficiency in grasslands of differing vegetation height and structure. *Journal of Applied Ecology* 45: 1357-1363.
- Brown VK, Gibson WD & Kathirithamby J **1992**. Community organisation in leaf hoppers. *Oikos* 65: 97-106.
- Cattin MF, Blandenier G, Banasek-Richter C & Bersier LF **2003**. The impact of mowing as a management strategy for wet meadows on spider (Araneae) communities. *Biological Conservation* 113: 179-188.
- Chambers BQ & Samways MJ **1998**. Grasshopper response to a 40-year experimental burning and mowing regime, with recommendations for invertebrate conservation management. *Biodiversity and Conservation* 7: 985-1012.
- Dekoninck W, de Koninck H, Baugnee JY & Maelfait J-P **2007**. Ant biodiversity conservation in Belgian calcareous grasslands: active management is vital. *Belgian Journal of Zoology* 137: 137-146.
- Delescaille LM **2005**. La gestion des pelouses sèches en Région wallonne. *Biotechnologie, Agronomie, Société et Environnement* 9: 119-124.
- Dennis RLH, Shreeve TG & Sheppard DA **2007**. Species conservation and landscape management: a habitat perspective. In: *Insect conservation biology* (Stewart EJE, New TR & Lewis OT eds.): 92-126. CABI, Wallingford, United Kingdom.
- Di Giulio M, Edwards PJ & Meister E **2001**. Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *Journal of Applied Ecology* 38: 310-319.
- Dolek M & Geyer A **2002**. Conserving biodiversity on calcareous grasslands in the Franconian Jura by grazing: a comprehensive approach. *Biological Conservation* 104: 351-360.
- Dostálek J & Frantík T **2008**. Dry grassland plant diversity conservation using low-intensity sheep and goat grazing management: case study in Prague (Czech Republic). *Biodiversity and Conservation* 17: 1439-1454.
- Gardiner T & Hill J **2006**. Mortality of Orthoptera caused by mechanical mowing of grassland. *British Journal of Entomology and Natural History* 19: 38–40.
- Gibson CWD, Hamblen C & Brown VK **1992**. Changes in Spider (Araneae) Assemblages in Relation to Succession and Grazing Management. *Journal of Applied Ecology* 29: 132-142
- Greenslade PJM **1964**. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology* 33: 301-310
- Hopwood JL **2008**. The contribution of roadside grassland restorations to native bee conservation. *Biological Conservation* 141: 2632-2640.
- Humbert JY, Ghazoul J & Walter T **2009**. Meadow harvesting techniques and their impacts on field fauna. *Agriculture, Ecosystems & Environment* 130: 1-8.
- Kampmann D, Herzog F, Jeanneret Ph, Konold W, Peter M, Walter T, Wildi O, Lüscher A **2008**. Mountain grassland biodiversity: Impact of site conditions versus management type. *Journal for Nature Conservation* 16: 12-25.

- Kondoh M **2001**. Unifying the relationships of species richness to productivity and disturbance. *Proceedings of the Royal Society of London, Series B* 268: 269-271.
- Marini L, Fontana P, Scotton M & Klimek S **2008**. Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. *Journal of Applied Ecology* 45: 361-370.
- Morris MG **1979**. Responses of grassland invertebrates to management by cutting 2. Heteroptera. *Journal of Applied Ecology* 16: 417-432.
- Morris MG **1981**. Responses of grassland invertebrates to management by cutting, IV. Positive responses of Auchenorrhyncha. *Journal of Applied Ecology* 18: 763-771.
- Morris MG **2000**. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. *Biological Conservation* 95: 129-142.
- Morris MG & Lakhani KH **1979**. Responses of grassland invertebrates to management by cutting 1. Species diversity of Hemiptera. *Journal of Applied Ecology* 16: 77-98.
- Morris MG & Plant R **1983**. Responses of grassland invertebrates to management by cutting 5. Changes in Hemiptera following cessation of management. *Journal of Applied Ecology* 20: 157-178.
- Morris MG, Clarke RT & Rispin W **2005**. The success of a rotational grazing system in conserving the diversity of chalk grassland Auchenorrhyncha. *Journal of Insect Conservation* 9: 363-374.
- Munguira ML & Thomas JA **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.
- New TR **1995**. *An introduction to invertebrate conservation*. Oxford University Press, United Kingdom.
- Noordijk J, Sýkora KV & Schaffers AP **2008**. The conservation value of sandy highway verges for arthropods – implications for management. *Proceedings of the Netherlands Entomological Society Meeting* 19: 75-93.
- Öckinger E, Hammarstedt O, Nilsson SG & Smith HG **2006**. The relationship between local extinctions of grassland butterflies and increased soil nitrogen levels. *Biological Conservation* 128: 564-573.
- Parr TW & Way JM **1988**. Management of roadside vegetation: the long-term effects of cutting. *Journal of Applied Ecology* 25: 1073-1087.
- Ries L, Debinski DM & Wieland ML **2001**. Conservation value of roadside prairie restoration to butterfly communities. *Conservation Biology* 15: 401-411.
- Roberts MJ **1998**. *Spinnengids* (translation and adaptation for the Netherlands by Noordam AP). Tirion Publishers, Baarn, the Netherlands.
- Robinson RA & Sutherland WJ **2002**. Post-war changes in arable farming and biodiversity in Great-Britain. *Journal of Applied Ecology* 39: 157-176.
- Rudmann-Maurera K, Weyandb A, Fischerc M & Stöcklina J **2008**. The role of landuse and natural determinants for grassland vegetation composition in the Swiss Alps. *Basic and Applied Ecology* 9: 494-503.
- Samways MJ **2005**. *Insect diversity conservation*. Cambridge University Press, Cambridge, United Kingdom.
- Sayer M **2002**. *Einfluss von Pflegenmaßnahmen auf die Entwicklung der Tierwelt in Straßenbegleitflächen*. Bundesministerium für Verkehr, Bau- und Wohnungswesen, Bonn, Germany.

- Schaffers AP **2002**. Soil, biomass, and management of semi-natural vegetation. Part I. Interrelationships. *Plant Ecology* 158: 229-246.
- Schaffers AP, Vesseur MC & Sýkora KV **1998**. Effects of delayed hay removal on the nutrient balance of roadside plant communities. *Journal of Applied Ecology* 35: 349-364.
- Schneider C & Fry G **2005**. Estimating the consequences of land-use changes on butterfly diversity in a marginal agricultural landscape in Sweden. *Journal for Nature Conservation* 13: 247-256.
- Schwab A, Dubois D, Fried PM & Edwards PJ **2002**. Estimating the biodiversity of hay meadows in north-eastern Switzerland on the basis of vegetation structure. *Agriculture, Ecosystems and Environment* 93: 197-209.
- Sýkora KV, de Nijs LJ & Pelsma TAHM **1993**. *Plantengemeenschappen van Nederlandse wegbermen*. Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht, the Netherlands.
- Sýkora KV, Kalwij JM & Keizer P-J **2002**. Phytosociological and floristic evaluation of a 15-year ecological management of roadside verges in the Netherlands. *Preslia* 74: 421-436.
- Schmitt T & Rákossy L **2007**. Changes of traditional agrarian landscapes and their conservation implications: a case study of butterflies in Romania. *Diversity and Distributions* 13: 855-862.
- Terry AC, Ashmore MR, Power SA, Allchin EA & Heil GW **2004**. Modelling the impacts of atmospheric nitrogen deposition on *Calluna*-dominated ecosystems in the UK. *Journal of Applied Ecology* 41: 897-909.
- Thomas JA & Morris MG **1994**. Patterns, mechanisms and rates of extinction among invertebrates in the United Kingdom. *Philosophical transactions of the Royal society of London, Series B* 344: 47-54.
- Thomas JA, Telfer MG, Roy DB, Preston CD, Greenwood JJD, Asher J, Fox R, Clarke RT & Lawton JH **2004**. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* 303: 1879-1881.
- Thorens P **1993**. Effets de la fauche sur une population du Criquet *Chorthippus mollis* (Charp.) (Orthoptera, Acrididae) dans une prairie du pied sud du Jura Suisse. *Bulletin de la Société Entomologique Suisse* 66 : 173-182.
- Tikka PM, Högmänder H & Koski PS **2001**. Road and railway verges serve as dispersal corridors for grassland plants. *Landscape Ecology* 16: 659-666.
- 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.
- van de Haterd RJW, van den Hengel B & Keizer P-J **2009**. Lange termijn effecten van maaibeheer in wegbermen. *De Levende Natuur* 110: 88-94.
- van Wingerden WKRE, Musters JCM & Maaskamp FIM **1991**. The influence of temperature on the duration of egg development in west european grasshoppers orthoptera acrididae. *Oecologia* 87: 417-423.
- van Wingerden WKRE, van Kreveld AR & Bongers W **1992**. Analysis of species composition and abundance of grasshoppers (Orth. Acrididae) in natural and fertilized grasslands. *Journal of Applied Entomology* 113: 138-152.
- Vermeulen HJW **1994**. Corridor function of a road verge for dispersal of stenotopic heathland ground beetles (Carabidae). *Biological Conservation* 69: 339-349.

- WallisDeVries MF, Poschlod P & Willems JH **2002**. Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation*, 104, 265–273.
- Wamelink GWW, de Jong JJ, van Dobben HF & van Wijk MN **2007**. Decreasing deposition will reduce costs for nature management. *Journal for Nature Conservation* 15: 131-143.
- Way JM **1977**. Roadside verges and conservation in Britain: a review. *Biological Conservation* 12: 65-74.
- Wenzel M, Schmitt T, Weitzel M & Seitz A **2006**. The severe decline of butterflies on western German calcareous grasslands during the last 30 years: A conservation problem. *Biological Conservation*, 128, 542–552.

## APPENDIX A

**A-1.** Average number of **spider species** caught in the plots at the three locations under the studied management treatments. Means are based on the back-transformed values of the estimated marginal means of the GLM tests. Significant GLM tests are given in bold. Values not sharing the same letter are different for that year ( $P < 0.05$ ).

Location		0	1M	2M	1M+	2M+
<b>Low-productive</b>						
2003	# species	8.79	7.93	8.98	7.56	8.77
2005	# species	9.20	9.59	9.39	9.17	9.39
2007	# species	9.13	8.31	7.36	8.55	7.77
<b>Medium-productive</b>						
2003	# species	5.82	5.67	6.35	5.32	5.36
2005	# species <sup>†</sup>	<b>9.95<sup>ab</sup></b>	<b>8.77<sup>a</sup></b>	<b>9.76<sup>a</sup></b>	<b>10.14<sup>ab</sup></b>	<b>11.52<sup>b</sup></b>
2007	# species	9.72	11.94	13.36	12.67	13.17
<b>High-productive</b>						
2003	# species	5.15	4.58	4.55	4.75	4.75
2005	# species	6.09	7.36	6.11	5.97	6.26
2007	# species	4.67	5.61	5.52	5.79	6.76

<sup>†</sup>  $F_{4,16} = 3.22$ ,  $P = 0.041$

**A-2.** Average number of **ground beetle species** caught in the plots at the three locations under the studied management treatments. Means are based on the back-transformed values of the estimated marginal means of the GLM tests. Significant GLM tests are given in bold. Values not sharing the same letter are different for that year ( $P < 0.05$ ).

Location		0	1M	2M	1M+	2M+
<b>Low-productive</b>						
2003	# species	10.98	8.77	9.91	9.53	9.09
2005	# species	11.68	11.32	11.26	10.28	10.50
2007	# species <sup>†</sup>	<b>12.13<sup>a</sup></b>	<b>12.10<sup>a</sup></b>	<b>15.53<sup>b</sup></b>	<b>12.48<sup>a</sup></b>	<b>12.74<sup>a</sup></b>
<b>Medium-productive</b>						
2003	# species	12.02	12.61	12.70	11.72	15.11
2005	# species	14.65	13.48	15.31	14.89	16.09
2007	# species	11.75	13.00	14.81	13.17	15.37
<b>High-productive</b>						
2003	# species	13.60	14.19	13.54	13.85	13.85
2005	# species	7.06	6.26	7.17	7.65	8.15
2007	# species	3.74	2.87	5.81	2.95	7.17

<sup>†</sup>  $F_{4,16} = 3.24$ ,  $P = 0.040$

**A-3.** Average number of **weevil species** caught in the plots at the three locations under the studied management treatments. Means are based on the back-transformed values of the estimated marginal means of the GLM tests. Significant GLM tests are given in bold. Values not sharing the same letter are different for that year ( $P < 0.05$ ).

Location		0	1M	2M	1M+	2M+
<b>Low-productive</b>						
2003	# species	1.35	1.17	0.25	0.43	0.78
2005	# species	0.00	0.52	0.52	0.32	0.43
2007	# species	0.15	0.43	0.15	0.32	0.32
<b>Medium-productive</b>						
2003	# species	7.77	6.98	9.16	5.32	9.76
2005	# species <sup>1</sup>	<b>5.45<sup>ab</sup></b>	<b>4.12<sup>a</sup></b>	<b>7.23<sup>bc</sup></b>	<b>6.98<sup>c</sup></b>	<b>9.18</b>
2007	# species <sup>2</sup>	<b>2.52<sup>a</sup></b>	<b>4.22<sup>a</sup></b>	<b>6.52<sup>b</sup></b>	<b>6.33<sup>b</sup></b>	<b>8.03<sup>b</sup></b>
<b>High-productive</b>						
2003	# species	6.03	6.67	5.17	3.74	6.66
2005	# species <sup>3</sup>	<b>2.64<sup>a</sup></b>	<b>3.68<sup>a</sup></b>	<b>3.64<sup>a</sup></b>	<b>4.19<sup>b</sup></b>	<b>6.43<sup>b</sup></b>
2007	# species <sup>4</sup>	<b>0.65</b>	<b>1.46<sup>b</sup></b>	<b>2.06<sup>bc</sup></b>	<b>3.28<sup>bc</sup></b>	<b>4.07<sup>c</sup></b>

<sup>1</sup>  $F_{4,16} = 3.64$ ,  $P = 0.027$

<sup>2</sup>  $F_{4,16} = 6.71$ ,  $P = 0.002$

<sup>3</sup>  $F_{4,16} = 3.39$ ,  $P = 0.034$

<sup>4</sup>  $F_{4,16} = 4.77$ ,  $P = 0.010$

**A-4.** Average number of **ant species** caught in the plots at the three locations under the studied management treatments. Means are based on the back-transformed values of the estimated marginal means of the GLM tests. Significant GLM tests are given in bold. Values not sharing the same letter are different for that year ( $P < 0.05$ ).

Location		0	1M	2M	1M+	2M+
<b>Low-productive</b>						
2003	# species	2.03	1.55	2.10	2.29	1.35
2005	# species	1.35	1.35	2.25	1.70	2.25
2007	# species	1.35	0.52	1.93	0.64	1.17
<b>Medium-productive</b>						
2003	# species	4.19	5.43	3.79	4.30	5.94
2005	# species	3.18	4.14	3.23	3.34	3.18
2007	# species <sup>1</sup>	<b>4.65<sup>ab</sup></b>	<b>5.52<sup>c</sup></b>	<b>4.30<sup>b</sup></b>	<b>5.94<sup>c</sup></b>	<b>5.15<sup>abc</sup></b>
<b>High-productive</b>						
2003	# species	2.25	2.73	2.73	2.29	2.90
2005	# species	2.37	2.95	4.25	2.73	3.58
2007	# species	2.73	2.37	2.57	3.33	2.25

<sup>1</sup>  $F_{4,16} = 2.79$ ,  $P = 0.062$

## APPENDIX B

**B-1.** Average number of **plant species** in the plots at the three locations under the studied management treatments. Significant GLM tests are given in bold. Values not sharing the same letter are different for that year ( $P < 0.05$ ).

Location		0	1M	2M	1M+	2M+
<b>Low-productive</b>						
2003	# species	15.6	16.0	14.2	14.8	15.2
2005	# species	14.2	14.8	14.4	14.8	13.2
2007	# species	15.6	15.8	14.4	15.4	15.6
<b>Medium-productive</b>						
2003	# species	21.8	23.0	21.2	21.2	22.6
2005	# species	22.2	24.0	23.6	22.6	24.2
2007	# species <sup>1</sup>	<b>22.2<sup>ab</sup></b>	<b>20.4<sup>a</sup></b>	<b>28.0<sup>c</sup></b>	<b>26.6<sup>bc</sup></b>	<b>34.2<sup>d</sup></b>
<b>High-productive</b>						
2003	# species	22.4	19.4	21.4	21.0	20.8
2005	# species	18.0	16.2	17.4	17.2	16.0
2007	# species	14.6	16.0	18.0	16.2	19.4

<sup>1</sup>  $F_{4,16} = 11.93$ ,  $P < 0.001$

**B-2.** Average number of **flowering plant species** in the plots at the three locations under the studied management treatments. Means are based on the back-transformed values of the estimated marginal means of the GLM tests. Significant GLM tests are given in bold. Values not sharing the same letter are different for that month ( $P < 0.05$ ).

Location		0	1M	2M	1M+	2M+
<b>Low-productive</b>						
2007 June	# species	4.07	2.94	2.47	4.04	3.37
2007 Sept	# species <sup>1</sup>	<b>10.41<sup>b</sup></b>	<b>8.79<sup>ab</sup></b>	<b>7.34<sup>a</sup></b>	<b>9.21<sup>b</sup></b>	<b>8.77<sup>ab</sup></b>
<b>Medium-productive</b>						
2007 June	# species <sup>2</sup>	<b>8.87<sup>a</sup></b>	<b>9.39<sup>ab</sup></b>	<b>12.25<sup>c</sup></b>	<b>12.05<sup>bc</sup></b>	<b>15.34<sup>c</sup></b>
2007 Sept	# species <sup>3</sup>	<b>6.66<sup>a</sup></b>	<b>9.16<sup>ab</sup></b>	<b>10.18<sup>b</sup></b>	<b>9.75<sup>b</sup></b>	<b>14.68<sup>c</sup></b>
<b>High-productive</b>						
2007 June	# species <sup>4</sup>	<b>3.33<sup>a</sup></b>	<b>3.79<sup>ab</sup></b>	<b>5.23<sup>ab</sup></b>	<b>5.52<sup>ab</sup></b>	<b>8.39<sup>b</sup></b>
2007 Sept	# species <sup>5</sup>	<b>1.83<sup>a</sup></b>	<b>2.06<sup>a</sup></b>	<b>2.57<sup>a</sup></b>	<b>3.04<sup>ab</sup></b>	<b>7.09<sup>b</sup></b>

<sup>1</sup>  $F_{4,16} = 3.68$ ,  $P = 0.026$

<sup>2</sup>  $F_{4,16} = 6.33$ ,  $P = 0.003$

<sup>3</sup>  $F_{4,16} = 7.32$ ,  $P = 0.002$

<sup>4</sup>  $F_{4,16} = 4.43$ ,  $P = 0.013$

<sup>5</sup>  $F_{4,16} = 9.79$ ,  $P < 0.001$



**B-3.** Average number of **flowers** in the plots at the three locations under the studied management treatments. Means are based on the back-transformed values of the estimated marginal means of the GLM tests. Significant GLM tests are given in bold. Values not sharing the same letter are different for that month ( $P < 0.005$ ).

Location		0	1M	2M	1M+	2M+
<b>Low-productive</b>						
2007 June	abundance <sup>1</sup>	<b>102.73<sup>b</sup></b>	<b>86.92<sup>ab</sup></b>	<b>101.47<sup>b</sup></b>	<b>72.95<sup>ac</sup></b>	<b>62.13<sup>c</sup></b>
2007 Sept	abundance	274.78	243.64	227.42	286.61	237.56
<b>Medium-productive</b>						
2007 June	abundance <sup>2</sup>	<b>134.91<sup>a</sup></b>	<b>379.47<sup>b</sup></b>	<b>657.26<sup>b</sup></b>	<b>477.57<sup>b</sup></b>	<b>3682.43<sup>c</sup></b>
2007 Sept	abundance <sup>3</sup>	<b>139.75<sup>b</sup></b>	<b>62.59<sup>a</sup></b>	<b>182.17<sup>b</sup></b>	<b>172.44<sup>b</sup></b>	<b>185.16<sup>b</sup></b>
<b>High-productive</b>						
2007 June	abundance <sup>4</sup>	<b>39.52<sup>a</sup></b>	<b>64.44<sup>ab</sup></b>	<b>112.52<sup>b</sup></b>	<b>84.20<sup>a</sup></b>	<b>539.99<sup>c</sup></b>
2007 Sept	abundance <sup>5</sup>	<b>19.55<sup>a</sup></b>	<b>20.43<sup>a</sup></b>	<b>47.97<sup>ab</sup></b>	<b>32.34<sup>a</sup></b>	<b>89.18<sup>b</sup></b>

<sup>1</sup>  $F_{4,16} = 3.97$ ,  $P = 0.020$

<sup>2</sup>  $F_{4,16} = 29.76$ ,  $P < 0.001$

<sup>3</sup>  $F_{4,16} = 8.12$ ,  $P = 0.001$

<sup>4</sup>  $F_{4,16} = 8.17$ ,  $P = 0.001$

<sup>5</sup>  $F_{4,16} = 3.70$ ,  $P = 0.026$

**B-4.** Average **standing plant-biomass** in the plots at the three locations under the studied management treatments. Means are based on the back-transformed values of the estimated marginal means of the GLM tests. Significant GLM tests are given in bold. Values not sharing the same letter are different for that month ( $P < 0.005$ ).

Location		0	1M	2M	1M+	2M+
<b>Low-productive</b>						
2007 June	(g / m <sup>2</sup> ) <sup>1</sup>	<b>48.58<sup>b</sup></b>	<b>26.31<sup>a</sup></b>	<b>25.93<sup>a</sup></b>	<b>23.13<sup>a</sup></b>	<b>24.47<sup>a</sup></b>
2007 Sept	(g / m <sup>2</sup> ) <sup>2</sup>	<b>96.83<sup>c</sup></b>	<b>89.02<sup>bc</sup></b>	<b>72.58<sup>a</sup></b>	<b>75.02<sup>ab</sup></b>	<b>77.41<sup>ab</sup></b>
<b>Medium-productive</b>						
2007 June	(g / m <sup>2</sup> ) <sup>3</sup>	<b>448.17<sup>c</sup></b>	<b>412.64<sup>c</sup></b>	<b>345.68<sup>bc</sup></b>	<b>342.44<sup>b</sup></b>	<b>251.90<sup>a</sup></b>
2007 Sept	(g / m <sup>2</sup> ) <sup>4</sup>	<b>619.05<sup>c</sup></b>	<b>657.00<sup>c</sup></b>	<b>344.71<sup>b</sup></b>	<b>659.37<sup>c</sup></b>	<b>165.97<sup>a</sup></b>
<b>High-productive</b>						
2007 June	(g / m <sup>2</sup> ) <sup>5</sup>	<b>834.81<sup>d</sup></b>	<b>608.35<sup>c</sup></b>	<b>544.55<sup>bc</sup></b>	<b>500.60<sup>b</sup></b>	<b>404.13<sup>a</sup></b>
2007 Sept	(g / m <sup>2</sup> ) <sup>6</sup>	<b>888.63<sup>b</sup></b>	<b>838.16<sup>b</sup></b>	<b>404.53<sup>a</sup></b>	<b>774.26<sup>b</sup></b>	<b>334.29<sup>a</sup></b>

<sup>1</sup>  $F_{4,16} = 8.79$ ,  $P = 0.001$

<sup>2</sup>  $F_{4,16} = 4.48$ ,  $P = 0.013$

<sup>3</sup>  $F_{4,16} = 22.18$ ,  $P < 0.001$

<sup>4</sup>  $F_{4,16} = 112.80$ ,  $P < 0.001$

<sup>5</sup>  $F_{4,16} = 17.64$ ,  $P < 0.001$

<sup>6</sup>  $F_{4,16} = 23.77$ ,  $P < 0.001$

**B-5. Average vegetation height** in the plots at the three locations under the studied management treatments. Means are based on the back-transformed values of the estimated marginal means of the GLM tests. Significant GLM tests are given in bold. Values not sharing the same letter are different for that month ( $P < 0.005$ ).

Location		0	1M	2M	1M+	2M+
<b>Low-productive</b>						
2007 June	cm	2.56	2.20	2.33	2.36	2.39
2007 Sept	cm <sup>1</sup>	<b>8.50<sup>c</sup></b>	<b>5.57<sup>b</sup></b>	<b>4.61<sup>a</sup></b>	<b>7.27<sup>bc</sup></b>	<b>5.36<sup>ab</sup></b>
<b>Medium-productive</b>						
2007 June	cm	52.71	48.03	44.32	40.54	33.55
2007 Sept	cm <sup>2</sup>	<b>66.21<sup>c</sup></b>	<b>59.22<sup>c</sup></b>	<b>17.63<sup>b</sup></b>	<b>50.63<sup>c</sup></b>	<b>12.28<sup>a</sup></b>
<b>High-productive</b>						
2007 June	cm <sup>3</sup>	<b>72.88<sup>b</sup></b>	<b>71.54<sup>b</sup></b>	<b>72.54<sup>b</sup></b>	<b>60.94<sup>a</sup></b>	<b>56.89<sup>a</sup></b>
2007 Sept	cm <sup>4</sup>	<b>55.08<sup>d</sup></b>	<b>49.60<sup>d</sup></b>	<b>31.75<sup>b</sup></b>	<b>41.24<sup>c</sup></b>	<b>24.53<sup>a</sup></b>

<sup>1</sup>  $F_{4,16} = 3.78$ ,  $P = 0.024$

<sup>2</sup>  $F_{4,16} = 59.73$ ,  $P < 0.001$

<sup>3</sup>  $F_{4,16} = 13.75$ ,  $P < 0.001$

<sup>4</sup>  $F_{4,16} = 42.12$ ,  $P < 0.001$

**B-6. Vegetation heterogeneity** (standard deviation of the vegetation height measurements) in the plots at the three locations under the studied management treatments. Means are based on the back-transformed values of the estimated marginal means of the GLM tests. Significant GLM tests are given in bold. Values not sharing the same letter are different for that month ( $P < 0.005$ ).

Location		0	1M	2M	1M+	2M+
<b>Low-productive</b>						
2007 June	st. deviation	0.42	0.34	0.49	0.27	0.35
2007 Sept	st. deviation	8.23	3.29	2.96	7.32	4.58
<b>Medium-productive</b>						
2007 June	st. deviation <sup>1</sup>	<b>32.00<sup>c</sup></b>	<b>16.90<sup>ab</sup></b>	<b>17.58<sup>b</sup></b>	<b>13.28<sup>a</sup></b>	<b>14.54<sup>ab</sup></b>
2007 Sept	st. deviation <sup>2</sup>	<b>35.62<sup>c</sup></b>	<b>13.69<sup>b</sup></b>	<b>4.91<sup>a</sup></b>	<b>14.36<sup>b</sup></b>	<b>3.20<sup>a</sup></b>
<b>High-productive</b>						
2007 June	st. deviation	13.07	12.32	11.94	12.56	15.26
2007 Sept	st. deviation <sup>3</sup>	<b>18.83<sup>c</sup></b>	<b>11.40<sup>bc</sup></b>	<b>8.75<sup>ab</sup></b>	<b>9.32<sup>ab</sup></b>	<b>5.82<sup>a</sup></b>

<sup>1</sup>  $F_{4,16} = 16.04$ ,  $P < 0.001$

<sup>2</sup>  $F_{4,16} = 49.60$ ,  $P < 0.001$

<sup>3</sup>  $F_{4,16} = 6.06$ ,  $P = 0.004$



4



# OPTIMIZING GRASSLAND MANAGEMENT FOR FLOWER-VISITING INSECTS IN ROADSIDE VERGES

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**Summary.** The decline of flower-visiting insects is a threat to ecological processes and to the services these insects provide. Roadside verges in the Netherlands span approximately 80,000 km and are often covered with semi-natural grasslands. As such, they also provide a suitable habitat for many insects, but this has received little attention so far. We investigated the effects of different management treatments on flower-visiting insects. We studied flower visitation in a 3 year old experimental set-up with five mowing treatments each replicated five times. Management types were: no management and mowing once or twice per year with and without the removal of hay, representing common forms of management and neglect. During an entire growing season, both flowers – number of species and inflorescences – as well as insects – total abundance and actual flower visits – were investigated. Mowing twice per year with removal of hay showed highest values for all measured variables and this effect persisted throughout the growing season. The early summer cut proved to be very important for insect feeding opportunities, due to the re-flowering of plants later in the growing season. Flower abundance showed high correlations with both plant species richness and the number of insect visits. Although overall, mowing twice a year with hay removal was the most beneficial treatment for flower-visiting insects, these plots were entirely devoid of flowers for some period right after mowing, indicating that a rotational scheme might further promote insect diversity and abundance.

**Key words.** diversity, flower-abundance, semi-natural grassland, insect conservation, mowing, roadside verge, vegetation management

## Introduction

Flower-visiting insects are of major significance for the functioning of natural ecosystems and for the services they provide for agriculture, such as crop pollination and pest control (Kratowil 2003; Kremer & Chaplin-Kramer 2007). Unfortunately, these insects are at risk of severe decline (Goulson *et al.* 2005; Biesmeijer *et al.* 2006; Pauw 2007; Grixti *et al.* 2009). Not only habitat destruction, but also the fragmentation of the natural and semi-natural landscapes is a main threat to biodiversity. Despite some pollinators being highly mobile, there are strong indications that the decline of this group is partly related to fragmentation (Steffan-Dewenter & Tscharntke 1999; Donaldson *et al.* 2002).

Although anthropogenic, semi-natural grassland is one of the most important ecosystems in Europe for both flowering plants and flower-visiting insects (Cremene *et al.* 2005; Schmitt & Rákossy 2007). This vegetation is under severe pressure as traditional land-use is increasingly replaced by either highly intensive agricultural practices or by abandonment (Öckinger *et al.* 2006; Marini *et al.* 2008). To enlarge insect habitats and to reduce fragmentation, it has often been proposed to create various linear refuges with grassy vegetation (Nicholls *et al.* 2001; Pywell *et al.* 2005; Öckinger & Smith 2007; Söderström & Hedblom 2007). Such habitats are of great importance, especially in the Netherlands where the landscape is highly anthropogenic and natural areas are scarce and highly scattered (Opdam *et al.* 2006; Hanski & Pöyry 2007). Promising habitats for grassland plants and flower-visiting insects in these landscapes are roadside verges (Munguira & Thomas 1992; Schaffers & Sýkora 2002; Saarinen *et al.* 2005), which may harbour relatively high species richness of plants and arthropods (Helden & Leather 2004; Hopwood 2008). In addition, their linear outline and omnipresence can easily turn them into corridors or stepping stones, thus creating ecological networks in the landscape (Ries *et al.* 2001; Tikka *et al.* 2001).

In semi-natural grassland, some form of management is essential to maintain high species richness (Stefanescu *et al.* 2005; Öckinger *et al.* 2006; Härdtle *et al.* 2006; Dekoninck *et al.* 2007). Most roadside verges in the Netherlands are regularly managed, not only to secure traffic safety but also to maintain plant diversity. In medium to highly productive grassland, this is done by hay-making once or twice per year. The importance of management for plant diversity in roadside verges has already been thoroughly investigated (Schaffers 2002; Sýkora *et al.* 2002). However, the effects of vegetation management on insects are less well studied and understood. Since a pollination crisis might be a true risk for many areas (Steffan-Dewenter *et al.* 2005; Biesmeijer *et al.* 2006), studying management effects on pollinating insects has become a matter of increasing urgency.



**Figure 1.** The studied roadside verge. The plots and different flower abundances can be seen.

In this paper, we explore which grassland management is most favourable for flower visitation. After applying five management treatments during three years, we studied flower density and diversity and number of actual flower visits by insects.

## Methods

### *Study site and experimental design*

The experiment was conducted in a verge of highway A76, close to the city of Heerlen in the most southern region of the Netherlands (Province of Limburg, 50°51'N–5°57'E). On the east, the verge is bordered by the highway, in the west by arable land. The original vegetation consisted of a species-rich hay-meadow *Arrhenatheretrum elatioris*, on a lime-rich soil (see Schaffers & Sýkora 2002). In the Netherlands, this plant community is at present almost limited to roadside verges and river embankments (Liebrand & Sýkora 1996; Sýkora *et al.* 2002).

On an initially homogenous roadside stretch five different forms of management were applied in contiguous plots of 12 by 15 m (Fig. 1), with small machinery and hand rakes. Treatments were: no management (0), mowing once per year in early autumn (mid-September) without hay removal (1M) or with hay removal (1M+), mowing twice a year in early summer (beginning of July) as well as early autumn without hay removal (2M) or with hay removal (2M+). These treatments reflect common management practises in Dutch roadside verges (1M+, 2M+) and forms of neglect or irregular management (0, 1M, 2M) (Sýkora *et al.* 2002).

Each treatment was replicated five times in a randomised block design. Consequently, 25 adjacent plots, totalling up to a length of 300 m, were created. Management treatments started in 2004, while the data was collected in 2006, the third year of the experiment. During the entire experiment, the parts of the verge surrounding the plots were uniformly managed by hay-making in September.

#### *Data collection*

Each plot was subdivided into four quadrants, and in the middle of each quadrant a subplot of 1 by 1 m was established. Subplots were demarcated by inconspicuous sticks. In these subplots we counted flowering plants and flower-visiting insects. We consecutively visited the same quadrant in all 25 plots before moving on to the next quadrant. At least one subplot of each treatment (i.e., one block), was surveyed on a particular day. Data obtained in the four subplots of each plot were pooled and regarded as one sample. An entire survey of all subplots (i.e., 100) makes one round and several rounds were made. The first round took place between the 8<sup>th</sup> of May and the 23<sup>rd</sup> of June, the second between the 30<sup>th</sup> of July and the 16<sup>th</sup> of August and the third between the 1<sup>st</sup> of September and the 6<sup>th</sup> of September. An additional quick round was made from the 15<sup>th</sup> to 17<sup>th</sup> of July, right after the first mowing event when the 2M and 2M+ plots harboured almost no flowers at all. This round provided insight in flower abundance of the other plots at the moment of mowing in the 2M and 2M+ plots. No measurements were carried out after the second mowing event (early autumn), because this was after the flight season of most insects. Differences in time-span between rounds were due to weather conditions. Surveys were limited to days with 'good' weather; i.e., a minimal temperature of 18°C, not too much wind (< 3 Beaufort), and less than 50% cloud cover.

During the survey of a subplot, flowering plant species were noted (flower diversity) and the number of flowers was counted (flower abundance). For Asteraceae, Apiaceae and most Fabaceae (except *Lathyrus hirsutus* and *Vicia sativa*) the number of flower heads was counted instead of the number of individual flowers. After the flower count, a 2 min break was taken before the start of the insect counting to compensate for possible disturbances by movements of the observer. Foraging insects were studied during 15 min. Each individual entering the subplot and starting to forage was counted (as a measure of attractiveness of the flower composition). The possibility existed that the same individual entered the subplot more than once, but it was impossible to follow the insects outside the subplots. We defined each individual landing on or otherwise touching a flower as a 'visit', and also counted all these visits (as a measure of food availability). We noted the insect's taxonomical group and the flower species visited. In case an insect fed on a plant with flower heads we assigned foraging to classes; noting 5 visits when less than 33% of the flowers in the flower head were visited, 10 visits if 33–67% was visited, and 15 visits when 67–100% was visited. Insects were subdivided into eight groups: bees (Apoidea, excl. *Bombus* spp.), bumblebees (*Bombus* spp.), flies (Diptera excl.



Syrphidae), hoverflies (Syrphidae), beetles (Coleoptera), ichneumon and braconid wasps (Ichneumonoidea), sawflies (Tenthredinidae), and butterflies (Lepidoptera).

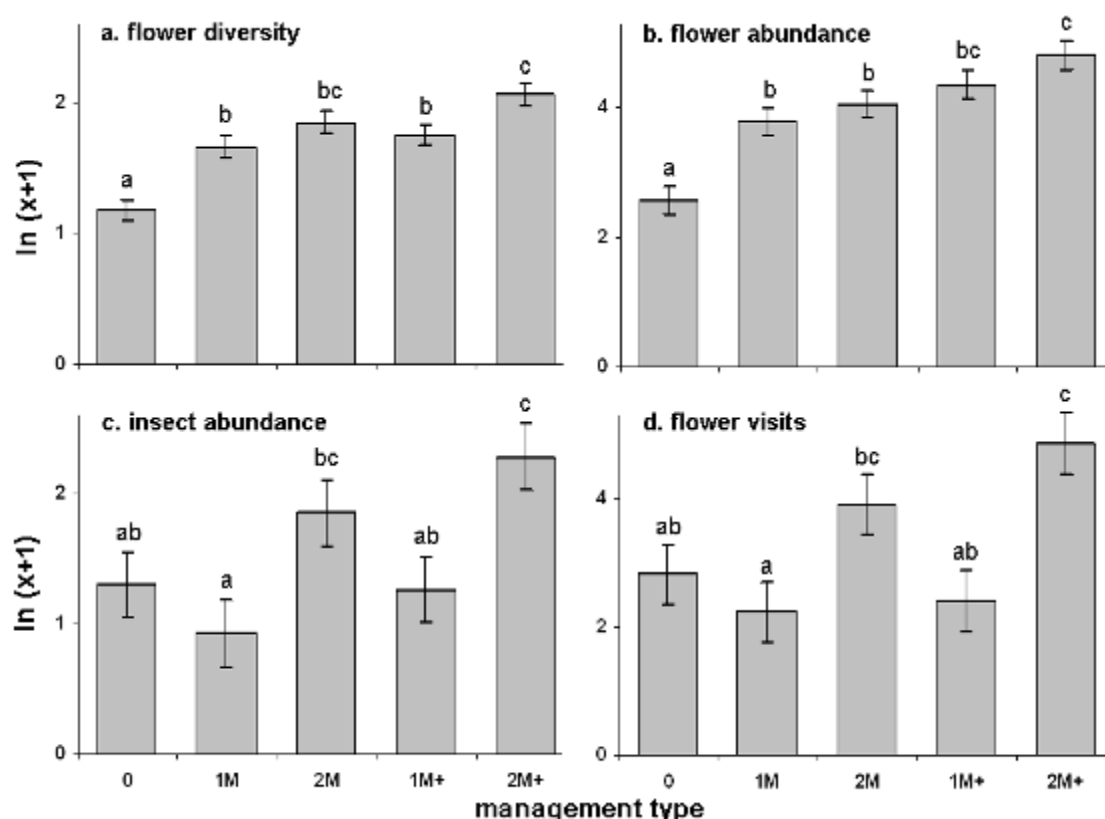
### Statistical analyses

Data on flower diversity and abundance, the number of insects visiting the subplots and the number of visits were  $\ln$  transformed to meet statistical requirements. Analyses were done using SPSS 15.0. Repeated measures General Linear Model (RM-GLM) tests, and LSD post-hoc tests were used to test for differences in flower and insect counts between the management types over the three main rounds. Rounds were also analysed separately using GLM to detect differences within each of the three rounds. Block was always included as a fixed factor, but it had no significant effect in any of the analyses. Linear regressions were performed to investigate relationships within the separate rounds between flower diversity and flower abundance, and between flower abundance and insect abundance and visits.

## Results

### Flower diversity and abundance

We counted 11,378 inflorescences during the main rounds and 769 in the round right after mowing and 37 flowering species were recorded (Appendix A).



**Figure 2.** Effects of management type on (a) flower diversity, (b) flower abundance, (c) insect abundance and (d) number of flower visits. Estimated marginal means of  $\ln$ -transformed values and standard errors given are based on the RM-GLM. Means not sharing the same letter are significantly different ( $P < 0.05$ ).

Flower diversity differed significantly between rounds ( $F_{1,16} = 55.67$ ,  $P < 0.001$ ). This effect was independent of management type (round x management:  $F_{4,16} = 1.06$ ,  $P = 0.407$ ). Management had a significant effect on flower diversity ( $F_{4,16} = 16.55$ ,  $P < 0.001$ ). Highest diversity was found where mowing occurred twice (particularly when cuttings were removed in 2M+), whereas the plots where no management occurred had lowest diversity (Fig. 2a).

Flower abundance also differed significantly between rounds ( $F_{1,16} = 65.13$ ,  $P < 0.001$ ). Overall, flower abundance was strongly affected by management type ( $F_{4,16} = 14.72$ ,  $P < 0.001$ ). It was very low where no management took place and highest where cuttings were removed after mowing, particularly when mowing occurred twice in 2M+ (Fig 2b). As can be seen by inspecting the separate rounds, differences between treatments were largest in the first and third round, whereas in the second round treatment effects are less pronounced (Table 1; round x management interaction:  $F_{4,16} = 3.22$ ,  $P = 0.041$ ).

A very strong positive correlation was observed between flower diversity and the abundance of flowers (Fig. 3). This indicates that forms of management resulting in high flower abundance are also likely to promote high plant diversity.

#### *Flower visitation*

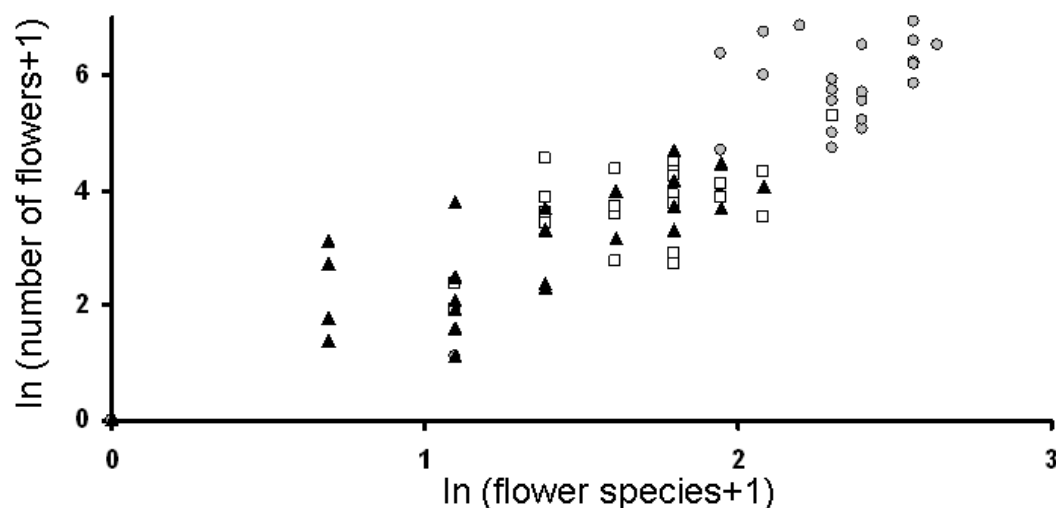
A total of 470 insect individuals were observed to make 11,802 visits during the three rounds while in the round right after mowing 109 individuals and 2456 visits were noted. Insects visited 29 plant species (Appendix A).

The number of individual insects feeding in the plots (insect abundance) did not differ between rounds ( $F_{1,16} = 3.41$ ,  $P = 0.083$ ) and no interaction between round and management was found ( $F_{4,16} = 1.82$ ,  $P = 0.175$ ), but insect abundance differed between management types ( $F_{4,16} = 4.48$ ,  $P = 0.013$ ). Abundance was highest when mowing occurred twice, particularly where the cuttings were removed in 2M+, whereas unmanaged plots and plots mown only once showed low insect abundance, particularly when the cutting was not removed (Fig. 2c; Table 1).

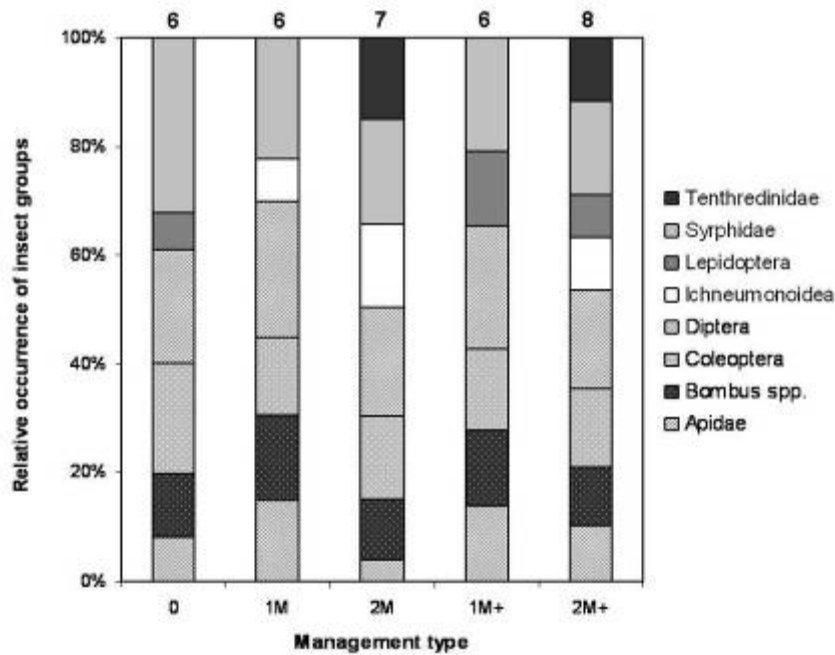
Similar to insect abundance, the number of flower visits did not differ between rounds ( $F_{1,16} = 1.05$ ,  $P = 0.322$ ), and no interaction between round and management was found (round x management:  $F_{4,16} = 0.90$ ,  $P = 0.487$ ). The number of visits differed between management types ( $F_{4,16} = 5.52$ ,  $P = 0.005$ ). It was again highest under a management of two cuts per year, particularly in 2M+ where the cuttings were removed (Fig. 2d). Just after mowing, 2M and 2M+ are very unsuitable for insects almost by definition, but in round two – which started only 3 weeks after the first mowing event – 2M+ already tended to attract the greatest numbers of insects (Table 1), although the difference was not yet significant. Moreover, plots that received a cut in early summer (the plots mown twice) remained strikingly attractive for flower-visiting insects in early autumn (Table 1, round three). The 2M+ treatment also is the only treatment that was visited by representatives from all eight insect groups (Fig. 4). Both insect abundance and the number of flower visits showed a significant positive relation to flower abundance (Fig. 5).

**Table 1.** Mean flower abundance, flower diversity, insect abundance and number of flower visits per management type during the growing season. All data are back-transformed values, indicating mean number per 4 m<sup>2</sup> for flower abundance and diversity and mean number per 4 m<sup>2</sup> per h for insect individuals and visits. Significances of the one-way ANOVA models are given, \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ . Means were compared using LSD post-hoc tests, with values not sharing the same letter indicating significant differences ( $P < 0.05$ ).

	Management type				
	0	1M	2M	1M+	2M+
<b>Round one</b>					
# flowers ***	14.96 <sup>a</sup>	322.76 <sup>b</sup>	218.20 <sup>b</sup>	477.19 <sup>b</sup>	650.97 <sup>b</sup>
# flowering species **	3.31 <sup>a</sup>	8.39 <sup>b</sup>	9.38 <sup>b</sup>	8.30 <sup>b</sup>	12.20 <sup>b</sup>
# insect individuals	3.85	1.23	4.10	3.14	8.21
# visits	13.88	3.22	39.45	12.87	72.70
<b>Right after mowing</b>					
# flowers ***	8.12 <sup>a</sup>	28.67 <sup>ab</sup>	0 <sup>c</sup>	58.15 <sup>b</sup>	0.25 <sup>c</sup>
# flowering species ***	2.46 <sup>a</sup>	3.62 <sup>a</sup>	0 <sup>b</sup>	3.66 <sup>a</sup>	0.15 <sup>b</sup>
# insect individuals **	1.69 <sup>ab</sup>	6.54 <sup>b</sup>	0 <sup>a</sup>	5.96 <sup>b</sup>	0 <sup>a</sup>
# visits ***	12.60 <sup>a</sup>	164.67 <sup>b</sup>	0 <sup>c</sup>	57.56 <sup>ab</sup>	0 <sup>c</sup>
<b>Round two</b>					
# flowers	16.29	32.45	25.31	65.02	60.56
# flowering species **	2.35 <sup>a</sup>	4.81 <sup>b</sup>	3.85 <sup>b</sup>	5.49 <sup>b</sup>	4.81 <sup>b</sup>
# insect individuals	4.05	4.10	6.39	5.49	12.46
# visits	71.97	58.74	44.60	43.26	243.69
<b>Round three</b>					
# flowers *	7.08 <sup>a</sup>	7.00 <sup>a</sup>	31.79 <sup>b</sup>	14.03 <sup>ab</sup>	45.06 <sup>b</sup>
# flowering species **	1.36 <sup>a</sup>	1.69 <sup>a</sup>	4.05 <sup>b</sup>	2.19 <sup>a</sup>	5.30 <sup>b</sup>
# insect individuals **	1.01 <sup>a</sup>	0.43 <sup>a</sup>	5.82 <sup>b</sup>	0.65 <sup>a</sup>	6.46 <sup>b</sup>
# visits **	3.26 <sup>a</sup>	2.19 <sup>a</sup>	63.07 <sup>b</sup>	1.16 <sup>a</sup>	113.43 <sup>b</sup>



**Figure 3.** Flower abundance in relation to the total number of flowering species. For clarity, the highly overlapping trend lines for the three rounds are not depicted. All three linear relationships were found to be significant, round one (grey circles):  $R^2 = 0.77$ ,  $P < 0.001$ , round two (squares):  $R^2 = 0.47$ ,  $P < 0.001$ ; and round three (black triangles):  $R^2 = 0.64$ ,  $P < 0.001$ .



**Figure 4.** The distribution of the eight insect groups over the five management types based on the In-transformed data of the visits. Above each bar the total number of insect groups encountered is given.

## Discussion

### *Flower-visiting insects*

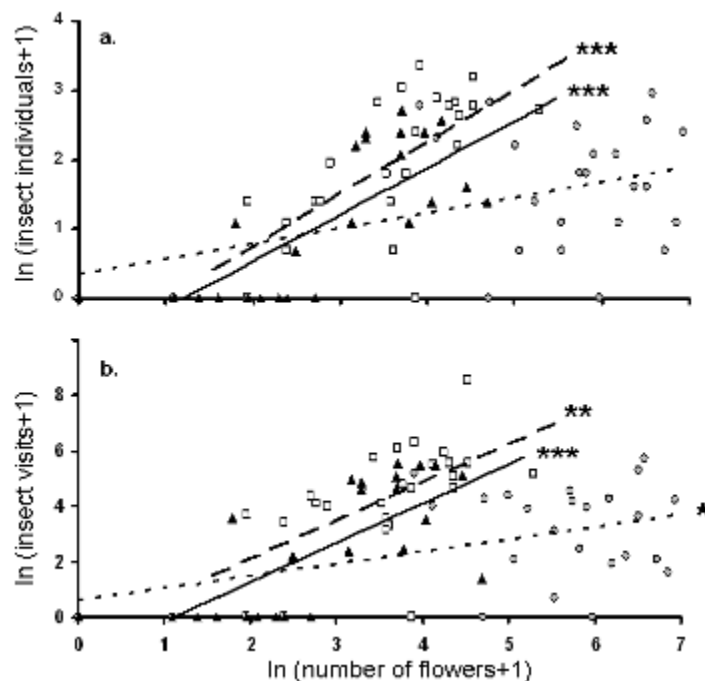
Management type 2M+ clearly provided the best feeding opportunities for flower-visiting insects throughout the year, judging from the insect abundances and number of flower visits. It also was the only treatment that attracted representatives from all eight insect groups under study. These effects are most likely due to the highest number of flowers under this treatment, as this proved to be a strong determinant for the abundance of flower-visitors (see also Hegland & Boeke 2006; Saarinen *et al.* 2005; Pywell *et al.* 2005; Sjödin 2007). Mowing twice per year with removal of the cuttings thus seems the most recommendable management practice for roadside verges on (moderately) nutrient-rich soils with potential or actual *Arrhenatherion* grasslands. Fortunately, hay-making twice a year is also commonly applied as botanical management by many road management authorities. When nutrient-poor conditions prevail, a more extensive management may suffice (CHAPTER 9).

In both the 2M and 2M+ plots, re-flowering late in the growing season appeared to be very important for flower-visitors because these plots were very attractive to insects in round three. In many other landscape elements (including nature reserves), flowers have largely disappeared by this time at the end of the growing season. Because of this, the common practice in roadsides to mow twice per year can be of great importance in providing flower resources for insects later in their life-cycle or for second generation adults in bivoltine species.

Management type 2M+ not only showed highest insect visitation, but it rendered highest flower diversity as well, reflecting underlying plant species richness, and is therefore the most recommendable practice also for botanical

diversity goals (see also Schaffers 2002). Mowing and removal of the clippings is a necessity for the conservation (or restoration) of species-rich grasslands, especially on relatively nutrient-rich soils or when the soil is enriched by atmospheric deposition of nutrients (Berendse *et al.* 1993; Wamelink 2007), as is the case for all Dutch roadside verges. Although the different management treatments in this study had only been applied for 3 years, a botanical degradation relative to 2M+ could already be observed, particularly for the plots without management. Mowing without the removal of hay also showed lower flower (plant) diversity but not yet significant. This is probably due to the relatively short duration of this experiment and a continuation of this practise will, in the long run, almost certainly lead to the disappearance of species-rich grassland (Schaffers *et al.* 1998; Sýkora *et al.* 2002).

There are many indications that the results of this study are widely applicable under grassland conditions with many perennial forbs. Various studies on plant diversity show similar positive effects of mowing (e.g., Parr & Way 1988; Schaffers 2002). In addition, we surveyed flowers (but not insects) in June and August in another roadside verge in the central-eastern part of the Netherlands, with exactly the same experimental set-up and management treatments but on a nutrient-rich clay soil and where mowing treatments continued for one more year (CHAPTER 3). There, we obtained similar or even stronger results for the flower counts; their number was highest in 2M+ plots both for June (5–27 times as many flowers as in 0, 1M, 1M+, 2M) and for September (1–3 times as many flowers as the other treatments).

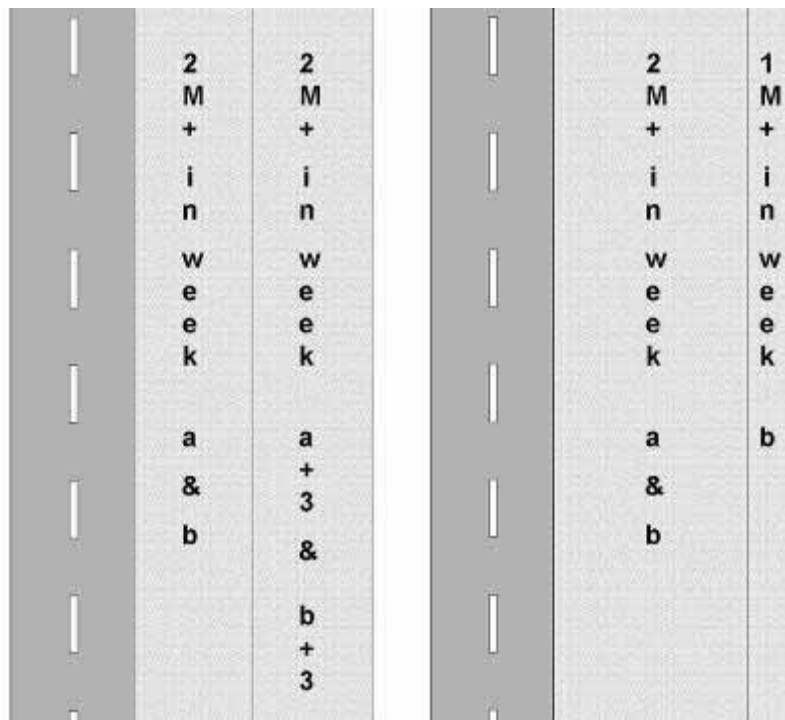


**Figure 5.** (a) Insect abundance and (b) flower visits in relation to flower abundance. The separate rounds are given in the graphs, round one: grey circles and dotted lines, round two: squares and striped lines, round three: black triangles and continuous lines. Significant linear relationships could be deduced. Insect individuals vs. flowers in round one:  $R^2 = 0.03$ ,  $P = 0.446$ , in round two:  $R^2 = 0.43$ ,  $P < 0.001$ , and in round three:  $R^2 = 0.57$ ,  $P < 0.001$ . Insect visits vs. flowers in round 1:  $R^2 = 0.16$ ,  $P = 0.046$ , in round 2:  $R^2 = 0.35$ ,  $P < 0.001$ , in round 3:  $R^2 = 0.51$ ,  $P < 0.001$ . For all regressions  $n = 25$ .

*Other aspects of insect conservation*

In this study, we only recorded insect feeding occurrences and attraction. The insects counted will mainly have been individuals for which the roadside is the main habitat, as the surrounding area mainly consists of arable fields and the road itself (see also Hopwood 2008), but it is also possible that insects were attracted from other areas nearby. Of course, there is a great deal more to conserving an insect's habitat than food alone: for instance they need to rest, mate, hibernate, pupate and hide from predators (e.g., Dennis *et al.* 2007). In all cases the vegetation plays an important role as many of the above mentioned functions are provided by plants. Paradoxically, direct effects of mowing might therefore harm insects, but our study shows that indirect effects of management are very important in the long run and a lack of management might eventually lead to the disappearance of suitable habitat (Morris 1981; Fenner & Palmer 1998; Caittin *et al.* 2003; Schmidt *et al.* 2008). Notwithstanding the positive effects of the 2M+ management on food availability, the sudden complete removal of nectar and pollen sources, lasting for days in the beginning of July, might be disastrous for short-lived and/or highly sedentary species, even though re-flowering already occurred after a few weeks. In addition, high mortality might be expected for larvae or pupae of flower-visiting insects caused by mowing (e.g., Valtonen & Saarinen 2005; Johst *et al.* 2006).

Some form of rotational management will therefore almost certainly benefit insects (e.g., Morris & Plant 1983; Morris & Rispin 1988; Chambers & Samways 1998; WallisDeVries *et al.* 2002). As different species have different periods in which they require food, rest, shelter, host plants, etc., a rotational management scheme is likely to be effective for the conservation of a wider range of insects than non-rotational management. When only specific parts of an area are mown in annual succession, continuous feeding opportunities for nectar or pollen eating insects are provided throughout the growing season. In roadside verges, however, rotational management is complicated by two reasons: (1) Many semi-natural grasslands in the Netherlands need hay management twice per year to retain high plant diversity (e.g., Schaffers 2002; see present results also). Since hay-meadow vegetation is largely limited to roadside verges, these botanical aspects are very important (Sýkora *et al.* 2002). A rotational management in which parts of the verge remain unmanaged in some years could negatively affect plant diversity in the entire verge (Hinsch & Poethke 2007; CHAPTER 3). (2) Management of roadside verges is not performed by nature conservation organisations but is generally put out to contractors. Large vehicles are used and extensive lengths of verges are mown on the same day. A detailed rotational management of the more than 80,000 km of (non-urban) roadsides in the Netherlands is simply not feasible. Mowing schemes should therefore be simple and easily implemental (Morris 1991).



**Figure 6.** Two alternative management schemes that would tailor vegetation management in roadside verges more to the needs of flower-visiting insects without negatively affecting floristic diversity.

#### *Management implications*

Taking the presented results and the above mentioned botanical values and practical considerations into account, we propose two rotational schemes that allow nectar and pollen dependent insects to persist in the verges throughout the season and might enhance the survival of vulnerable life-stages, like larvae and pupae. (1) One alternative is to divide a verge into two longitudinal strips of the same width each receiving 2M+ management but with a small time-shift (e.g., 3 weeks; see Fig. 6a). This way, flowering plants are always present and botanical values are protected or even promoted because seed-set may become feasible for more plant species. As an extra advantage, this management is easily applicable as one strip could be mown when the machines move in one direction and the other when they return. (2) As a second alternative, we suggest to manage almost the entire verge with 2M+, while on a narrow strip only (e.g., 10% of the total width) 1M+ is applied (Fig. 6b). Although plant diversity will probably decrease in this strip, the vegetation would still retain the character of a hay-meadow. Moreover, during the early summer mowing event the actual area mown is reduced, cutting back on management costs. The first alternative is most beneficial for insect feeding opportunities and plant diversity, while the second option will likely increase the chances of successful insect reproduction.

Further experiments remain necessary to test the validity of the recommended management options for other grassland types and specific insect groups. A major challenge will be to find management options that deliver best results for both insect reproduction and feeding opportunities. At this moment, however, our results and recommendations may already help to improve conditions for a threatened group of insects.

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## References

- Berendse F, Aerts R & Bobbink R **1993**. Atmospheric nitrogen deposition and its impact on terrestrial ecosystems. In: *Landscape Ecology of a Stressed Environment* (Opdam P & Vos CC eds.): 104-121. Chapman and Hall, London, UK.
- Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J & Kunin WE **2006**. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313: 351-354.
- Cattin MF, Blandenier G, Banasek-Richter C & Bersier LF **2003**. The impact of mowing as a management strategy for wet meadows on spider (Araneae) communities. *Biological Conservation* 113: 179-188.
- Chambers BQ & Samways MJ **1998**. Grasshopper response to a 40-year experimental burning and mowing treatment, with recommendations for invertebrate conservation management. *Biodiversity and Conservation* 7: 985-1012.
- Cremene C, Groza G, Rakosy L, Schileiko AA, Baur A, Erhardt A & Baur B **2005**. Alterations of steppe-like grasslands in Eastern Europe: a threat to regional biodiversity hotspots. *Conservation Biology* 19: 1606-1618.
- Dekoninck W, de Koninck H, Baugnee JY, Maelfait J-P **2007**. Ant biodiversity conservation in Belgian calcareous grasslands: active management is vital. *Belgian Journal of Zoology* 137: 137-146.
- Dennis RLH, Shreeve TG & Sheppard DA **2007**. Species conservation and landscape management: a habitat perspective. In: *Insect conservation biology* (Stewart AJA, New TR & Lewis OT eds.): 92-126. CABI, Wallingford, UK.
- Donaldson J, Nänni I, Zachariades C & Kemper J **2002**. Effects of habitat fragmentation and plant reproductive success in renosterveld shrublands of South Africa. *Conservation Biology* 16: 1267-1276.
- Fenner M & Palmer L **1998**. Grassland management to promote diversity: creation of a patchy sward by mowing and fertilizer treatments. *Field Studies* 9: 313-324.
- Gibson CWD, Hamblen C & Brown VK **1992**. Changes in spider Araneae assemblages in relation to succession and grazing management. *Journal of Applied Ecology* 29: 132-142.
- Goulson D, Hanley ME, Darvill JS, Ellis JS & Knight ME **2005**. Causes of rarity in bumblebees. *Biological Conservation* 122: 1-8.
- Gixti JC, Wong LT, Cameron SA & Favret C **2009**. Decline of bumble bees (*Bombus*) in the North American Midwest. *Biological Conservation* 142: 75-84.
- Hanski I & Pöyry J **2007**. Insect populations in fragmented habitats. In: *Insect conservation biology* (Stewart AJA, New TR & Lewis OT eds.): 175-202. CABI, Wallingford, UK.
- Härdtle W, Redecker B, Assmann T & Meyer H **2006**. Vegetation responses to environmental conditions in floodplain grasslands: Prerequisites for preserving plant species diversity. *Basic and Applied Ecology* 7: 280-288.
- Hegland SJ & Boeke L **2006**. Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. *Ecological Entomology* 31: 532-538.



- Helden AJ & Leather SR **2004**. Biodiversity on urban roundabouts - Hemiptera, management and the species-area relationship. *Basic and Applied Ecology* 5: 367-377.
- Hinsch M & Poethke H-J **2007**. Consequences of cyclic vegetation management for arthropod survival: simulation experiments. *Basic and Applied Ecology* 8: 321-331.
- Hopwood JL **2008**. The contribution of roadside grassland restorations to native bee conservation. *Biological Conservation* 141: 2632-2640
- Johst K, Dreschler M, Thomas J & Settele J **2006**. Influence of mowing on the persistence of two endangered large blue butterfly species. *Journal of Applied Ecology* 43: 333-342.
- Kratochwil A **2003**. Bees (Hymenoptera, Apoidea) as key-stone species: specifics of resource and requisite utilisation in different habitat types. *Berichte der Reinhold-Tüxen-Gesellschaft* 15: 59-77.
- Kremer C & Chaplin-Kramer R **2007**. Insects as providers of ecosystem services: crop pollination and pest control. In: *Insect conservation biology* (Stewart AJA, New TR & Lewis OT eds.): 349-382. CABI, Wallingford, UK.
- Liebrand CIJM & Sýkora KV **1996**. Restoration of semi-natural, species-rich grasslands on river dikes after reconstruction. *Ecological Engineering* 7: 315-326.
- Marini L, Fontana P, Scotton M & Klimek S **2008**. Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. *Journal of Applied Ecology* 45: 361-370.
- Morris MG **1981**. Responses of grassland invertebrates to management by cutting. IV. Positive responses of Auchenorrhyncha. *Journal of Applied Ecology* 18: 763-771.
- Morris GM **1991**. The management of reserves and protected areas. In: *The scientific management of temperate communities for conservation* (Spellerberg IF, Goldsmith FB & Morris MG eds.): 323-347. Blackwell Scientific Publications, Oxford, UK.
- Morris MG & Plant R **1983**. Responses of grassland invertebrates to management by cutting. V. Changes in Hemiptera following cessation of management. *Journal of Applied Ecology* 20: 157-177.
- Morris MG & Rispin WE **1988**. A beetle fauna of oolitic limestone grassland, and the responses of species to conservation management by different cutting treatments. *Biological Conservation* 43: 87-105.
- Munguira ML & Thomas JA **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.
- Nicholls CI, Parrella M & Altieri A **2001**. The effects of a vegetational corridor on the abundance and dispersal of insect biodiversity within a northern California organic vineyard. *Landscape Ecology* 16: 133-146.
- Öckinger E, Hammarstedt O, Nilsson SG & Smith HG **2006**. The relationship between local extinctions of grassland butterflies and increased soil nitrogen levels. *Biological Conservation* 128: 564-573.
- Öckinger E & Smith HG **2007**. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology* 44: 50-59
- Opdam P, Steingröver E & van Rooij S **2006**. Ecological networks: A spatial concept for multi-actor planning of sustainable landscapes. *Landscape and Urban Planning* 75: 322-332.
- Pauw A **2007**. Collapse of a pollination web in small conservation areas. *Ecology* 88: 1759-1769.

- Parr TW & Way JM **1988**. Management of Roadside Vegetation: The Long-Term Effects of Cutting. *Journal of Applied Ecology* 25: 1073-1087.
- Pywell RF, Warman EA, Carvell C, Sparks TH, Dicks LV, Bennet D, Wright A. Critchley CNR & Sherwood A **2005**. Providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation* 121: 479-494.
- Ries L, Debinski DM & Wieland ML **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.
- Schaffers AP **2002**. Soil, biomass, and management of semi-natural vegetation. Part II. Factors controlling species diversity. *Plant Ecology* 158: 247-268.
- Schaffers AP & Sýkora KV **2002**. Synecology of species-rich plant communities on roadside verges in the Netherlands. *Phytocoenologia* 32: 29-83.
- Schaffers AP, Vesseur MC & Sýkora KV **1998**. Effects of delayed hay removal on the nutrient balance of roadside plant communities. *Journal of Applied Ecology* 35: 349-364.
- Schmidt MH, Rocker S, Hanafi J & Gigon A **2008**. Rotational fallows as overwintering habitat for grassland arthropods: the case of spiders in fen meadows. *Biodiversity and Conservation* 17: 3003-3012.
- Schmitt T & Rákossy L **2007**. Changes of traditional agrarian landscapes and their conservation implications: a case study of butterflies in Romania. *Diversity and Distributions* 13: 855-862.
- Sjödin NE **2007**. Pollinator behavioural responses to grazing intensity. *Biodiversity and Conservation* 16: 2103-2121.
- Söderström B & Hedblom M **2007**. Comparing movement of four butterfly species in experimental grassland strips. *Journal of Insect Conservation* 11: 333-342.
- Stefanescu C, Peñuelas J & Filella I **2005**. Butterflies highlight the conservation value of hay meadows highly threatened by land-use change in a protected Mediterranean area. *Biological Conservation* 126: 234-246.
- Steffan-Dewenter I & Tscharntke T **1999**. Effects of habitat isolation on pollinator communities and seed set. *Oecologia* 121: 432-440.
- Steffan-Dewenter I, Potts SG & Packer L **2005**. Pollinator diversity and crop pollination services are at risk. *Trends in Ecology & Evolution* 20: 651-652
- Sýkora KV, Kalwij JM & Keizer P-J **2002**. Phytosociological and floristic evaluation of a 15-year ecological management of roadside verges in the Netherlands. *Preslia* 74: 421-436.
- Tikka PM, Högmander H & Koski PS **2001**. Road and railway verges serve as dispersal corridors for grassland plants. *Landscape Ecology* 16: 659-666.
- 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.
- van der Meijden R **2005**. *Heukels' Flora van Nederland*. Wolters Noordhoff, Groningen, Nederland.
- WallisDeVries MF, Poschod P & Willems JH **2002**. Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation* 104: 265-273.
- Wamelink W **2007**. *Simulation of vegetation dynamics as affected by nitrogen deposition*. PhD-thesis, Wageningen University, Wageningen, the Netherlands.

**Appendix A.** The flowering plant species recorded in this study, including their total number of flowers in each management type (the five plots of each type were pooled for this appendix). The groups observed to visit each plant species are given in superscript; A: bees (*Apidea* s.l. excl. *Bombus* spp.), B: bumblebees (*Bombus* spp.), C: flies (Diptera excl. Syrphidae), D: hoverflies (Syrphidae), E: beetles (Coleoptera), F: ichneumon and braconid wasps (Ichneumonoidea), G: sawflies (Tenthredinidae), and H: butterflies (Lepidoptera). Nomenclature for plants follows van der Meijden (2005).

Species	management type				
	0	1M	1M+	2M	2M+
<i>Rubus caesius</i> L. <sup>ACDE</sup>	20				
<i>Achillea millefolium</i> L. <sup>CD</sup>	37	1			
<i>Origanum vulgare</i> L. <sup>ABCDH</sup>	84		2		
<i>Cirsium arvense</i> (L.) Scop.	4			1	
<i>Centaurea jacea</i> L. <sup>ABDH</sup>	8	10	3		1
<i>Epilobium</i> spp. s.l. <sup>A</sup>	4	45	1		
<i>Pulicaria dysenterica</i> (L.) Bernh. <sup>D</sup>		9			
<i>Geranium molle</i> L.		1	1	1	
<i>Clinopodium vulgare</i> L. <sup>BCDH</sup>	26	9	28		2
<i>Vicia tetrasperma</i> (L.) Schreb. <sup>AB</sup>	23	360	265	174	223
<i>Vicia hirsuta</i> (L.) S.F.Gray <sup>ACE</sup>	15	1077	1197	239	213
<i>Lathyrus hirsutus</i> L. <sup>ABCE</sup>	2	258	388	232	297
<i>Lathyrus pratensis</i> L. <sup>ABDEH</sup>	65	212	735	33	396
<i>Bellis perennis</i> L. <sup>C</sup>	4	21	14	35	46
<i>Daucus carota</i> L. <sup>ABCDEFG</sup>	14	41	89	137	127
<i>Picris hieracioides</i> L. <sup>ABCDH</sup>	65	36	69	74	86
<i>Leucanthemum vulgare</i> Lamk. <sup>CDEFH</sup>	56	24	37	64	217
<i>Cerastium fontanum</i> Baumg. <sup>DE</sup>	13	35	61	53	130
<i>Plantago lanceolata</i> L. <sup>CDE</sup>	3	4	6	77	286
<i>Trifolium dubium</i> Sibth. <sup>ACEH</sup>		12	6	166	1636
<i>Vicia sativa</i> subsp. <i>nigra</i> (L.) Ehrh.		12	66	40	97
<i>Ranunculus repens</i> L. <sup>ADE</sup>	3	26		41	5
<i>Centaureum erythraea</i> Rafn <sup>BD</sup>	2			6	18
<i>Hypochaeris radicata</i> L. <sup>D</sup>		1	1	3	3
<i>Agrimonia eupatoria</i> L. <sup>C</sup>		1		14	
<i>Prunella vulgaris</i> L.		2	4		4
<i>Crepis biennis</i> L. <sup>BE</sup>		23		28	1
<i>Trifolium pratense</i> L. <sup>BCH</sup>		1	5	1	78
<i>Linum catharticum</i> L.		1		4	14
<i>Myosotis discolor</i> Pers.		9			37
<i>Lotus corniculatus</i> L. <sup>AB</sup>		4	152	9	21
<i>Lapsana communis</i> L. <sup>BCD</sup>			26		13
<i>Heracleum sphondylium</i> L. <sup>CDFG</sup>			2	6	2
<i>Jacobaea vulgaris</i> P.Gaertn <sup>ACD</sup>			9	3	
<i>Carduus crispus</i> L. <sup>B</sup>				60	
<i>Rhinanthus angustifolius</i> C.C.Gmel.				70	
<i>Trifolium repens</i> L.					4





5



# DIVERSITY OF GROUND BEETLES AND SPIDERS IN ROADSIDE VERGES WITH GREY HAIR-GRASS VEGETATION

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**Summary.** Roadside verges in densely populated areas are often a significant addition to the total semi-natural area and as such may contribute to the conservation of biodiversity. Furthermore, they can enhance the ecological cohesion of a region, especially when the existing nature reserves are small and/or highly fragmented. We investigated the occurrence of ground beetles and spiders in six highway verges with grey hair-grass vegetation in the Veluwe region, the Netherlands. Total species number in the verges was similar to the values found in nearby nature reserves with comparable vegetation, but the ground beetles tended to be more abundant in the reserves. Many stenotopic species were present in the verges, confirming the significant conservation value of this habitat. However, compared with the nature reserves, there were fewer species of stenotopic ground beetles and the stenotopic spiders were less abundant in the verges. From our knowledge of the biology and ecology of the species captured, it seems likely that this is attributable to differences in 'habitat quality'. In the verges, species preferring bare sand are scarcer, and the weighted mean body length of ground beetles is shorter than in nature reserves. This suggests that the sward in the road verges is too dense and the suitable vegetation too patchy to sustain some of the stenotopic species. Habitat analyses support this contention: Compared with the nature reserves, the verges had proportionally less bare sand, more herb and tree cover and the grey hair-grass vegetation patches were smaller. The strategy suggested to promote stenotopic species entails removing encroaching trees and shrubs from the verges in order to expand the nutrient-poor zone and create pioneer conditions. Subsequent management should aim at maintaining the road verges as extensions of nutrient-poor habitat.

**Key words.** Araneae, Carabidae, diversity, management, roadside verges, Spargulo-Corynephorum, stenotopic species, the Netherlands

## Introduction

The Netherlands is the most densely populated country in Europe (excluding the mini-states Monaco, Vatican City, Malta and San Marino), having an average of more than 400 inhabitants per square km and almost one car for every two persons. It has a very dense road network, around 1.8 km/km<sup>2</sup> outside the urban areas, which means that one of the main threats to biodiversity is landscape fragmentation (e.g., Mader *et al.* 1990; Forman & Alexander 1998; Spellenberg 2002; Gelbard & Harrison 2003). However, it also means that roadside verges make up an estimated 1.7% of the land area, which is not a negligible amount given that unforested natural and semi-natural areas make up only about 4% of the land area (Schaffers 2000).

The substantial areas of roadside verges can benefit biodiversity in three ways. (1) They may provide a suitable habitat for plants and small animals, especially invertebrates (Eversham & Telfer 1994; Major *et al.* 1999; Spellenberg 2002). It has been shown that in intensive agricultural or urban landscapes they may be more important to biodiversity than the hinterland (Keals & Majer 1991; De Bonte *et al.* 1997; Forman & Alexander 1998). (2) Roadsides may effectively increase the size of nature reserves, particularly if the vegetation in the nature reserve and the verge corresponds, thereby enabling larger populations or additional subpopulations of species to be sustained (Keals & Majer 1991; Vermeulen 1993). (3) Roadside verges may act as ecological corridors, enabling or improving dispersal of certain species (Getz *et al.* 1978; Vermeulen & Opdam 1995; Tikka *et al.* 2001; Delgado García *et al.* 2007). It is for these reasons that studies on the ecological value of road verges are important for effective nature management, particularly in countries with large areas under intensive agricultural use, highly fragmented nature reserves, and/or a dense road network.

In this paper, ground beetle and spider communities in six roadside verges and adjacent nature reserves are compared. At all the locations, we took samples in grey hair-grass vegetation (*Spergulo-Corynephorum*), a pioneer community of acid drift sands characteristic of inland dunes in the Netherlands. We compare the species numbers, abundances and evenness, and describe the biological characteristics of the species and compare habitat quality. The focus is on the hypothesis that roadside verges are of lower quality for stenotopic species. In the verges, the expectation is to find a lower species number or abundance, over-representation of certain species (low evenness), few large species, or the absence of poor dispersers (de Vries *et al.* 1996; den Boer 1990).

## Methods

### *Study area and sampling design*

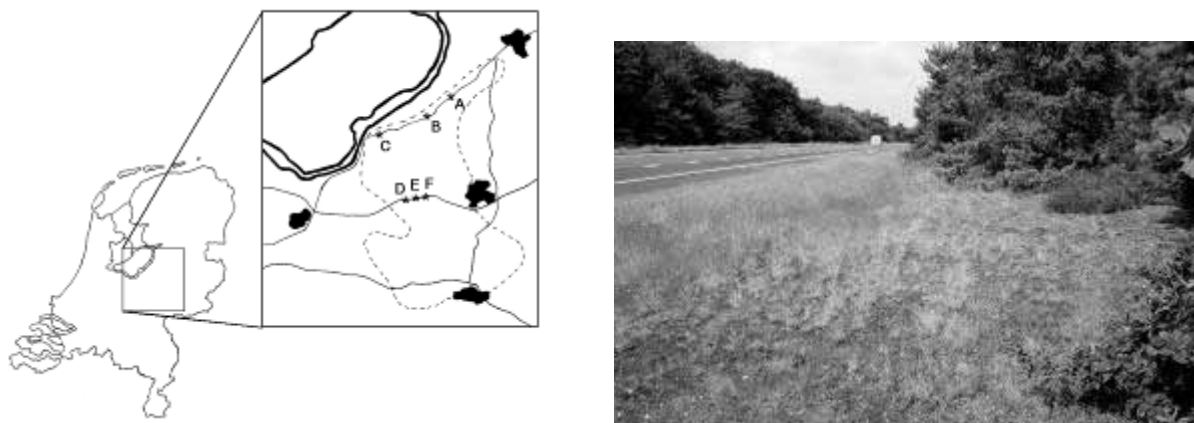
At six locations epigeic ground beetles and spiders were sampled in highway verges and nearby nature reserves, using pitfall traps. All the locations were in the Veluwe, an area of approximately 90,000 ha in the central part of the Netherlands between



52°00'N–52°30'N and 5°30'E–6°15'E (Fig. 1). This region consists of nutrient-poor, acidic, Pleistocene sands deposited during the last two ice ages. Although forests are abundant, the area is also of national importance because of the characteristic fauna living in the mosaics of drift sand, heathland, and nutrient-poor grassland.

Several highways run through the region. Their verges are seldom mown because of the nutrient-poor soil. Vegetation succession has resulted in mosaics of mosses, grasses, heather, and pine and oak trees. Although grey hair-grass vegetation used to be common in the verges in this area for many years, most of this vegetation has disappeared due to vegetation succession, which is accelerated by atmospheric nitrogen deposition (Ketner-Oostra *et al.* 2006).

For sampling, six roadside verges, constructed between 1960 and 1972, which still contained one or more patches of well developed grey hair-grass vegetation were selected (Fig. 1). In this vegetation type, mosses (*Campylopus introflexus* and *Polytrichum piliferum*), lichens (e.g., *Cladonia* spp. and *Cladina portentosa*), grasses (e.g., *Festuca ovina* s.l. and *Agrostis vinealis*) and herbs (e.g., *Rumex acetosella* and *Spergula morisonii*) can be abundant, but the sites were always selected on the basis of the presence of the character species of this vegetation type: grey hair-grass (*Corynephorus canescens*) (Weeda *et al.* 1996; Schaffers & Sýkora 2002). We also sampled vegetation patches at distances between 50 and 100 m from the roadside verge in adjacent nature reserves. These sites are more subjected to disturbances such as nature management, grazing, military tank training and/or recreation. In this way, we compared verges, which were expected to harbour a relatively high diversity of stenotopic species, with a potential species pools.



**Figure 1.** Sampling locations in the Veluwe. The inset shows highways and towns. The dashed line delineates the sandy soils of the Veluwe. The letters indicate the six locations where both roadside verges and the adjacent nature reserves were sampled. The locations are named after the nature reserves, A: 'De Haere', B: 'Hulshorsterzand', C: 'Beekhuizerzand', D: 'Caitwickerzand', E: 'Nieuw Milligsche zand', and F: 'Bremmert'. The photo shows a grey hair-grass vegetation patch in the verge at Caitwickerzand.

*Arthropod sampling*

At each location in the roadside verge and nature reserve, a series of four pitfall traps was placed in patches of grey hair-grass vegetation. The traps were operational from mid-May until mid-October at most locations in 2004; in 2006 they were operational during this period at one location. The traps were 10 cm in diameter, 9 cm deep and half-filled with a 3% formalin solution. A plastic lid placed approximately 2 cm above each trap kept out the rain and reduced evaporation. The catches were collected every two or three weeks.

All ground beetles and non-webbuilding spiders were identified to species using Boeken *et al.* (2002) and Roberts (1998). For the nomenclature of spiders we followed Platnick (2006). The catches of all four traps of a series were bulked and analysed as one sample.

*Ecological and biological traits*

From the catches we identified a subset of species typical of nutrient-poor conditions. Ground beetle species with a known preference for heathland, grey hair-grass vegetation and low vegetation on sandy soils (according to Turin *et al.* 1991; Turin 2000), were considered to be stenotopic for heathland/drift sand areas, and thus target species for conservation. Two species from this group, *Calathus micropterus* and *Pterostichus diligens* were ignored, as they can also be abundant in young forests. Our selection of stenotopic spider species of nutrient-poor conditions was based on Bauchhenss (1990), Hängi *et al.* (1995), Roberts (1998) and Bonte *et al.* (2003). The selection of the spiders was verified by comparison with distribution patterns in the Netherlands (Database European Invertebrate Survey - the Netherlands). Those ground beetle and spider species not included in the subset were mostly eurytopic species and species with a preference for forest or forest edges and nutrient-rich grassland.

The sex of all identified specimens was recorded, so we could test whether the sex ratios of the species in the roadside verges and nature reserves were different. Using species abundances and species size, we calculated the weighted mean body length for each site. Mean body length of ground beetle species was derived from Boeken *et al.* (2002). Mean body length of spider species (female size was used) was derived from Roberts (1998). Our aim was to establish whether smaller species predominated in the verges. The dispersal capacity of the stenotopic ground beetles recorded was also assessed, making a distinction between poor dispersers (species that have never been found flying in the Netherlands) and good dispersers (species that have been recorded flying in the Netherlands) (Turin 2000 and personal observations). This data was used to test whether fewer poorly dispersing species are found in the verges.

### *Environmental variables*

The percentage of the ground covered with bare sand, litter, mosses, herbs and young trees or by overhanging branches was estimated for a quadrant of 16 m<sup>2</sup> around each pitfall trap. In the same quadrant the plant species composition was recorded. The cover of each vascular plant, moss or lichen species was estimated, using a nine-point modified Braun-Blanquet scale (cf. Barkman *et al.* 1964). The distance from each trap to the nearest tree was recorded. We measured the size of the patch of grey hair-grass vegetation, up to a maximum value of 10,000 m<sup>2</sup> in some nature reserves, in order to prevent a too skewed distribution.

### *Data analysis*

Differences between the roadside verges and nature reserves in species number, abundance and evenness of 'total species' and 'stenotopic species' were studied on a pair-wise basis with Wilcoxon signed rank tests. In all analyses, we tested the hypothesis that values are higher in the nature reserves (one-sided tests). Species number is used as a measure of diversity, while evenness is used to explore the variability in species abundances (Magurán 2004). Because the efficiency of pitfall traps might differ between species and the randomness of a sample is therefore not guaranteed, we used the Brillouin index of diversity to calculate evenness (Norris 1999; Southwood & Henderson 2000).

An RDA analysis was performed on all stenotopic species, with nature reserve and roadside verge as the only explanatory variable and locations as covariables. The data were centred by species, not by samples. The location covariables (explaining 49.3% of the variation) were entered as nominal variables, implicitly leading to a pair-wise analysis of nature reserve *vs.* roadside verge. In order to reveal which species occur mainly in roadside verges or in nature reserves, the species shown on the graph are those with a fit higher than 9% on the first axis and that occur in more than one site. The significance of the explanatory variable was tested using a Monte Carlo permutation test (4,999 permutations, ter Braak & Šmilauer 1998).

Differences between the sex ratios of the stenotopic ground beetles and spiders in the roadside verges and the nature reserves were tested using Chi-squared tests. For each sampling series, weighted mean body length for each of the two arthropod groups was calculated. The hypothesis that ground beetles in nature reserves have a longer weighted mean body length than in roadside verges was tested using Wilcoxon signed rank tests. The latter test was also used to compare the species numbers and abundances of ground beetles classed as poor dispersers (never found flying) in either verges or reserves.

Plant species composition around the pitfall traps was analysed with TWINSpan (version 2.3). Environmental conditions were analysed using general linear models (GLM) to detect differences between nature reserves and roadside verges; in order to control for effects of location, location was included as a fixed factor. If necessary, data were transformed to meet assumptions of normality.

**Table 1.** The stenotopic ground beetles and non-webbuilding spiders of heath/driftsand areas, and the number of individuals caught in pitfall traps at the six locations. For the non-stenotopic species see appendices 1 and 2.

Species	Location		Hulshor-sterzand		Caitwicker-zand		De Haere		Beekhuizer-zand		N. Milligsche zand		Bremmert	
	reserve	verge	reserve	verge	reserve	verge	reserve	verge	reserve	verge	reserve	verge	reserve	verge
<b>Carabidae</b>														
<i>Amara consularis</i> (Duftschmid)	.	.	.	.	.	.	.	.	4	.	1	3	.	.
<i>Amara equestris</i> (Duftschmid)	.	8	5	3	1	.	.	.	3	3	.	.	5	2
<i>Broscus cephalotus</i> (L.)	1	.	.	.	.	.	.	.	1	.	.	.	.	.
<i>Calathus ambiguus</i> (Paykull)	3	.	206	.	.	.	.	.	31	.	3	3	192	.
<i>Cicindela campestris</i> L.	2	2	1	.	10	.	.	.	.	.	.	1	1	.
<i>Cicindela hybrida</i> L.	2	.	.	.	1	.	.	.	3	.	.	.	15	.
<i>Cicindela sylvatica</i> L.	.	.	.	.	4	.	.	.	.	.	.	.	.	.
<i>Cymindis macularis</i> Mannerh.	5	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Harpalus anxius</i> (Duftschmid)	11	16	20	50	6	5	.	.	4	.	6	42	14	12
<i>Harpalus latus</i> (L.)	.	1	.	.	.	.	.	.	.	2	1	.	.	.
<i>Harpalus neglectus</i> Serville	3	.	.	.	.	1	.	.	32	.	3	6	2	.
<i>Harpalus rufipalpis</i> Sturm	.	27	.	10	2	6	.	.	4	37	7	96	2	9
<i>Harpalus servus</i> (Duftschmid)	2	.	5	.	1	.	.	.	13	.	.	.	1	.
<i>H. smaragdinus</i> (Duftschmid)	1	6	1	1	1	.	.	.	3	.	3	39	5	2
<i>Harpalus solitarius</i> Dejean	.	2	.	.	.	.	.	.	16	.	.	.	.	4
<i>Masoreus wetterhallii</i> (Gyllen.)	.	9	.	3	.	.	.	.	.	1	5	1	.	1
<i>Notiophilus germinyi</i> Fauvel	77	.	.	30	25	59	.	.	6	16	1	4	4	24
<i>Olisthopus rotundatus</i> (Pay.)	.	3	.	.	2	4	.	.	.	.	1	6	1	2
<i>Poecilus lepidus</i> (Leske)	31	41	18	9	12	4	.	.	4	16	64	43	34	37



Table 1. Continued.

Species	Location		Hulshor-sterzand		Caitwicker-zand		De Haere		Beekhuizer-zand		N. Milligsche zand		Bremmert	
	reserve	verge	reserve	verge	reserve	verge	reserve	verge	reserve	verge	reserve	verge	reserve	verge
<b>Araneae</b>														
<i>Aelurillus v-insignitus</i> (Simon)	1	.	.	.	10	1	.	.	1	.	3	2	.	.
<i>Agelena labyrinthica</i> (Clerck)	.	.	1	.	.	.	.	.	.	.	.	.	.	.
<i>Agroeca proxima</i> (O. P.-Cam.)	2	.	.	.	1	.	.	.	.	.	.	.	.	.
<i>Alopecosa barbipes</i> (Sund.)	6	.	40	6	16	37	21	21	2	3	12	21	.	.
<i>Alopecosa fabrilis</i> (Clerck)	17	22	18	.	15	23	3	.	1	3	14	19	.	.
<i>Arctosa perita</i> (Latreille)	6	.	.	.	.	.	12	.	.	.	1	.	.	.
<i>Atypus affinis</i> Eichwald	1	1	1	24	4	.	2	1	.	.	.	.	.	.
<i>Cheiracanthium erraticum</i> (W.)	.	.	.	2	.	.	.	1	.	.	.	.	.	.
<i>Ch. virescens</i> (Sundevall)	.	2	.	.	.	.	.	.	.	2	.	2	.	.
<i>Drassodes cupreus</i> (Blackwall)	.	.	.	.	1	4	.	4	.	.	1	1	.	.
<i>Haplodrassus dalmatensis</i> (L.K.)	14	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>H. signifer</i> (C. L. Koch)	2	3	9	8	6	6	2	4	6	15	9	16	.	.
<i>Micaria dives</i> (Lucas)	1	.	.	.	4	1	.	.	.	.	.	.	.	.
<i>Micaria fulgens</i> (Walckenaer)	.	.	.	.	.	.	2	.	.	.	.	1	.	.
<i>Micaria silesiaca</i> L. Koch	.	.	.	.	1	.	.	.	1	1	9	21	.	.
<i>Ozyptilla scabricula</i> (Westring)	.	.	.	.	.	2	.	.	.	.	.	.	.	.
<i>Pardosa monticola</i> (Clerck)	26	27	62	9	3	3	17	8	389	202	112	29	.	.
<i>Pellenes tripunctatus</i> (Walck.)	2	1	.	2	.	2	.	.	5	1	1	1	.	.
<i>Phaeocedus braccatus</i> (L. K.)	.	3	.	3	.	.	.	2	.	.	.	1	.	.
<i>Phlegra fasciata</i> (Hahn)	1	1	.	.	.	1	.	4	1	.	.	.	.	.
<i>Sitticus distinguendus</i> (Simon)	.	.	.	.	1	.	1	.	.	.	.	.	.	.
<i>S. saltator</i> (O. P.-Cambridge)	8	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Steatoda albomaculata</i> (D. G.)	.	.	1	.	.	.	3	.	.	.	3	1	.	.
<i>Talavera aequipes</i> (O. P.-Ca.)	.	.	.	.	1	.	.	.	.	.	.	.	.	.
<i>Talavera petrensis</i> (C. L. Koch)	8	.	5	.	2	.	2	.	.	1	4	2	.	.
<i>Tegenaria agrestis</i> (Walcken.)	6	1	4	2	1	.	9	2	.	1	2	4	.	.
<i>Thanatus formicinus</i> (Clerck)	.	.	.	2	.	.	.	.	.	.	.	.	.	.
<i>Xysticus ninnii</i> Thorell	.	.	.	.	3	.	.	.	.	.	1	.	.	.
<i>Zelotes electus</i> (C. L. Koch)	6	4	.	.	5	17	5	9	4	1	.	5	.	.
<i>Zelotes longipes</i> (L. Koch)	57	16	61	3	30	38	28	40	45	45	66	106	.	.

## Results

### Ground beetle and spider diversity

We collected a total of 57 ground beetle and 65 spider species, and 4551 and 2999 individuals of each, respectively. There was no statistical difference between the nature reserves and the roadside verges in terms of the total numbers of species of ground beetle ( $Z = -0.368$ ,  $P = 0.36$ ) and spiders ( $Z = -0.420$ ,  $P = 0.34$ ). Though ground beetles tended to be more abundant in the nature reserves, this was not statistically significant ( $Z = -1.483$ ,  $P = 0.07$ ). For the spiders, no differences could be detected in the number of individuals ( $Z = -0.734$ ,  $P = 0.23$ ). In the nature reserves, the evenness

tended to be less, i.e., there was great variability in the species abundances, for the ground beetles ( $Z = -1.572$ ,  $P = 0.06$ ), but not for the spiders ( $Z = -1.153$ ,  $P = 0.12$ ).

#### *Stenotopic species*

Forty-nine species were classed as stenotopic for nutrient-poor conditions: 19 were ground beetles and 30 were spiders (Table 1 and Appendices 1 & 2). Analysing only these species yielded the following results (Fig. 2). The number of ground beetle species was higher in the nature reserves than roadside verges ( $Z = -1.826$ ,  $P = 0.03$ ), although the total number of individuals did not differ ( $Z = -0.153$ ,  $P = 0.13$ ). For the stenotopic spiders, no difference in species number could be detected ( $Z = -1.084$ ,  $P = 0.14$ ), but there was a tendency to fewer individuals of this group to be in the verges ( $Z = -1.572$ ,  $P = 0.06$ ). There were no statistically significant differences in evenness in the two groups between the sites in the nature reserves and the roadside verges (ground beetles:  $Z = -1.153$ ,  $P = 0.12$ ; spiders:  $Z = -0.734$ ,  $P = 0.22$ ).

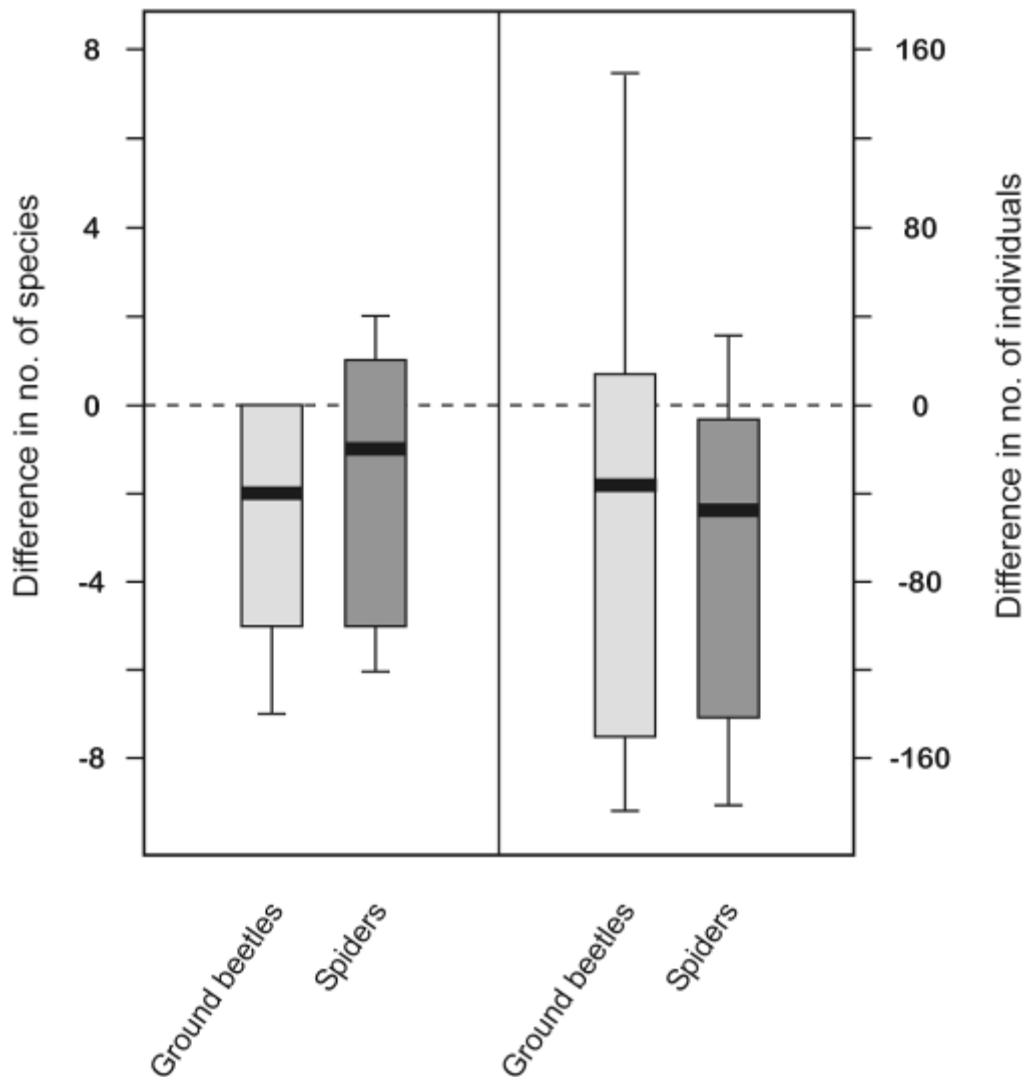
The RDA ordination of only the stenotopic ground beetles and spiders reveals the species with a strong occurrence in the nature reserves or roadside verges (Fig. 3, first axis explains 34.0% of the variation after fitting covariables,  $P < 0.005$ ). The species most clearly associated with the nature reserves are *Harpalus servus*, *Calathus ambiguus*, *Talavera petrensis*, *Cicindela hybrida* and *Arctosa perita*. Those most clearly associated with road verges are *Harpalus rufipalpis*, *Phaeocedus braccatus*, *Cheiracanthium virescens*, *Masoreus wetterhallii* and *Olisthopus rotundatus*.

If a detailed subdivision based on habitat preference is constructed for the stenotopic ground beetles (according to Turin *et al.* 1991), some patterns emerge (Table 2). Heathland species were found on 39 occasions, with a species occurring either in a verge or in the reserve at a location and 20 (51%) of these occurrences were in roadside verges. Moreover, each heathland species was found in at least two roadside verges. Species with a preference for nutrient-poor grasslands were found on 36 occasions; 16 (44%) of these were for roadside verges. Most of the nutrient-poor grassland species were found in at least one roadside verge, except for *Broscus cephalotus*, for which only two individuals were collected in a reserve. Drift sand species were found on 39 occasions; only 13 (33%) of these occurrences were in roadsides. Four of the eight drift sand species were not recorded in any of the verges.

#### *Biological traits*

We found no statistically significant difference between the verges and the nature reserves in the sex ratios of the stenotopic ground beetles ( $\chi^2 = 2.257$ ,  $P = 0.13$ ) or the spiders ( $\chi^2 = 0.992$ ,  $P = 0.32$ ).

The weighted mean body length of the stenotopic ground beetles was shorter in the roadside verges than in the nature reserves: 8.64 and 9.70 mm, respectively ( $Z = -1.782$ ,  $P = 0.04$ ). In contrast, the stenotopic spiders had a longer mean body length in the verges than the reserves: 8.04 mm versus 7.62 mm ( $Z = -2.201$ ,  $P = 0.01$ ).



**Figure 2.** Box-and-Whisker plot of pair-wise differences in species number (left) and abundance (right) of stenotopic ground beetles (pale grey bars) and spiders (dark grey bars) in six roadside verges, with the adjacent nature reserves as a reference (horizontal dotted line).

Only seven of the stenotopic ground beetle species recorded were poor dispersers, i.e., have never been observed in flight in the Netherlands: *Broscus cephalotes*, *Cymindis macularis*, *Harpalus neglectus*, *Masoreus wetterhallii*, *Notiophilus germinyi*, *Olisthopus rotundatus* and *Poecilus lepidus*. We found no statistically significant difference between the nature reserves and the roadside verges in their species number ( $Z = -0.000$ ,  $P = 1.00$ ) and abundance ( $Z = -0.314$ ,  $P = 0.75$ ).

#### *Environmental analysis*

TWINSPAN analyses of the plant species composition around the pitfall traps did not reveal a clear distinction between the sites in the nature reserves and the roadside verges (data not shown). This indicates that the sampled vegetation patches in the nature reserves and roadside verges do not differ greatly in plant species composition. The grey hair-grass vegetation patches in roadside verges could nonetheless be regarded as of poorer quality: they have a smaller area of bare sand,

more cover of herbs, and greater proximity to trees (Table 3). Since 'total surface of the vegetation patch' and 'cover of young trees and overhanging branches' could not be transformed to a normal distribution, and the nested, pair-wise design is not suitable for standard non-parametric tests, we used both GLM and Mann-Whitney U tests to approximate the statistical differences. Both patch size and cover of young trees and overhanging branches appeared to be less in the verges ( $P < 0.05$  in all cases).

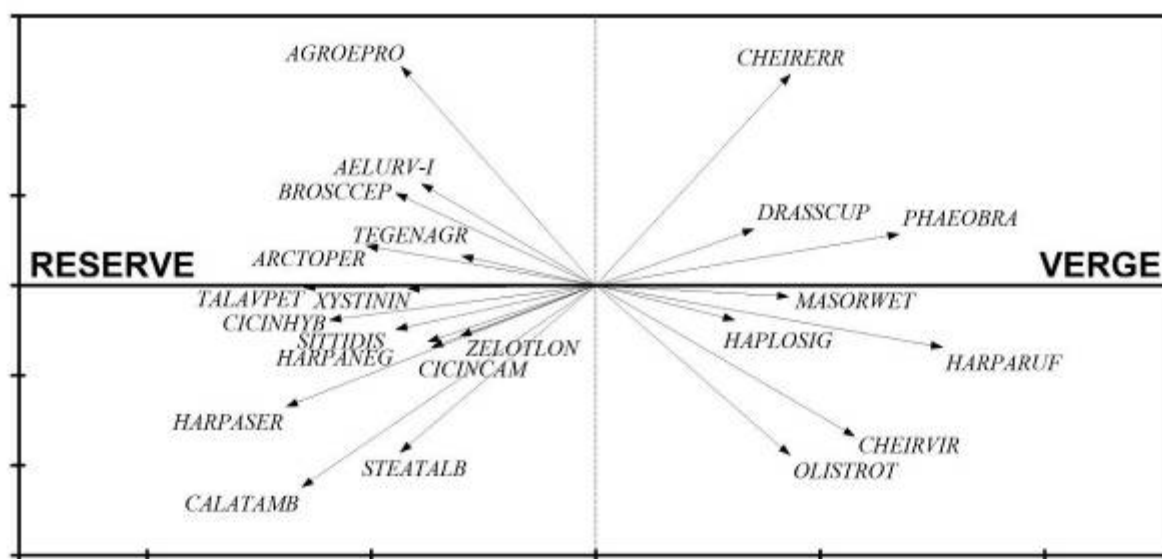
## Discussion

The finding that there was not much difference between roadsides and the adjacent nature reserves in the total number of ground beetle and spider species is not unexpected, because in the grey hair-grass vegetation patches in the verges are species that originated from adjacent vegetations, forest on one side and a strip of nutrient-rich grassland close to the road on the other side. In the nature reserves, *Calathus erratus* and *C. ambiguus* can be very abundant, which explains why in these sites ground beetles tend to be more abundant and the observed evenness is smaller. These species are characteristically abundant when large patches of homogeneous and moss-rich grey hair-grass vegetation are present (e.g., van Essen 1993).

**Table 2.** Ecological characterization and occurrence of the stenotopic ground beetles at the six locations. The second column gives the number of nature reserves where a species was found; the third column gives the number of verges where the species was found.

<b>Heathland species</b>	<b>no. reserves (19)</b>	<b>no. verges (20)</b>
<i>Amara equestris</i>	4	4
<i>Cicindela campestris</i>	4	2
<i>Harpalus latus</i>	1	2
<i>Harpalus solitarius</i>	1	2
<i>Olisthopus rotundatus</i>	3	4
<i>Poecilus lepidus</i>	6	6
<b>Nutrient-poor grassland species</b>	<b>no. reserves (20)</b>	<b>no. verges (16)</b>
<i>Amara consularis</i>	2	1
<i>Broscus cephalotus</i>	2	0
<i>Harpalus anxius</i>	6	5
<i>Harpalus smaragdinus</i>	6	4
<i>Harpalus rufipalpis</i>	4	6
<b>Driftsand species</b>	<b>no. reserves (26)</b>	<b>no. verges (13)</b>
<i>Calathus ambiguus</i>	5	1
<i>Cicindela hybrida</i>	4	0
<i>Cicindela sylvatica</i>	1	0
<i>Cymindis macularis</i>	1	0
<i>Harpalus neglectus</i>	4	2
<i>Harpalus servus</i>	5	0
<i>Masoreus wetterhallii</i>	1	5
<i>Notiophilus germinyi</i>	5	5





**Figure 3.** RDA ordination of the stenotopic species, with nature reserve / roadside verge as the explanatory variable and location as a covariable. Only species with a clear preference for nature reserves or roadside verges are shown (>9% fit on the first axis and occurring in more than one location). AELURV-I: *Aelurillus v-insignitus*, AGROEPROX: *Agroeca proxima*, ARCTOPER: *Arctosa perita*, BROSCCEP: *Broscus cephalotus*, CALATAMB: *Calathus ambiguus*, CHEIRERR: *Cheiracanthium erraticum*, CHEIRVIR: *C. virescens*, CICINCAM: *Cincindela campestris*, CICINHYB: *C. hybrida*, DRASSCUP: *Drassodes cupreus*, HAPLOSIG: *Haplodrassus signifer*, HARPANEG: *Harpalus neglectus*, HARPARUF: *H. rufipalpis*, HARPASER: *H. servus*, MASORWET: *Masoreus wetterhallii*, OLISTROT: *Olistophus rotundatus*, PHAEOBRA: *Phaeocedus braccatus*, SITTIDIS: *Sitticus distinguendus*, STEATALB: *Steatoda albomaculata*, TALAVPET: *Talavera petrensis*, TEGENAGR: *Tegenaria agrestis*, XISTININ: *Xisticus ninnii*, ZELOTLO: *Zelotes longipes*.

Numerous specialist species find suitable habitats in heathy highway verges in the Veluwe region (see also Vermeulen 1993; Noordijk & Boer 2007). In this study several ground beetle species with nature conservation value were found in quite high numbers: examples are *Amara equestris*, *Harpalus anxius*, *H. smaragdinus*, *H. solitarius*, *Poecilus lepidus* and *Olisthopus rotundatus*. These species are rare and/or in decline in the Netherlands (Desender & Turin 1989). In the roadside verges, we also found several rare spiders, e.g., *Micaria silesiaca*, *Ozyptilla scabricula*, *Pellenes tripunctatus* and *Phaeocedus braccatus* (Roberts 1998).

Although roadside verges apparently provide a suitable habitat for many stenotopic species, the number of ground beetle species and the abundance of spider species are lower there than in the adjacent nature reserve (Fig. 2). In addition, the species composition differs: in particular, some species with a preference for open vegetation with bare sand tend to be lacking in the verges (Table 2). A similar pattern emerges when only the species most characteristic of the nature reserves and roadside verges are considered (Fig. 3). The ground beetles *Harpalus servus*, *Cicindela hybrida* and *Calathus ambiguus* and the spiders *Talavera petrensis* and *Arctosa perita* were closely associated with the nature reserves; all are known to have an optimum in, or even to be restricted to, vegetation with bare sand (Roberts 1998; Turin 2000). The stenotopic species most clearly associated with the verges, the ground beetles

**Table 3.** Mean values for the environmental variables measured around individual pitfall traps. Data given for nature reserves and roadside verges are back-transformed averages. Test statistics are derived from GLM tests (controlling for the effects of location).

	transformation	nature reserves	roadside verges		
Sand cover (%)	$\ln(x+1)$	20.33	4.21	$F_1 = 28.54$	$P < 0.001$
Litter cover (%)	$\ln(x+1)$	9.04	9.67	$F_1 = 3.56$	$P = 0.07$
Moss cover (%)	$-\ln(100-(x-1))$	70.38	71.29	$F_1 = 0.04$	$P = 0.85$
Herb cover (%)	$\ln$	14.69	24.42	$F_1 = 10.49$	$P < 0.01$
Distance nearest tree (m)	$\ln$	11.25	4.15	$F_1 = 31.65$	$P < 0.001$

*Harpalus rufipalpis*, *Masoreus wetterhallii* and *Olisthopus rotundatus* and the spiders *Phaeocedus braccatus* and *Cheiracanthium virescens*, are also all known to be abundant in more closed vegetation types (Bauchhenss 1990; Roberts 1998; Turin 2000; Bonte *et al.* 2002). Angold (1997) has argued that the fumes from car exhausts affect heathland vegetation alongside roads negatively, because they cause eutrophication that boosts the growth of grasses and vascular plants and reduces the abundance and health of lichens.

In the verges studied, the grey hair-grass vegetation patches were more closed and contained less bare sand than in the nature reserves. There was more herb cover and occasionally even small trees were present. In the nature reserves, the conditions for grey hair-grass vegetation are more favourable: more dynamic (blowing sand, grazing, recreational activities), less eutrophication from traffic and targeted nature management. Furthermore, the smaller size of the vegetation patches in the roadside verges probably also negatively influences the species diversity, because the probability of colonisation is lower and that of the populations dying out is higher (Hopkins & Webb 1984; de Vries *et al.* 1996).

The smaller size of the grey hair-grass vegetation patches in the verges might also explain why the stenotopic ground beetles there had a smaller weighted mean body length. Large stenotopic species logically need larger areas than small stenotopic species, in order for them to obtain sufficient food and accommodate their larger home ranges (Tscharncke *et al.* 2002; Biederman 2003). On the other hand, the weighted mean body length of the stenotopic spiders was significantly greater in the verges. Unlike ground beetles, which often deposit their eggs, hibernate and rest in the soil (Turin 2000), spiders need structural complexity in which to construct silken webs or sacs for hibernation, resting, moulting and oviposition (Roberts 1998). So we would argue that although grey hair-grass vegetation in nature reserves might provide ample structure for small spiders, larger species possibly benefit from the structurally more complex vegetation in the verges (Halaj *et al.* 1990; Rypstra *et al.* 1999).

Some of the verges in this study were richer in stenotopic ground beetles in the past, especially in species with a preference for sandy conditions (Vermeulen 1993; Noordijk *et al.* 2005). Over the years these species have declined. It is clear that the remaining patches of grey hair-grass vegetation are declining both in area and in

quality as a result of vegetation succession. Yet it is the early successional stages that are especially important for many target species in the Veluwe region (see also Small *et al.* 2003; Riksen *et al.* 2006). The management strategy required in order to create larger areas of open vegetation entails removing invading trees from the verges and selective sod-cutting. Occasional and/or rotational mowing with removal of the cuttings can subsequently be applied to maintain open swards. The mechanical disturbance associated with this type of management will further contribute to the creation of sandy places. If these advised restoration measures are applied over a considerable length of verge, the roadsides could turn into extensive strips of open habitats for stenotopic arthropods, and thus function as ecological corridors connecting heathland and/or drift sand areas (more details in CHAPTER 9).

Perhaps the diversity of stenotopic species in roadside verges will always be lower than in nature reserves, due to area effects. Nevertheless, this study shows that a high percentage, 73%, of the stenotopic species from nature reserves can also be found in verges, demonstrating that these verges effectively contribute to the maintenance of characteristic arthropod species. This effect should be enhanced by appropriate vegetation management.

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## References

- Angold PG **1997**. The impact of a road upon adjacent heathland vegetation: effects on plant species composition. *Journal of Applied Ecology* 34: 409-417.
- Barkman JJ, Doing H & Segal S **1964**. Kritische Bemerkungen und Vorschläge zur quantitativen Vegetationsanalyse. *Acta Botanica Neerlandica* 13: 394-419.
- Bauchhenss E **1990**. Central European xerotherm habitats and their epigaeic spider fauna – an autecological approach. *Abhandlungen des Naturwissenschaftlichen Vereinigung Hamburg* 31/32: 153-162.
- Biedermann R **2003**. Body size and area-incidence relationships: is there a general pattern. *Global Ecology and Biogeography* 12: 381-387.
- Boeken M, Desender K, Drost B, van Gijzen T, Koese B, Muilwijk J, Turin H & Vermeulen R **2002**. *De loopkevers van Nederland and Vlaanderen* (Coleoptera: Carabidae). Stichting Jeugdbondsuitgeverij, Utrecht, the Netherlands.
- Bonte D, Baert L & Maelfait J-P **2002**. Spider assemblage structure and stability in a heterogeneous coastal dune system (Belgium). *Journal of Arachnology* 30: 331-343.
- Bonte D, Criel P, van Thournout I & Maelfait J-P **2003**. Regional and local variation of spider assemblages (Araneae) from coastal grey dunes along the North Sea. *Journal of Biogeography* 30: 901-911.

- de Bonte AJ, Hazebroek E, van den Hengel LC, Keijzer P-J, Sýkora KV & Schaminée JHJ **1997**. *Botanical quality of roadside verges in the Agricultural landscape*. Report no. W-DWW-97-092. Rijkswaterstaat, Dienst Weg- en Waterbouw, Delft, the Netherlands.
- Delgado García JD, Arévalo JR & Fernández-Palacios JM **2007**. Road effects on the abundance of the lizard *Gallotia gallotia* (Sauria: Lacertidae) in two Canary Islands forests. *Biodiversity and Conservation* 16: 2949-2963.
- den Boer PJ **1990**. The survival value of dispersal in terrestrial arthropods. *Biological Conservation* 54: 175-192.
- Desender K & Turin H **1989**. Loss of habitats and changes in the composition of the ground and tiger beetle fauna in four West European countries since 1950 (Coleoptera: Carabidae, Cicindelidae). *Biological Conservation* 48: 277-294.
- de Vries HH, den Boer PJ & van Dijk ThS **1996**. Ground beetle species in heathland fragments in relation to survival, dispersal, and habitat preference. *Oecologia* 107: 332-342.
- Eversham BC & Telfer MG **1994**. Conservation value of roadside verges for stenotopic heathland Carabidae: corridors or refugia? *Biodiversity and Conservation* 3: 538-545.
- Forman RTT & Alexander LE **1998**. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29: 207-231.
- Gelbard JL & Harrison S **2003**. Roadless habitats as refuges for native grasslands: interactions with soil, aspect, and grazing. *Ecological Applications* 13: 404-415.
- Getz LL, Cole FR & Gates DL **1978**. Interstate roadsides as dispersal routes for *Microtus pennsylvanicus*. *Journal of Mammalogy* 59: 208-212.
- Halaj J, Ross DW & Moldenk AR **2000**. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. *Oikos* 90: 139-152.
- Hänggi A, Stöckli E & Nentwig W **1995**. *Habitats of Central European spiders. Characterisation of the habitats of the most abundant spider species of Central Europe and associated species*. Miscellanea Faunistica Helvetica 4. Centre Suisse de Cartographie de la Faune, Neuchâtel, Switzerland.
- Hopkins PJ & Webb NR **1984**. The composition of the beetle and spider faunas on fragmented heathlands. *Journal Applied Ecology* 21: 935-946.
- Keals N & Majer JD **1991**. The conservation status of ant communities along the Wubin-Perenjori Corridor. In: *Nature conservation 2: the role of corridors* (Saunders DA & Hobbs RJ eds.): 387-393. Surrey Beatty & sons, Sydney, Australia.
- Ketner-Oostra R, van der Peijl MJ & Sýkora KV **2006**. Restoration of lichen diversity in grass-dominated vegetation of coastal dunes after wildfire. *Journal of Vegetation Science* 17: 147-156.
- Mader HJ, Schell C & Kornacker P **1990**. Linear barriers to arthropod movements in the landscape. *Biological Conservation* 54: 209-222.
- Maguran AE **2004**. *Measuring biological diversity*. Blackwell Publishing, Malden, United States of America.
- Major RE, Smith D, Cassis G, Gray M & Colgan DJ **1999**. Are roadside strips important reservoirs of invertebrate diversity? A comparison of the ant and beetle faunas of roadside strips and the large remnant woodlands. *Australian Journal of Zoology* 47: 611-624.
- Noordijk J, Vermeulen R & Heijerman Th **2005**. Ground beetles in changing roadside verges. *De Levende Natuur* 106: 255-258.
- Noordijk J & Boer P **2007**. Mieren in Veluwebermen: soortenrijkdom en aanbevelingen voor beheer (Hymenoptera: Formicidae). *Nederlandse Faunistische Mededelingen* 27: 23-50.

- Norris KC **1999**. Quantifying change through time in spider assemblages: sampling methods, indices and sources of error. *Journal of Insect Conservation* 3: 309-325.
- Platnick NI **2006**. *World spider catalog, version 7.0*. available at: <http://research.amnh.org/entomology/spiders/catalog/INTRO1.html>. [accessed on 23.xi.2006]
- Riksen M, Ketner-Oostra R, van Turnhout C, Nijssen M, Goossens D, Jungerius PD & Spaan W **2006**. Will we lose the last active inland drift sands of Western Europe? The origin and development of the inland drift-sand ecotype in the Netherlands. *Landscape Ecology* 21: 431-447.
- Roberts MJ **1998**. *Spinnengids* (translation and adaptation for the Netherlands by Noordam A.P.). Tirion Publishers, Baarn, the Netherlands.
- Rypstra AL, Carter PE, Balfour RA & Marshall SD **1999**. Architectural features of agricultural habitats and their impact on the spider inhabitants. *Journal of Arachnology* 27: 371-377.
- Schaffers AP **2000**. *Ecology of roadside plant communities*. PhD thesis, Wageningen University, the Netherlands.
- Schaffers AP & Sýkora KV **2002**. Synecology of species-rich plant communities on roadside verges in the Netherlands. *Phytocoenologia* 32: 29-83.
- Small EC, Sadler JP & Telfer MG **2003**. Carabid assemblages on urban derelict sites in Birmingham, UK. *Journal of Insect Conservation* 6: 233-246.
- Southwood R & Henderson PA **2000**. *Ecological methods*. Blackwell Science, Oxford, United Kingdom.
- Spellenberg IF **2002**. *Ecological effects of roads*. Land Reconstruction and Management, Vol. 2. Science Publisher, Enfield, USA.
- ter Braak CJF & Šmilauer P **1998**. *CANOCO Reference manual and user's guide to Canoco for Windows. Software for canonical community ordination (version 4)*. Centre for Biometry, Wageningen, the Netherlands.
- Tikka PM, Högmander H & Koski PS **2001**. Road and railway verges serve as dispersal corridors for grassland plants. *Landscape Ecology* 16: 659-666.
- Tscharntke T, Steffan-Dewenter I, Kreuss A & Thies C **2002**. Characteristics of insect populations on habitat fragments: A mini review. *Ecological Research* 17: 229-239.
- Turin H **2000**. *De Nederlandse loopkevers - verspreiding en ecologie (Coleoptera: Carabidae)*. Nederlandse Fauna 3. Museum Naturalis, KNNV Uitgeverij, European Invertebrate Survey-Nederland, Leiden, the Netherlands.
- Turin H, Alders K, den Boer PJ, van Essen S, Heijerman Th, Laane W & Penterman E **1991**. Ecological characterization of carabid species (Coleoptera, Carabidae) in the Netherlands from thirty years of pitfall sampling. *Tijdschrift v. Entomologie* 134: 279-303.
- van Essen S **1993**. *Loopkeverinventarisatie Dwingelderveld 1991*. Staatsbosbeheer, Biologisch Station Wijster, Natuurmonumenten, the Netherlands.
- Vermeulen HJW **1993**. The composition of the carabid fauna on poor sandy road-side verges in relation with comparable open areas. *Biodiversity and Conservation* 2: 331-350.
- Vermeulen HJW & Opdam PFM **1995**. Effectiveness of roadside verges as dispersal corridors for small ground-dwelling animals: a simulation study. *Landscape and Urban Planning* 31: 233-248.
- Weeda EJ, Doing H & Schaminée JHJ **1996**. *Koelerio-Coryneporeta*. In: *De vegetatie van Nederland 3* (Schaminée JHJ, Stortelder AHF & Weeda EJ eds.): 61-144. Opulus Press, Uppsala, Sweden.

**Appendix 1.** The ground beetle species recorded that are not stenotopic for sandy nutrient-poor conditions. For the stenotopic species, see Table 1.

<i>Abax ater</i> (Villers)	<i>Calathus melanocephalus</i> (L.)	<i>Loricera pilicornis</i> (Fabricius)
<i>Amara communis</i> (Panzer)	<i>Calathus micropterus</i> (Duftschmid)	<i>Nebria brevicollis</i> (Fabricius)
<i>Amara eanea</i> (Degeer)	<i>Calathus rotundicollis</i> (Dejean)	<i>Notiophilus aquaticus</i> (L.)
<i>Amara familiaris</i> (Duftschmid)	<i>Carabus nemoralis</i> Herbst	<i>Notiophilus palustris</i> (Duftschmid)
<i>Amara lunicollis</i> Schieodte	<i>Carabus problematicus</i> Herbst	<i>Oxypselaphus obscurus</i> (Herbst)
<i>Amara plebeja</i> (Gyllenhal)	<i>Carabus violaceus</i> L.	<i>Poecilus cupreus</i> (L.)
<i>Bembidion lampros</i> (Herbst)	<i>Clivina fossor</i> (L.)	<i>Poecilus versicolor</i> (Sturm)
<i>Bembidion properans</i> (Stephens)	<i>Cychrus caraboides</i> (L.)	<i>Pseudoophonus rufipes</i> (Degeer)
<i>Bembidion quadrimaculatum</i> (L.)	<i>Harpalus affinis</i> (Schrank)	<i>Pterostichus niger</i> (Schaller)
<i>Bembidion tetracolum</i> Say	<i>Harpalus laevipes</i> Zetterstedt	<i>Pterostichus vernalis</i> (Panzer)
<i>Bradycellus harpalinus</i> (Serville)	<i>Harpalus rubripes</i> (Duftschmid)	<i>Syntomus foveatus</i> (Geoffroy)
<i>Calathus erratus</i> (C.R. Sahlberg)	<i>Harpalus tardus</i> (Panzer)	<i>Trechus quadristriatus</i> (Schrank)
<i>Calathus fuscipes</i> (Goeze)	<i>Leistus ferrugineus</i> (L.)	

**Appendix 2.** The non-webbuilding spider species recorded that are not stenotopic for sandy nutrient-poor conditions. For the stenotopic species see Table 1.

<i>Agroeca brunnea</i> (Blackwall)	<i>Evarcha falcata</i> (Clerck)	<i>Pisaura mirabilis</i> (Clerck)
<i>Alopecosa cuneata</i> (Clerck)	<i>Heliophanus flavipes</i> (Hahn)	<i>Steatoda phalerata</i> (Panzer)
<i>Alopecosa pulverulenta</i> (Clerck)	<i>Micaria pulicaria</i> (Sundevall)	<i>Tibellus oblongus</i> (Walckenaer)
<i>Clubiona comta</i> C.L. Koch	<i>Neon reticulatus</i> (Blackwall)	<i>Trochosa terricola</i> Thorell
<i>Clubiona diversa</i> O.P. -Cambridge	<i>Ozyptila praticola</i> (C.L. Koch)	<i>Xerolycosa nemoralis</i> (Westring)
<i>Clubiona reclusa</i> O.P. -Cambridge	<i>Pardosa lugubris</i> (Walckenaer)	<i>Xysticus cristatus</i> (Clerck)
<i>Coelotes terrestris</i> (Wider)	<i>Pardosa nigriceps</i> (Thorell)	<i>Xysticus erraticus</i> (Blackwall)
<i>Drassodes pubescens</i> (Thorell)	<i>Pardosa palustris</i> (L.)	<i>Xysticus ferrugineus</i> Menge
<i>Drassylus pusillus</i> (C.L. Koch)	<i>Pardosa pullata</i> (Clerck)	<i>Xysticus kochi</i> Thorell
<i>Euophrys frontalis</i> (Walckenaer)	<i>Pardosa saltans</i> Töpfer-Hofmann	<i>Zelotes petrensis</i> (C. L. Koch)
<i>Euryopis flavomaculata</i> (C.L. Koch)	<i>Philodromus cespitum</i> (Walckenaer)	<i>Zelotes subterraneus</i> (C. L. Koch)
<i>Evarcha arcuata</i> (Clerck)	<i>Pirata hygrophilus</i> Thorell	





6





# HABITAT AND MOVEMENT CORRIDORS TO IMPROVE LANDSCAPE CONNECTIVITY FOR HEATHLAND CARABIDS

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**Summary.** Heathland and drift sand areas in the Netherlands are declining in size and quality, and becoming increasingly fragmented. The connectivity of the landscape for threatened insects might be improved by creating networks of corridors. We studied carabid beetles in heathy roadside verges and newly-created linear forest clearings, and compared this with heathland nature reserves and forests. The clearings were created in between the roadside verges and the nature reserves half-way the study period. Species composition and abundance in the four landscape elements involved (roadsides, forest clearings, nature reserves and forests) were assessed using pitfall and window traps. Principal Component Analysis showed that the carabid species composition in roadside verges differed from that in nature reserves, both before and after the creation of the connecting forest clearings. Of the 29 target species selected from the pitfall traps, 19 were nonetheless present in the roadside verges. In addition, the occurrence of teneral individuals and flightless species indicate that the verges provide valuable habitat where reproduction takes place. Forests acted as barriers for many target carabids. In the pitfalls traps in forest clearings, target carabids were encountered in similar amounts as in the nature reserves and roadside verges, but teneral individuals were only found for two species. In contrast, flying carabids were far more abundantly caught in the forest clearing corridors than in adjacent verges or nature reserves. This indicates that these linear forest clearings are particularly used by dispersing carabids. It is concluded that roadside verges can act as *habitat corridors* and that linear forest clearings are particularly used as *movement corridors*. This way, these structures offer a simple solution for increasing the connectivity of fragmented landscapes for a threatened insect group.

**Key words.** Carabidae, ecological network, forest clearing, insect conservation, the Netherlands, roadside verge

## Introduction

During the last 150 years, over 90% of the total area of heathland and drift sand in the Netherlands has been lost (van Duuren *et al.* 2003). It has been replaced by agriculture or by forests through forestation and vegetation succession. The remaining sites are losing quality through eutrophication and acidification caused by atmospheric deposition of nitrogen and sulphur (Bobbink *et al.* 1998; Ketner-Oostra *et al.* 2006). Since nutrient-poor conditions are becoming increasingly rare in the Netherlands, remaining heathland and drift sand areas are very important habitats and refuges for certain species (e.g., Riksen *et al.* 2006) and these habitats have also been designated European target ecosystems for conservation (European Community 1992). Not only does the reduction in their total area have severe implications; the resulting fragmentation and isolation also poses threats for the biodiversity (Noss & Csuti 1997; Hilty *et al.* 2006).

Carabid beetles (or ground beetles, Coleoptera: Carabidae) form a highly diverse insect family, with approximately 370 species occurring in the Netherlands (Turin 2000). Many vegetation types have their own specialized carabids (Turin *et al.* 1991; Schaffers *et al.* 2008). Habitat fragmentation is an important factor causing the decline of specialist species (Turin & den Boer 1988; de Vries & den Boer 1990; de Vries *et al.* 1996) and species of heathland and drift sand are among the carabids most severely in decline (Turin & Heijerman 1997). Although no official conservation policy – for example a red list – does exist for carabids in the Netherlands, in this paper we consider stenotopic species of nutrient-poor open vegetations and species of open areas showing a decline in our country as target species for conservation management of heathlands and drift sands.

The construction of corridors is often proposed as a means to alleviate fragmentation effects on species (Beier & Noss 1998; Haddad & Baum 1999). In highly fragmented landscapes, such corridors could improve the exchange of individuals between remaining sites, thereby enabling colonization of unoccupied sites or strengthening existing populations (Hilty *et al.* 2006; Hanski & Pöyry 2007). Different types of corridor can be distinguished: e.g., habitat corridors, which link discrete nature reserves by similar vegetation, thus increasing the habitat area and enhancing the opportunities for target species to live and reproduce, and movement corridors, which are primarily designed to facilitate movements of individuals of target species from one habitat patch to another (Anderson & Jenkins 2006). A corridor might be a movement corridor for one species and a habitat corridor for another species.

In this paper, we study two linear landscape elements on their potential role as ecological corridor. First, we examine to what extent roadside verges with high-quality nutrient-poor vegetation patches are suitable habitat for target carabids. This provides insight into the potential corridor function of long stretches of suitable verge. Ecological conditions of verges might not be suitable for target species due to the negative effects of the linear outline and resulting ecotonal effects, the inferior

quality of the vegetation, the small size and the disturbance, pollution and kills caused by traffic (Gish & Christensen 1973; Munguira & Thomas 1992; Angold 1997; Forman *et al.* 2002; Spellerberg 2002). Secondly, we examine ground-dwelling and flying carabids in linear forest clearings connecting two open areas. This gives insight into the potential corridor function of open linear structures through a forested landscape – for example recreational or forestry paths, fire lanes, or strips of tree-free vegetation under power lines. Such linear structures are expected to have a positive effect on dispersal (e.g., Haddad & Tewksbury 2005), although this effect probably depends strongly on the quality and the width of the corridor. Also, due to the effects of the extensive ‘edge habitat’ in linear forest clearings, many target species possibly avoid these structures (Pryke & Samways 2001; Ewers & Didham 2008).

## Material & Methods

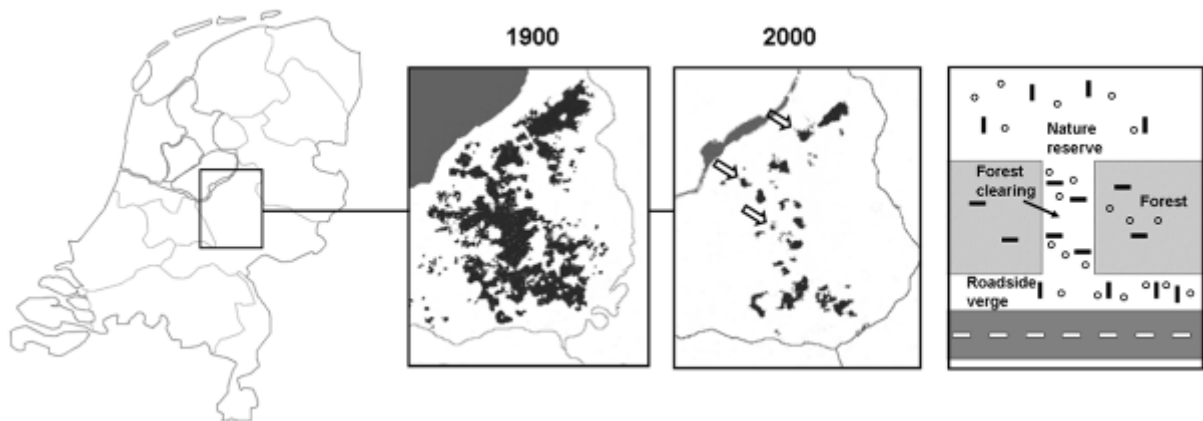
### *Study area*

Our study areas were located in the Veluwe (Fig. 1; all locations between 52°00′N–52°30′N and 5°30′E–6°15′E), an area in the centre of the Netherlands, with Pleistocene, sandy and acidic soils on which pine and oak forests, heath and drift sand typically occur (Weeda *et al.* 2002). Here, from the end of the 15th century until around 1900, the landscape was dominated by heathland and drift sand. Between around 1900 and 1970 many of these areas were afforested with conifers, leaving only fragments of open areas (Fig. 1), which are currently at threat from eutrophication and encroachment by trees.

The highway verges in this region were constructed using the local sandy soil and have therefore often been colonized by nutrient-poor plant communities such as dry inland heath (*Genisto-Callunetum*), nutrient-poor heathy grassland (*Thero-Airion*) and pioneer drift sand vegetation (*Spergulo-Corynephorretum*). Particularly in the first few decades after their construction, these verges contained relatively large stretches of habitat suitable for species typical of nutrient-poor habitats. The vegetation in these verges was not usually managed, as this seemed unnecessary given to the nutrient-poor conditions. At present, however, the valuable plant communities are disappearing, due to succession of the vegetation towards high and dense plant communities (Sýkora *et al.* 2002). The remaining nutrient-poor vegetation patches in the verges are very small and completely isolated from similar sites. Especially large roadside stretches with encroaching pine trees, already very close to the asphalt edge, seem major barriers for xero- and thermophilic species (see CHAPTER 9; Fig. 3).

### *General setup*

At three locations – Caitwickerzand, De Haere and Hulshorsterzand – all along highways, the roadside verge and a nearby nature reserve were sampled for carabids between 2003 and 2006. A linear forest clearing, created in the winter of 2004/2005 connecting the open area of the verge to the nature reserve, and the adjacent



**Figure 1.** Distribution of heathland and drift sand in the Veluwe region in the central part of the Netherlands in 1900 and 2000. The arrows indicate the study locations alongside highways. At each study location several landscape elements were sampled with pitfall (○) and window traps (—), the set-up of which is depicted in the right graph.

undisturbed forest were sampled as well (Table 1). The monitored roadside verges were selected on the basis of their vegetation quality; patches of well-developed *Genisto-Callunetum* (dry heath) and *Spergulo-Corynephorretum* (grey hair-grass) vegetation were chosen. These patches were isolated from other similar patches, both in nature reserves and in the verges, by vegetation types with higher standing biomass. The well-developed patches function as reference habitats, indicating the potential insect diversity in roadside verges in the Veluwe region. At the beginning of the fieldwork, the monitored road verges were all isolated from nearby nature reserves by Scots pine (*Pinus sylvestris*) forest. After sampling the road verges and nature reserves for two years, at each location a strip of forest was removed between the reserve and the verge. These linear forest clearings differed in size, orientation,

**Table 1.** Characteristics of the four studied landscape elements (nature reserve, roadside verge, forest and forest clearing) at each of the three study locations.

	Caitwickerzand	Hulshorsterzand	De Haere
<b>Nature reserve</b>			
<i>Dominant vegetation</i>	fixed drift sand	active drift sand & heath	heath & fixed drift sand
<i>Size of open area</i>	150 ha	300 ha	100 ha
<b>Roadside verge</b>			
<i>Dominant vegetation</i>	fixed drift sand & heath	fixed drift sand & heath	fixed drift sand & heath
<i>Size of open area</i>	170 m <sup>2</sup>	700 m <sup>2</sup>	220 m <sup>2</sup>
<b>Forest clearing</b>			
<i>Length x width</i>	200 m x 20 m	60 m x 20 m	100 m x 20 m
<i>Direction from nature reserve</i>	east-west	west-east	east-west
<i>Ground cover</i>	nutrient-poor grassland	bare sand	bare sand
<b>Forest</b>			
<i>Type of forest</i>	<i>Pinus sylvestris</i> & <i>Quercus robur</i>	<i>Pinus sylvestris</i>	<i>Pinus sylvestris</i>

and type of soil cover (Table 1). At two locations, the topsoil was also removed, to expose sand. At one location an existing patch of nutrient-poor grassland was enlarged and connected to both nature reserve and roadside verge by removing trees.

Carabid sampling was done with pitfall and window traps. The pitfall traps to capture ground-dwelling individuals were placed at least 10 m apart and were operational for four consecutive years, 2003-2006, from mid-May until mid-October. The traps were 10 cm in diameter, 9 cm deep and half-filled with a 3% formalin solution. A plastic lid was placed approximately 1½ cm above each trap to keep out the rain. The catches were collected every two or three weeks. Flying beetles were sampled using window traps consisting of a wooden frame containing a transparent perspex pane of 80 by 60 cm, fixed vertically, with its lower side 1 m above ground level (adapted from the description in Duelli *et al.* 1999). Under the panes plastic gutters were placed and they were half-filled with water that was saturated with salt; the gutters protruded 9 cm on either side. The samples were collected weekly.

#### *Study 1: Carabids in roadside verges and nature reserves*

Each of the three roadside verges was sampled with a series of 5 pitfall traps. The trap catches were subdivided into two periods: one period was prior to the creation of the forest clearing (2003 & 2004) and the other period was after the creation of the forest clearing (2005 & 2006).

Nearby nature reserves (ca. 60-200 m from the verges) were sampled as well, again using pitfall traps. These samples were also subdivided into before (2003 & 2004) and after the creation of the forest clearing (2005 & 2006). In De Haere and Hulshorsterzand 5 pitfall traps were used per year, while at Caitwickerzand 4 pitfall traps were used in the reserve.

All ground beetles were identified to species-level and for the roadside catches the presence of teneral was noted. Teneral beetles have recently emerged from the pupae, and are recognizable by the soft chitinous body parts and the underdeveloped colour of the body. Their presence was taken as proof of successful reproduction of the species in the verge. Before the connecting forest clearings were created the presence of flightless species (species that have never been observed flying in the Netherlands) in the roadside verges was used as a second indication that carabids were probably reproducing here, as the isolation of the suitable roadside patches would likely prevent walking carabids from reaching these sites (flight capability taken from Turin 2000 and personal observations).

#### *Study 2: Carabids in forest clearings*

Forests are expected to act as barriers that hinder the exchange of carabid individuals between open habitats. According to this hypothesis, very few target carabids would be found in the forests, and because forest clearings could be expected to substantially reduce the barrier effect, these clearings are expected to be frequently used by dispersing carabids. To study the effect of the created forest clearings,

sampling with both pitfall and window traps was done in the nature reserve, roadside verge, forest clearing and the undisturbed forest adjacent to the forest clearing (from now on these four habitat types will be called 'landscape elements'). The data were collected in 2005 for Caitwickerzand and De Haere and in 2006 for Hulshorsterzand (the clearings were created in winter 2004/2005). Some of the pitfall traps for study 1 were simultaneously used for study 2. All traps were operational from mid-April until mid-October.

Series of pitfall traps were used to sample ground-dwelling carabids. Three pitfall traps were placed in the forest, three at the 'beginning' of the forest clearing closer to the nature reserve (at distances of 10-40 m from the nature reserve), three at the opposite 'end' of the clearing (at 10-40 m from the roadside verge), three in the roadside verge closer to the forest clearing (at 10-30 m from the forest clearing) and three further away from the clearing (at 40-70 m from the forest clearing). In the nature reserve we placed six pitfall traps, except at Caitwickerzand where the catches of 4 pitfall traps were used. We took account of the presence of teneral individuals in the forest clearing.

Four window traps were placed in each landscape element. The window traps in the forest (at 20-40 m from the clearing) and forest clearing (evenly distributed over the length of the clearing) were oriented perpendicular to the direction of the linear forest clearing. The window traps in the nature reserves (at 20-60 m from the forest and clearings) and the roadside verges (at 20-60 m from the forest and clearings) were positioned perpendicular to the road. Flight as a movement strategy is relatively uncommon in carabid beetles and is limited to periods in which the flight muscles of the individuals are fully developed and weather conditions are optimal (van Huizen 1979; Nelemans 1987). This implies that in most species flight is only employed for dispersal or (re)colonization of suitable habitats (den Boer 1970; Boiteau *et al.* 2000; Turin 2000). Only few species are an exception to this and fly during their entire adult life. Such species, however, only constitute a small fraction of the catches presented in this study. Window traps in our study therefore mainly sample naturally dispersing carabids.

### *Analyses*

Principal Component Analysis in Canoco 4.5 (PCA, after checking the length of gradient) was used in both studies to identify the main gradients in carabid species composition of all species and their relationship to the landscape elements studied. In study 1, PCA was also used to detect changes in species composition within the roadside verges and the nature reserves before and after the construction of the forest clearing. The ordinations are based on the pooled catches per landscape element per location, divided by the number of traps used, to correct for the occasional differences therein. Carabid abundances were ln-transformed and only species with a fit higher than 25% in the first two dimensions are included in the graphs.

From all catches, a subset of 'target' species was selected, consisting of stenotopic species with a preference to drift sand, heathland and other nutrient-poor

open habitats (A1, B1 and B2 species in Turin 2000). In addition, other open habitat species (from Turin 2000) were included, but only those that show a clear decline in occurrence in the Netherlands (according to Desender & Turin 1989).

Repeated measures General Linear Model (RM-GLM) tests were used to test for differences in abundance and diversity between the roadside verges and nature reserves over the two periods. General Linear Models (GLM; ANOVA) and Tukey post-hoc tests were used to find differences in abundance and diversity between the four landscape elements of study 2. Levene's test was used to check for homogeneity of variance. To meet the normality assumption, carabid abundance data were ln-transformed. Data from individual traps were used as replicates to test for differences over the landscape elements. Location was always used as random factor in the models. All analyses were performed in SPSS 15.

## **Results**

### *Study 1: Carabids in roadside verges and nature reserves*

The pitfall traps in the verges collected 3851 individuals belonging to 76 species. Nineteen of these, with 1449 individuals, could be classified as target species (Table 2, and see Appendix A for the non-target species). Teneral individuals were collected for 10 of these 19 species. Eight of the 19 target species are flightless but nevertheless occurred in the verge patches during the first two years of the study when verges were still isolated from nature reserves (and any other area with open vegetation) by forest (Table 2). In the nature reserves, 6143 individuals belonging to 58 species were collected, of these, 24 species caught with 4658 individuals could be classified as target species. Ten of these did not occur in the verges (Table 2), but on the other hand 5 target species were observed in the verges that were not caught in the nature reserves.

Ordination on all carabids showed that the most important variation in species composition (reflected on the first axis) nevertheless relates to the difference between verges and nature reserves. The second axis mainly relates to differences between locations (Fig. 2; the first two axes together accounted for 55% of the variation in species composition). Species on the right-hand side of the graph were more common in the nature reserves. Species on the left-hand side of the graph were more abundant in the roadside verges with the exception of some species mainly found at the De Haere location. The two periods – before and after the creation of the forest clearing between reserve and verge – showed only minor differences in species composition (Fig. 2). Moreover, the temporal shifts in species composition in the verges tended to proceed in the same general direction as those within the reserves.

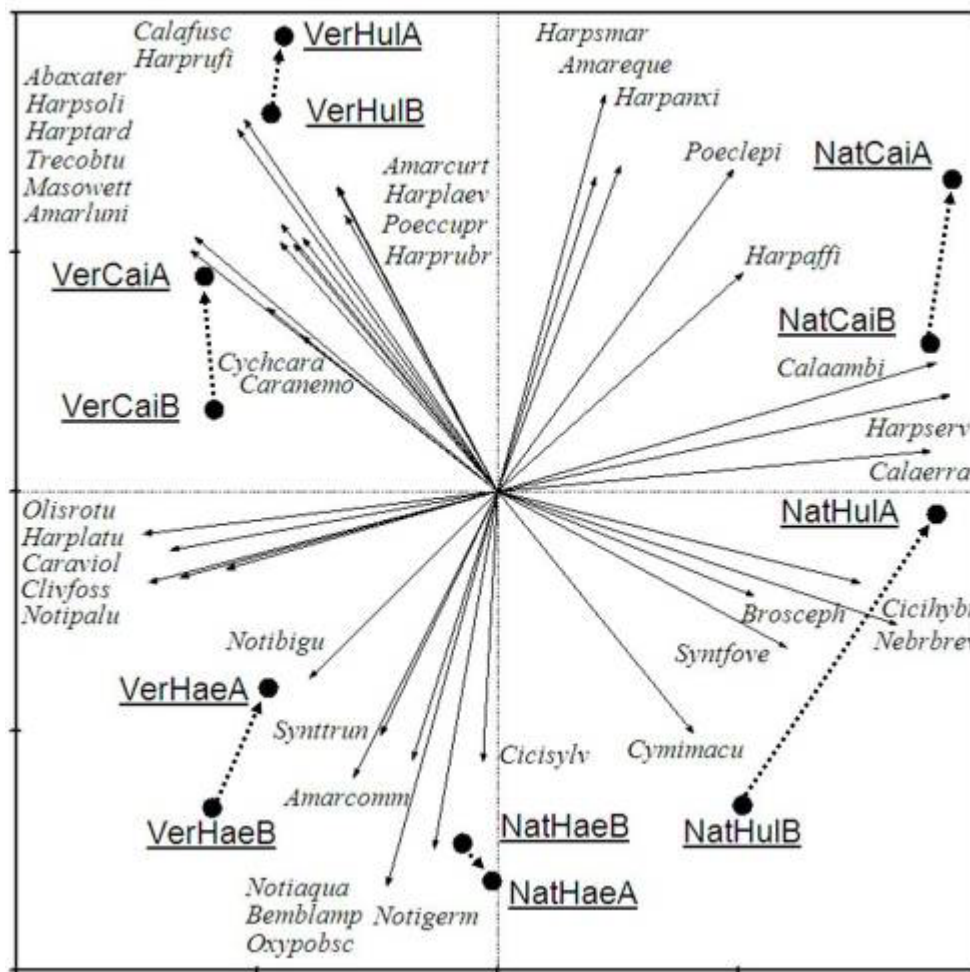
The abundance of all carabids differed between the roadside verges and the nature reserves, both in the period before and after the creation of the forest clearing, with the nature reserves having a higher abundance (before:  $F_{1,25} = 10.81$ ,  $P = 0.003$ ; after  $F_{1,25} = 7.25$ ,  $P = 0.012$ ). The number of all carabid species did not differ in both

**Table 2.** The average abundance of target carabids in pitfall traps in nature reserves and roadside verges (study 1). The values are summed for the three locations and divided by the total number of traps per landscape element (nature reserves = 56, roadside verges per period = 30). Locations where the species was found during the entire study are given using abbreviations after the species name; Ca = Caitwickerzand, Ha = De Haere, Hu = Hulshorsterzand. If in a roadside verge several individuals for a particular species were caught, the abundance is given in bold. If a species is flightless but was found in roadside verges during the first two years of the experiment (when these were still isolated patches of suitable habitat) the abundance is given underlined.

species	nature reserves '03-'06	verges '03-'04	verges '05-'06
<i>Amara consularis</i> (Duft.) [Ca, Ha, Hu]	0.04	0.00	0.10
<i>Amara convexior</i> Steph. [Ca]	0.00	0.00	0.03
<i>Amara curta</i> Dej. [Hu]	0.00	<u>0.03</u>	0.03
<i>Amara equestris</i> (Duft.) [Ca, Ha, Hu]	0.78	<b><u>0.43</u></b>	<b>0.60</b>
<i>Amara quenseli</i> Zimm. [Hu]	0.35	0.00	0.00
<i>Bembidion nigricorne</i> Gyll. [Ca, Ha, Hu]	0.09	0.00	0.00
<i>Bradycellus ruficollis</i> (Steph.) [Ha, Hu]	0.00	0.00	0.03
<i>Broscus cephalotes</i> (L.) [Hu]	0.22	0.00	0.00
<i>Calathus ambiguus</i> (Payk.) [Ca, Ha, Hu]	19.76	0.00	0.00
<i>Calathus erratus</i> (Sahlb.) [Ca, Ha, Hu]	50.33	<b><u>0.67</u></b>	<b>1.90</b>
<i>Cicindela campestris</i> L. [Ca, Ha, Hu]	0.46	0.23	0.00
<i>Cicindela hybrida</i> L. [Ca, Ha, Hu]	0.31	0.00	0.00
<i>Cicindela sylvatica</i> L. [Ha]	0.19	0.00	0.00
<i>Cymindis macularis</i> Mann. in Fisch.-W. [Ha, Hu]	0.19	0.00	0.00
<i>Harpalus anxius</i> (Duft.) [Ca, Ha, Hu]	4.39	<b>2.93</b>	<b>7.13</b>
<i>Harpalus latus</i> (L.) [Ca, Ha, Hu]	0.02	<b>0.23</b>	0.23
<i>Harpalus neglectus</i> Serv. [Ha, Hu]	0.54	<u>0.03</u>	0.13
<i>Harpalus rufipalpis</i> Sturm [Ca, Ha, Hu]	0.78	<b>5.17</b>	<b>5.67</b>
<i>Harpalus servus</i> (Duft.) [Ca, Hu]	0.63	0.00	0.00
<i>Harpalus smaragdinus</i> (Duft.) [Ca, Ha, Hu]	0.22	0.23	0.40
<i>Harpalus solitaris</i> Dej. [Ha, Hu]	0.00	0.07	0.10
<i>Harpalus tardus</i> (Panz.) [Ca, Ha, Hu]	0.74	<b>2.03</b>	4.37
<i>Masoreus wetterhallii</i> (Gyll.) [Ca, Ha, Hu]	0.00	<b><u>0.50</u></b>	<b>0.20</b>
<i>Nebria salina</i> Fairm.Lab. [Ca, Ha, Hu]	0.76	0.00	0.00
<i>Notiophilus aesthuans</i> (Dejean) [Ca]	0.02	0.00	0.00
<i>Notiophilus germinyi</i> Fauvel [Ca, Ha, Hu]	3.33	<b><u>3.43</u></b>	<b>2.70</b>
<i>Olisthopus rotundatus</i> (Payk.) [Ca, Ha, Hu]	0.22	<u>0.27</u>	<b>0.37</b>
<i>Poecilus lepidus</i> (Leske) [Ca, Ha, Hu]	4.24	<b><u>3.17</u></b>	3.47
<i>Pterostichus diligens</i> (Sturm) [Ca, Ha, Hu]	0.15	0.80	0.20

periods between the two landscape elements (before:  $F_{1,25} = 0.20$ ,  $P = 0.660$ ; after  $F_{1,25} = 2.19$ ,  $P = 0.151$ ). For only the target species similar patterns were obtained for abundance, in both periods the nature reserves had highest abundance (before:  $F_{1,25} = 18.46$ ,  $P < 0.001$ ; after  $F_{1,25} = 8.54$ ,  $P < 0.007$ ). The nature reserves had higher diversity of target species than the verges, in the period before the creation of the forest clearing this was only marginally so ( $F_{1,25} = 3.52$ ,  $P = 0.072$ ), but after the creation this became more noticeable ( $F_{1,25} = 5.30$ ,  $P = 0.030$ ).





**Figure 2.** PCA ordination of the carabid species composition of study 1: carabids in roadside verges and nature reserves caught with pitfall traps. Site codes (underlined): Ver = verge, Nat = nature reserve, Hae = De Haere, Cai = Caitwickerzand, Hul = Hulshorsterzand (Hul), B = sampled prior to creation of the corridor, A = sampled after creation of corridor. Carabid species codes are a combination of the first four letters of the genus name and the species name.

### Study 2: Carabids in the forest clearings

The pitfall traps in study 2 yielded 6190 individuals of 72 species. Of these, 27 species and 3262 individuals concerned target species. Although two additional landscape elements were sampled in this study (forest and forest clearing), no new target species were encountered as compared to study 1. With the pitfall traps in the forest clearings 18 target species were collected (Table 3, and see Appendix A for the non-target species), but for only two of these tenerals were found: *Harpalus rufipalpis* and *Nebria salina*.

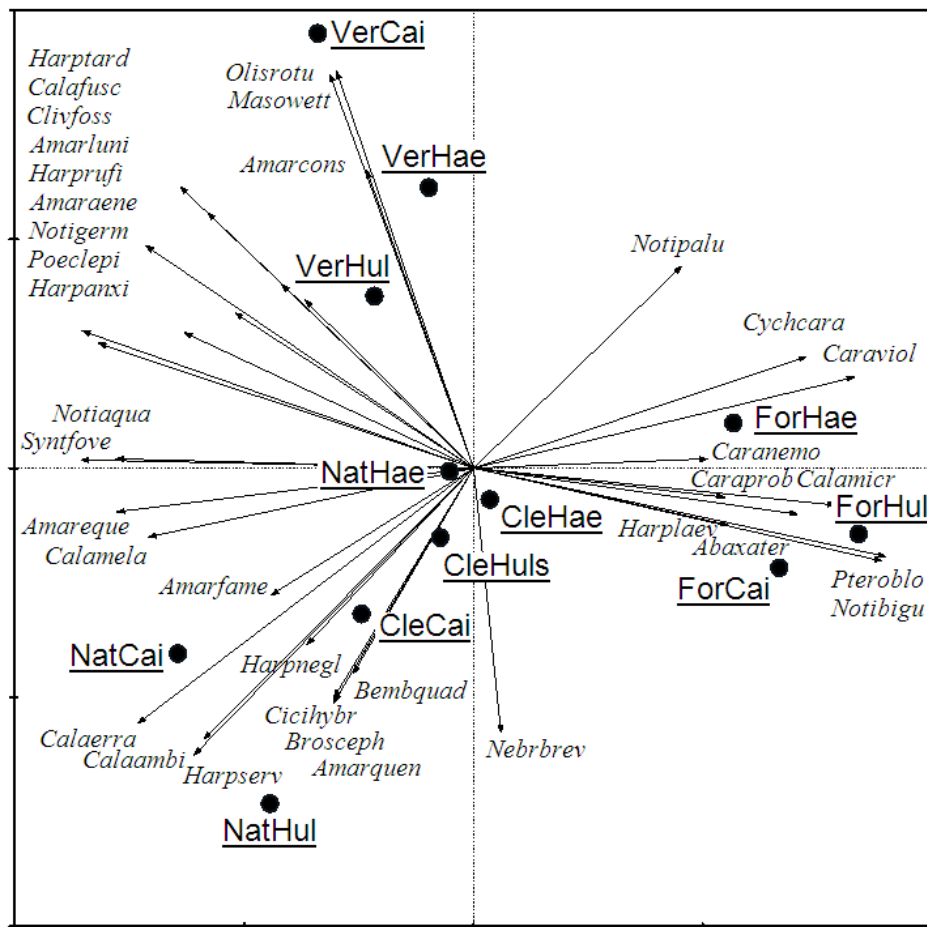
Ordination of all the species caught with the pitfall traps revealed that the first axis mainly separated the forests from the other landscape elements, i.e., the forests deviated most in species composition. The second axis separated the roadside verges from the nature reserves and forest clearings (Fig. 3, together the first two axes accounted for 52% of the variation in species composition).

**Table 3.** The average abundance of target carabids in pitfall traps in the forest clearings (study 2). The values are summed for the three locations and divided by the total number of traps per landscape element (= 18). Locations where the species was found during the entire study are given using abbreviations after the species name; Ca = Caitwickerzand, Ha = De Haere, Hu = Hulshorsterzand.

species	forest clearings
<i>Amara equestris</i> (Duft.) [Ca, Ha, Hu]	0.28
<i>Amara quenseli</i> Zimm. [Hu]	0.22
<i>Calathus ambiguus</i> (Payk.) [Ca, Hu]	0.11
<i>Calathus erratus</i> (Sahlb.) [Ca, Ha, Hu]	25.72
<i>Cicindela campestris</i> L. [Ca, Ha, Hu]	1.44
<i>Cicindela hybrida</i> L. [Ca, Ha, Hu]	0.11
<i>Cicindela sylvatica</i> L. [Ha]	0.17
<i>Harpalus anxius</i> (Duft.) [Ca, Ha, Hu]	0.72
<i>Harpalus neglectus</i> Serv. [Ha, Hu]	0.83
<i>Harpalus rufipalpis</i> Sturm [Ca, Ha, Hu]	3.44
<i>Harpalus servus</i> (Duft.) [Ca, Hu]	0.39
<i>Harpalus smaragdinus</i> (Duft.) [Ca, Ha, Hu]	0.61
<i>Harpalus solitarius</i> Dej. [Ha, Hu]	0.06
<i>Harpalus tardus</i> (Panz.) [Ca, Ha, Hu]	0.67
<i>Nebria salina</i> Fairm.Lab. [Ca, Ha, Hu]	3.28
<i>Notiophilus germinyi</i> Fauvel [Ca, Ha, Hu]	1.17
<i>Poecilus lepidus</i> (Leske) [Ca, Ha, Hu]	1.06
<i>Pterostichus diligens</i> (Sturm) [Ca, Ha, Hu]	0.28

Abundance and diversity of all carabids in the pitfall traps did not differ for the landscape elements (abundance:  $F_{3,55} = 1.26$ ,  $P = 0.297$ ; diversity:  $F_{3,55} = 2.40$ ,  $P = 0.078$ ) (Fig. 4a). However, when only the target species were considered marginally significant effect of landscape element could be found (abundance:  $F_{3,55} = 13.75$ ,  $P < 0.001$ ; diversity:  $F_{3,55} = 35.10$ ,  $P < 0.001$ ), with the forests harbouring fewer target carabids than the other landscape elements; only 25 individuals of three species were caught here (Fig. 4a).

The window traps yielded 639 individuals of 58 species, of which 13 species and 162 individuals were target species (Table 4, and see Appendix A for the non-target species). Eighteen of the 58 species caught in all window traps had not been found in the pitfall traps (of study 1 and 2 combined); they included three target species (*Amara lucida*, *A. nitida*, *A. tibialis*). Twelve of the 13 target species were also caught in the forest clearings, five of which were not caught in the pitfall traps here (Table 3 & 4). Only the *Cicindela* species have flight capacity during their entire life, so the majority of these catches represent dispersing individuals. Abundance and diversity of all carabids differed significantly between the landscape elements (abundance:  $F_{3,42} = 44.99$ ,  $P < 0.001$ ; diversity  $F_{3,42} = 6.88$ ,  $P = 0.001$ ). When only the target species were considered, the effects of landscape elements significantly affected abundance and diversity as well (abundance  $F_{3,42} = 16.91$ ,  $P < 0.001$ ; diversity  $F_{3,42} = 3.86$ ,  $P = 0.016$ ). The forest clearings were intensively used by flying carabids; in all cases highest abundance and diversity was found here (Fig. 4b). For the stenotopic species, approximately twice as many individuals were caught in the clearings



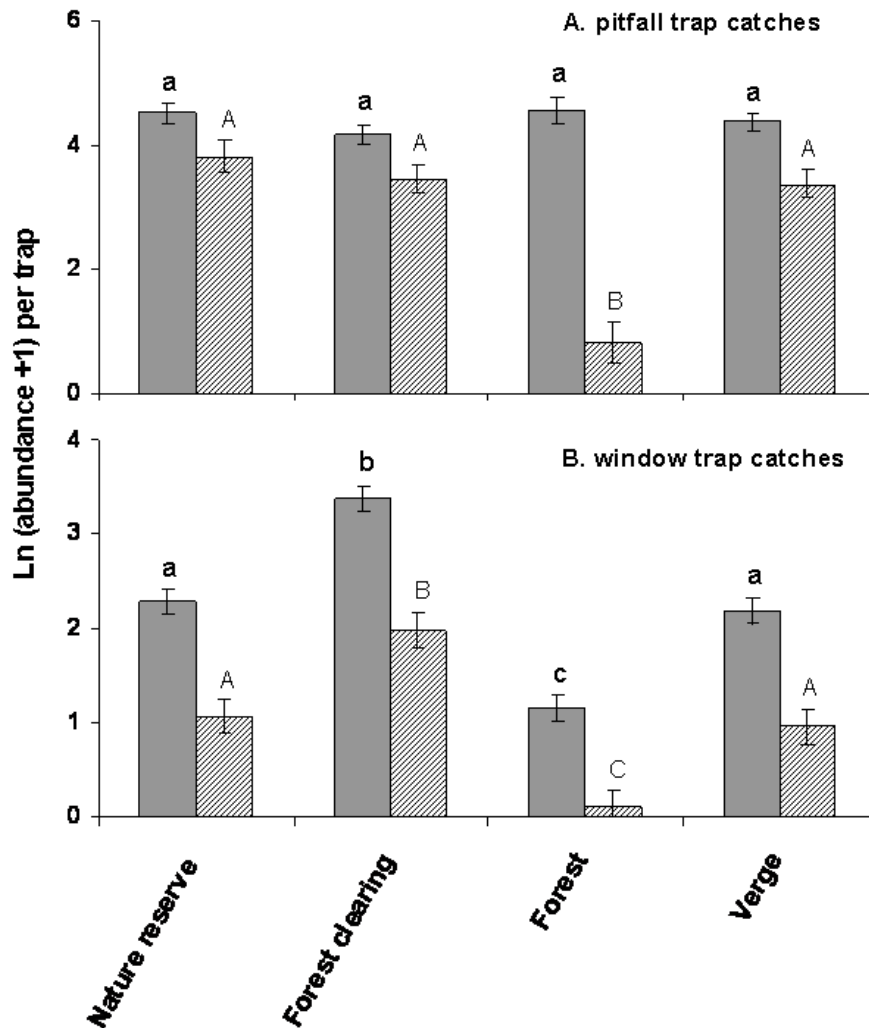
**Figure 3.** PCA ordination of the carabid species composition in the four landscape elements of study 2 based on the pitfall trap data. Site codes (underlined): Hae = De Haere, Cai = Caitwickerzand, Hul = Hulshorsterzand, Ver = verge, Nat = nature reserve, Cle = forest clearing, For = forest. Carabid species codes are a combination of first four letters of the genus name and the species name.

compared to the nature reserves and the roadside verges. In the forests, only 29 individuals, of which two target species individuals, were caught with the window traps (Fig. 4b).

## Discussion and Conclusion

### Roadside verges as corridors

The presence of teneral of many target species and flightless species in our roadside verge samples indicates that target carabids reproduce there. These species included several nationally rare species, such as *Amara equestris*, *Harpalus anxius*, *H. neglectus*, *Masoreus wetterhallii* and *Olisthopus rotundatus*; all are highly stenotopic. Most of the other species we found in the verges are likely to have resident populations here as well, as the vegetation seems appropriate and almost always several individuals



**Figure 4.** Estimated marginal means (predicted values of the GLM tests) for carabid abundance (per trap  $\pm$  s.e.) for the four landscape elements after correcting for location effects: a) Carabids in pitfall traps. b) Carabids in window traps. Grey bars: all species, hatched bars: target species. Means not sharing the same letter are significantly different at  $P < 0.05$  in post-hoc comparisons (in the case of target carabids in the pitfall traps, significance of the overall effect of landscape element was  $P = 0.063$ ).

were caught. Even though the vegetation in the verges possibly is of lower quality (Angold 1997) and some target species are absent (Table 2, CHAPTER 5), it is clear that for many carabids, verges provide suitable habitat (see also Vermeulen 1993; Eversham & Telfer 1994). Roadside verges carrying vegetation similar to the studied patches and stretching between separate nature reserves thus provide suitable habitat corridors for many target species. Similar conclusions can be drawn from previous studies. Noordijk and Boer (2007) described the ant species inhabiting roadside verges in the Veluwe region (these include the verges studied in this paper) and found many nests of species of high conservation concern, including some IUCN Red List species. Raemakers *et al.* (in prep.) studied arthropod overwintering in a roadside verge in the same region; they found many such species emerging from eggs, larvae and pupae from roadside verge soil, indicating successful reproduction of the species concerned.

**Table 4.** The average abundance of target carabids in window traps in the four landscape elements (study 2). The values are summed for the three locations and divided by the total number of traps per landscape element (= 12). Locations where the species was found during the entire study are given using abbreviations after the species name; Ca = Caitwickerzand, Ha = De Haere, Hu = Hulshorsterzand.

species	nature reserves	forest clearings	forests	verges
<i>Amara consularis</i> (Duft.) [Ca, Ha, Hu]	0.58	0.67	0.00	0.50
<i>Amara lucida</i> (Duft.) [Ca, Ha, Hu]	0.00	0.58	0.17	0.17
<i>Amara nitida</i> Sturm [Hu]	0.00	0.00	0.00	0.08
<i>Amara tibialis</i> (Payk.) [Ha]	0.00	0.08	0.00	0.00
<i>Bradycellus ruficollis</i> (Steph.) [Ha, Hu]	0.08	2.00	0.00	0.58
<i>Calathus ambiguus</i> (Payk.) [Ca, Ha, Hu]	1.83	0.00	0.00	0.00
<i>Cicindela campestris</i> L. [Ca, Ha, Hu]	0.08	0.25	0.00	0.00
<i>Cicindela hybrida</i> L. [Ca, Ha, Hu]	0.00	0.08	0.00	0.00
<i>Harpalus anxius</i> (Duft.) [Ca, Ha, Hu]	0.08	0.08	0.00	0.00
<i>Harpalus latus</i> (L.) [Ca, Ha, Hu]	0.00	0.08	0.00	0.00
<i>Harpalus rufipalpis</i> Sturm [Ca, Ha, Hu]	0.42	3.75	0.08	0.83
<i>Harpalus smaragdinus</i> (Duft.) [Ca, Ha, Hu]	0.08	0.17	0.00	0.00
<i>Harpalus solitarius</i> Dej. [Ha, Hu]	0.00	0.08	0.00	0.08
<i>Pterostichus diligens</i> (Sturm) [Ca, Ha, Hu]	0.00	0.08	0.00	0.00

After the forest clearings had been created, no important changes in species composition in the verges were detected and the difference in the abundance and diversity of target species between the nature reserves and roadside verges did not improve. The temporal shifts in species composition in the verges tended to proceed in the same direction as those within the nature reserves (Fig. 2), and should therefore probably be attributed to general changes in composition or abundance of certain species. Thus, an effect of the creation of corridors on the species composition in the verges could not be proved. It might be concluded that in roadside verges the habitats are different from those in the nature reserves and that the verges already harboured the species able to live here. Similar conclusions were drawn from a previous study, where many carabid species characteristic of heathland and nutrient-poor grassland were found to be present in the verges (CHAPTER 5). Yet some species – the ones characteristic of drift sands – were lacking, most likely because the vegetation in the verges was not suitable for them (CHAPTER 5). Probably, roadside verges cannot provide suitable habitats for all target species in this region.

#### *Forest clearings as corridors*

The carabid species composition of the newly-created forest clearings differed strongly from that in the forest (Fig. 3). One might have expected that forest species would still emerge from the soil after the trees had been cleared, but instead, quickly invading species of open areas – including many target species – dominated the catches. Several species were common in the forest clearings (either in the pitfall or window traps and see Table 3 & 4), e.g., *Harpalus rufipalpis*, *Cicindela campestris*, *Bradycellus verbasci*. In addition, several flightless target species were found here:

*Harpalus neglectus*, *Notiophilus germinyi*, *Poecilus lepidus* and *Calathus erratus*. Even some very stenotopic species of heathlands were found in the forest clearings, such as *Harpalus solitarius*, *H. anxius*, *Bradycellus ruficollis* and *Cicindela sylvatica*. In the pitfall traps, the total number of individuals from target species did not differ much between the forest clearing, nature reserve and roadside verge, but the species composition of these three landscape elements differed substantially (Fig. 3 & 4). In the forest clearings only two target species were occasionally encountered as teneral. The latter is not surprising, given the very recent origin of the forest clearings.

Forests appear to be barriers to both flying and ground-dwelling target carabids (Fig. 4). Only *Calathus erratus*, *Poecilus lepidus*, *Pterostichus diligens*, *Amara lucida* and *Harpalus rufipalpis* were found here, in very low numbers. The reluctance of insect species of open habitats to enter forests has been widely reported (e.g., Vermeulen 1994b; Schmitt *et al.* 2000; Fried *et al.* 2005). Especially for flight-incapable target species, forests can be important barriers, leading to fragmented populations. But also flight-capable species might still be negatively affected by forest in-between suitable habitats. It might seem unnecessary to create corridors for flight-capable species, since it could be argued that they can easily fly over forests. However, linear structures may have positive effects on flying insects, increasing the probability that individuals will end up at a certain site (Sutcliffe & Thomas 1996; Várkonyi *et al.* 2003; Fried *et al.* 2005; Townsend & Levey 2005). Suitable sites in fragmented landscapes are not easy to reach if dispersing individuals have to rely solely on chance. Open linear habitats might therefore truly compensate for the fragmentation of low vegetation habitats brought about by the planting of forests or natural succession towards them (Sutcliffe & Thomas 1996; Forrester *et al.* 2005), even if the vegetation in such corridors does not match the habitat of the target species (Haddad & Tewksbury 2005).

The abundances of walking and flying carabids in the forest clearings showed distinctly different patterns (Fig. 4). Compared with the nature reserves and roadside verges, in the forest clearings far more individuals were caught in the window traps than in the pitfall traps. This indicates that linear forest clearings are particularly used as movement corridors (see also Sutcliffe & Thomas 1996). The reason that linear forest clearings function so well might be that dispersing insects tend to follow edges (Fried *et al.* 2005). Another study of flying carabid beetles at two forest edges indicated that most individuals fly parallel to the edges (J. Noordijk, Th. Heijerman, R. Morssinkhof & B. Aukema, unpublished data, see CHAPTER 8 for the sampling set-up to measure directions of flying insects). The clearings in the present study therefore probably act as funnels, channelling the flight paths of many individuals. The guiding of flying carabids to other habitats seems to have a strong positive effect on colonization prospects, as van Huizen (1990) showed that females of many species fly when they are fertilized. Our window trap catches predominantly consisted of female individuals (ca. 60%).

These results indicate that small and linear forest clearings represent dispersal corridors for many target species, but reproduction sites for only a limited number.

The forest clearings were very recent and longer-lasting sampling may be needed to evaluate this last notion. Of course, movement corridors are only effective if dispersing individuals find suitable new habitat on the other side. In case of the studied roadside verges, many species were already present and the biotopes seem not suitable for other species that were not yet present. Nevertheless, forest clearings improve prospects for many open habitat carabids (see also Lemauiel & Roze 2000; Kuras *et al.* 2003; Koivula 2005; Koponen 2005; Lin *et al.* 2007). These findings and the fact that linear strips without trees are abundant in forested areas in the Netherlands indicate that good opportunities exist to create ecological networks.

### *Conclusion*

Both forest clearings and roadside verges appear to be useful landscape elements for heathland carabid species in the study region, either as a habitat or as movement corridor (see also Lin *et al.* 2007). If all verges in the Veluwe region were of the quality and appearance of the studied patches in this paper and if they extended between different nature reserves, they would undoubtedly function as large habitat extensions and habitat corridors (Vermeulen 1994a). If new linear forest clearings are to be created – e.g., for recreational or forestry paths, as fire breaks, for power lines or for timber harvest – constructing them to link up discrete heathland areas might offer target insects guidance to other suitable habitats (see also Forrester *et al.* 2005).

If the conditions in the verges in the Veluwe are to be suitable for the target species, some form of vegetation management is necessary. During the first few decades after their construction the roadside verges contained large open areas. However, vegetation succession is now moving into stages where standing biomass is increasing, species diversity decreasing and trees are beginning to encroach over large stretches (Sýkora *et al.* 2002; Noordijk *et al.* 2008). Clearly, roadside verges could harbour more target carabid species if they are kept open and managed in a way that sustains the nutrient-poor vegetation. The forest clearings, too, need to be managed appropriately to prevent vegetation succession. An advantage of structures created for human convenience is that they need to be kept open for purposes other than nature conservation, which makes it more likely that they will persist over time. Therefore, these landscape elements may provide suitable and sustainable corridors for threatened insects in fragmented landscapes.

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## References

- Anderson AB & Jenkins CN **2006**. *Applying nature's design: corridors as a strategy for biodiversity conservation*. Columbia University Press, New York, USA.
- Angold PG **1997**. The impact of a road upon adjacent heathland vegetation: effects on plant species composition. *Journal of Applied Ecology* 34: 409-417.
- Beier P & Noss RF **1998**. Do habitat corridors provide connectivity? *Conservation Biology* 12: 1241-1252.
- Bobbink R, Hornung M & Roelofs JGM **1998**. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology* 86: 717-738.
- Boiteau G, Bousquet Y & Osborn W **2000**. Vertical and temporal distribution of Carabidae and Elateridae in flight above an agricultural landscape. *Environmental Entomology* 29: 1157-1163.
- den Boer PJ **1970**. On the significance of dispersal power for populations of carabid-beetles (Coleoptera, Carabidae). *Oecologia* 4: 1-28.
- Desender K & Turin H **1989**. Loss of habitats and changes in the composition of the ground and tiger beetle fauna in four West European countries since 1950 (Coleoptera: Carabidae, Cicindelidae). *Biological Conservation* 48: 277-294.
- de Vries HH, den Boer PJ, van Dijk ThS **1996**. Ground beetle species in heathland fragments in relation to survival, dispersal, and habitat preference. *Oecologia* 107: 332-342.
- de Vries HH & den Boer PJ **1990**. Survival of populations of *Agonum ericeti* Panz. Coleoptera Carabidae in relation to fragmentation of habitats. *Netherlands Journal of Zoology* 40: 484-498.
- Duelli P, Obrist MK & Schmatz DR **1999**. Biodiversity evaluation in agricultural landscapes: above-ground insects. *Agriculture Ecosystems and Environment* 74: 33-64.
- European Community **1992**. *The habitats directive 92/43/EEC*. European Community, Brussels, Belgium.
- Eversham BC & Telfer MG **1994**. Conservation value of roadside verges for stenotopic heathland Carabidae: corridors or refugia? *Biodiversity and Conservation* 3: 538-545.
- Ewers RM & Didham RK **2008**. Pervasive impact of large-scale edge effects on a beetle community. *Proceedings of the National Academy of Sciences* 105: 5426-5429.
- Forrester JA, Leopold DJ & Hafner SD **2005**. Maintaining critical Habitat in a heavily managed landscape: effects of power line corridor management on Karner blue butterfly (*Lycaeides melissa samuelis*) habitat. *Restoration Ecology* 13: 488-498.
- Fried JH, Levey DJ & Hogsette JA **2005**. Habitat corridors function as both drift fences and movement conduits for dispersing flies. *Oecologia* 143: 645-651.
- Gish CD & Christensen RE **1973**. Cadmium, nickel, lead and zinc in earthworms from roadside soil. *Environmental Science and Technology* 7: 1060-1062.
- Haddad NM & Baum KA **1999**. An experimental test of corridor effects on butterfly densities. *Ecological Applications* 9: 623-633.
- Haddad NM & Tewksbury JJ **2005**. Low-quality habitat corridors as movement conduits for two butterfly species. *Ecological Applications* 15: 250-257.
- Hanski I & Pöyry J **2007**. Insect populations in fragmented habitats. In: *Insect conservation biology* (Stewart AJA, New TR & Lewis OT eds.): 175-202. CABI, Wallingford, UK.
- Hilty JA, Lidicker WZ & Merenlender AM **2006**. *Corridor ecology, the science and practice of linking landscapes for biodiversity conservation*. Island Press, Washington, USA.



- Ketner-Oostra R, van der Peijl MJ & Sýkora KV **2006**. Restoration of lichen diversity in grass-dominated vegetation of coastal dunes after wildfire. *Journal of Vegetation Science* 17: 147-156.
- Koivula MJ **2005**. Effects of forest roads on spatial distribution of boreal carabid beetles (Coleoptera: Carabidae). *Coleopterists Bulletin* 59: 465-487.
- Koponen S **2005**. Early succession of a boreal spider community after forest fire. *Journal of Arachnology* 33: 230-235.
- Kuras T, Benes J, Fric Z & Konvicka M **2003**. Dispersal patterns of endemic alpine butterflies with contrasting population structures: *Erebia epiphron* and *E. sudetica*. *Population Ecology* 45: 114-123.
- Lemauviel S & Roze F **2000**. Ecological study of pine forest clearings along the French Atlantic sand dunes: perspectives of restoration. *Acta Oecologia* 21: 179-192.
- Lin Y-C, James R & Doman PM **2007**. Conservation of heathland ground beetles (Coleoptera: Carabidae): the value of lowland coniferous plantations. *Biodiversity and Conservation* 16: 1337-1358.
- Munguira ML & Thomas JA **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.
- Nelemans MNE **1987**. Possibilities for flight in the carabid beetle *Nebria brevicollis* (F.) – the importance of food during larval growth. *Oecologia* 72: 502-509.
- Noordijk J & Boer P **2007**. Mieren in snelwegbermen op de Veluwe – soortenrijkdom en aanbevelingen voor beheer (Hymenoptera: Formicidae). *Nederlandse Faunistische Mededelingen* 27: 23-50.
- Noordijk J, Sýkora KV & Schaffers AP **2008**. Conservation value of sandy roadside verges for arthropods – implications for management. *Proceedings of the Netherlands Entomological Society Meeting* 19: 75-93.
- Noss RF & Csuti B **1997**. Habitat fragmentation. In: *Principles of conservation biology*, 2nd edition (Meffe G & Ronald CR eds.): 269-304. Sinauer Associates, Sunderland, USA.
- Pryke SR & Samways MJ **2001**. Width of grassland linkages for the conservation of butterflies in South African afforested areas. *Biological Conservation* 101: 85-96.
- Riksen M, Ketner-Oostra R, van Turnhout C, Nijssen M, Goossens D, Jungerius PD & Spaan W **2006**. Will we lose the last active inland drift sands of Western Europe? The origin and development of the inland drift-sand ecotype in the Netherlands. *Landscape Ecology* 21: 431-447.
- Schaffers AP **2000**. *Ecology of roadside plant communities*. PhD thesis, Wageningen University, the Netherlands.
- Schaffers AP, Raemakers IP, Sýkora KV & ter Braak CJF **2008**. Arthropod assemblages are best predicted by plant species composition. *Ecology* 89: 782-794.
- Schmitt T, Varga Z & Seitz A **2000**. Forests as dispersal barriers for *Erebia medusa* (Nymphalidae, Lepidoptera). *Basic and Applied Ecology* 1: 53-59.
- Spellerberg IF **2002**. *Ecological effects of roads*. The land reconstruction and management series, vol. 2. Science Publishers, Enfield, USA.
- Sýkora KV, Kalwij JM & Keizer P-J **2002**. A phytosociological and floristic evaluation of 15-year ecological management of roadside verges in the Netherlands. *Preslia* 74: 421-436.
- Sutcliffe OL & Thomas CD **1996**. Open corridors appear to facilitate dispersal by Ringlet Butterflies (*Aphantopus hyperantus*) between woodland clearings. *Conservation Biology* 10: 1359-1365.

- Townsend PA & Levey DJ **2005**. An experimental test of whether habitat corridors affect pollen transfer. *Ecology* 86: 466-475.
- Turin H **2000**. *De Nederlandse loopkevers, verspreiding en ecologie. (Coleoptera: Carabidae)*. Nederlandse Fauna 3. Nationaal Natuurhistorisch Museum Naturalis, Leiden, KNNV Uitgeverij, Utrecht, European Invertebrate Survey-Nederland, Leiden, the Netherlands.
- Turin H, Alders K, den Boer PJ, van Essen S, Heijerman Th, Laane W & Penterman E **1991**. Ecological characterization of carabid species (Coleoptera, Carabidae) in the Netherlands from thirty years of pitfall sampling. *Tijdschrift voor Entomologie* 134: 279-303.
- Turin H & den Boer PJ **1988**. Changes in the distribution of carabid beetles in The Netherlands since 1880. II. Isolation of habitats and long-term time trends in the occurrence of carabid species with different powers of dispersal (Coleoptera, Carabidae). *Biological Conservation* 44: 179-200.
- Turin H & Heijerman Th **1997**. Loopkevers. In: *Jaarboek Natuur 1997* (Veling K, Verheggen L, van Halder I & van Leeuwen BH eds.): 112-124. KNNV/VOFF, Utrecht/Wageningen, the Netherlands.
- van Duuren L, Eggink GJ, Kalkhoven J, Notenboom J, van Strien AJ & Wortelboer R **2003**. *Natuurcompendium 2003, Natuur in cijfers*. KNNV Uitgeverij, Utrecht, the Netherlands.
- van Huizen THP **1979**. Individual and environmental factors determining flight in carabid beetles. In: *On the Evolution of Behaviour in Carabid Beetles* (den Boer PJ, Thiele HU & Weber F eds.): 199-211. Miscellaneous Papers of the Agricultural University, Wageningen, the Netherlands.
- van Huizen THP **1990**. 'Gone with the wind': flight activity of carabid beetles in relation to wind direction and to the reproductive state of females in flight. In: *The role of ground beetles in ecological and environmental studies* (Stork ND ed.): 289-293. Intercept, Andover, UK.
- Várkonyi G, Kuussaari M & Lappalainen H **2003**. Use of forest corridors by boreal *Xestia* moths. *Oecologia* 137: 466-474.
- Vermeulen HJW **1993**. The composition of the carabid fauna on poor sandy road-side verges in relation with comparable open areas. *Biodiversity and Conservation* 2: 331-350.
- Vermeulen HJW **1994a**. Corridor function of a road verge for dispersal of stenotopic heathland ground beetles (Carabidae). *Biological Conservation* 69: 339-349.
- Vermeulen R **1994b**. The effects of different vegetation structures on the dispersal of carabid beetles from poor sandy heaths and grasslands. In: *Carabid beetles: ecology and evolution* (Desender K, Dufrêne M, Loureau M, Luff M & Maelfait J-P eds.): 387-392. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Weeda EJ, Schaminée JHJ & van Duuren L **2002**. *Atlas van de plantengemeenschappen in Nederland. Deel 2, Graslanden, zomen and droge heiden*. KNNV Publisher, Utrecht, the Netherlands.

**Appendix I.** Carabid species caught during this study not classified as target species. <sup>1</sup> = caught in pitfall trap, <sup>2</sup> = caught in window trap. Nomenclature follows Turin (2000).

<i>Abax ater</i> (Piller & Mitterpacher) <sup>1</sup>	<i>Bradycellus verbasci</i> (Duft.) <sup>1,2</sup>	<i>Nebria brevicollis</i> (F.) <sup>1</sup>
<i>Acupalpus brunnipes</i> (Sturm) <sup>2</sup>	<i>Calathus fuscipes</i> (Goeze) <sup>1</sup>	<i>Notiophilus aquaticus</i> (L.) <sup>1</sup>
<i>Acupalpus flavicollis</i> (Sturm) <sup>2</sup>	<i>Calathus melanocephalus</i> (L.) <sup>1,2</sup>	<i>Notiophilus biguttatus</i> (F.) <sup>1,2</sup>
<i>Agonum muelleri</i> (Hbst.) <sup>1,2</sup>	<i>Calathus micropterus</i> (Duft.) <sup>1</sup>	<i>Notiophilus palustris</i> (Duft.) <sup>1,2</sup>
<i>Amara aenea</i> (Degeer) <sup>1,2</sup>	<i>Calodromius spilotus</i> (Ill.) <sup>2</sup>	<i>Notiophilus rufipes</i> Curt. <sup>1,2</sup>
<i>Amara apricaria</i> (Payk.) <sup>2</sup>	<i>Carabus nemoralis</i> Müll. <sup>1</sup>	<i>Ophonus puncticeps</i> Steph. <sup>2</sup>
<i>Amara bifrons</i> (Gyll.) <sup>1</sup>	<i>Carabus problematicus</i> Hbst. <sup>1</sup>	<i>Ophonus rufibarbis</i> (F.) <sup>2</sup>
<i>Amara communis</i> (Panz.) <sup>1,2</sup>	<i>Carabus violaceus</i> L. <sup>1</sup>	<i>Oxypselaphus obscurus</i> (Hbst.) <sup>1</sup>
<i>Amara famelica</i> Zimm. <sup>1</sup>	<i>Clivina fossor</i> (L.) <sup>1,2</sup>	<i>Panagaeus cruxmajor</i> (L.) <sup>1</sup>
<i>Amara familiaris</i> (Duft.) <sup>1,2</sup>	<i>Cychrus caraboides</i> (L.) <sup>1</sup>	<i>Poecilus cupreus</i> (L.) <sup>1,2</sup>
<i>Amara lunicollis</i> Schdte. <sup>1,2</sup>	<i>Dromius agilis</i> (F.) <sup>1,2</sup>	<i>Poecilus versicolor</i> (Sturm) <sup>1</sup>
<i>Amara majuscula</i> Chaud. <sup>2</sup>	<i>Dromius quadrimaculatus</i> (L.) <sup>2</sup>	<i>Pterostichus melanarius</i> (Ill.) <sup>1</sup>
<i>Amara ovata</i> (F.) <sup>1,2</sup>	<i>Dyschirius globosus</i> (Hbst.) <sup>1</sup>	<i>Pterostichus niger</i> (Schall.) <sup>1</sup>
<i>Amara plebeja</i> (Gyll.) <sup>1</sup>	<i>Dyschirius politus</i> (Dej.) <sup>2</sup>	<i>Pterostichus nigrata</i> (Payk.) <sup>2</sup>
<i>Anisodactylus binotatus</i> (F.) <sup>2</sup>	<i>Harpalus affinis</i> (Schrk.) <sup>1,2</sup>	<i>Pterostichus oblongopunctatus</i> (F.) <sup>1</sup>
<i>Asaphidion curtum</i> (Heyd.) <sup>2</sup>	<i>Harpalus griseus</i> (Panz.) <sup>2</sup>	<i>Pterostichus vernalis</i> (Panz.) <sup>1,2</sup>
<i>Asaphidion flavipes</i> (L.) <sup>2</sup>	<i>Harpalus laevipes</i> Zett. <sup>1</sup>	<i>Syntomus truncatellus</i> (L.) <sup>1,2</sup>
<i>Badister sodalist</i> (Duft.) <sup>1</sup>	<i>Harpalus rubripes</i> (Duft.) <sup>1</sup>	<i>S. foveatus</i> (Geoffr. in Fourcr.) <sup>1</sup>
<i>Bembidion lampros</i> (Hbst.) <sup>1,2</sup>	<i>Harpalus rufipes</i> (Geer) <sup>1,2</sup>	<i>Paratachys micros</i> (Fisch.-W.) <sup>2</sup>
<i>Bembidion lunulatum</i> (Geoffr. in Fourcr.) <sup>2</sup>	<i>Laemostenus terricola</i> (Hbst.) <sup>1</sup>	<i>Trechus obtusus</i> Er. <sup>1</sup>
<i>Bembidion properans</i> (Steph.) <sup>1,2</sup>	<i>Leistus ferrugineus</i> (L.) <sup>1</sup>	<i>Trechus quadristriatus</i> (Schrk.) <sup>2</sup>
<i>Bembidion quadrimaculatum</i> (L.) <sup>1,2</sup>	<i>Leistus rufomarginatus</i> (Duft.) <sup>1</sup>	<i>Trichocellus placidus</i> (Gyll.) <sup>2</sup>
<i>Bradycellus harpalinus</i> (Serv.) <sup>1,2</sup>	<i>Loricera pilicornis</i> (F.) <sup>1,2</sup>	







7



# IMPACT OF A ROAD ON THE MOVEMENTS OF TWO GROUND BEETLE SPECIES

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**Abstract.** We studied the effects of a road on movement directions of the ground beetle (Coleoptera: Carabidae) species *Poecilus versicolor* and *Agonum sexpunctatum*. By using mark-recapture experiments and window traps, we determined the number of road crossings and the deviation in walking directions caused by the road. We found two effects of the road on walking behaviour: (i) The road is more or less a barrier to both species: *P. versicolor* showed resistance to cross the road and had a significant movement away from the road. We did not detect road crossings by *A. sexpunctatum*. (ii) Both species, but especially *A. sexpunctatum*, showed a high tendency to walk along the road in the adjacent verge and especially in the ditch. Of the two studied species, only one individual of *A. sexpunctatum* was caught flying close to the road, indicating that it might cross the road through the air. Furthermore, we visually sought for dead ground beetle specimens on two 100 m long transects along the road and we found several individuals of *P. versicolor*. Finally, we offer suggestions on how to use the observed walking behaviour for the benefit of nature management.

**Key words.** *Agonum sexpunctatum*, barrier effect, Carabidae, mark-recapture, *Poecilus versicolor*, provincial road, traffic casualties

## Introduction

Roads have many negative ecological effects, such as habitat destruction, and disturbance and pollution of the environment (for reviews see Forman & Alexander 1998; Spellerberg 2002). Beside this, roads also have a strong barrier effect: for many animals they are difficult or even impossible to cross and individuals may find death on the pavement. This has been shown in several studies for small and large animal species (Baur & Baur 1990; Mader *et al.* 1990; Dyer *et al.* 2002; Koivula & Vermeulen 2005). For the species in the remaining areas cut off by roads, this may lead to a loss of genetic variability of populations (Reh & Seitz 1990; Keller & Largiadèr 2003), which can increase the probability of local extinctions (e.g., Pulliam & Dunning 1997).

In 2005, we studied ground beetle movement patterns next to a provincial road running straight through the centre of the nature restoration area Mantingerveld, in the north of the Netherlands (Fig. 1a). In this area, the conversion of more than 2000 ha of heathland into arable land started in 1954 (Fig. 1c). In 1959, only 325 ha of heathland was left scattered throughout the area in five fragments (Fig. 1c). Habitat fragmentation and destruction became publicly noticed in the 1970s and 1980s. At that time, planning of restoration, enlargement, and reconnection of the remaining heathlands was started. In order to connect the five heathland remnants, the nature management organisation ‘*Natuurmonumenten*’ is restoring the in-between arable fields into heathlands and species-rich grassland, by top-soil removal and introduction of heather propagules (Aerts *et al.* 1995). This resulted in a more or less coherent and interconnected nature reserve with a total area of 1050 ha (Fig. 1d). However, the provincial road is still dividing the Mantingerveld in two parts.

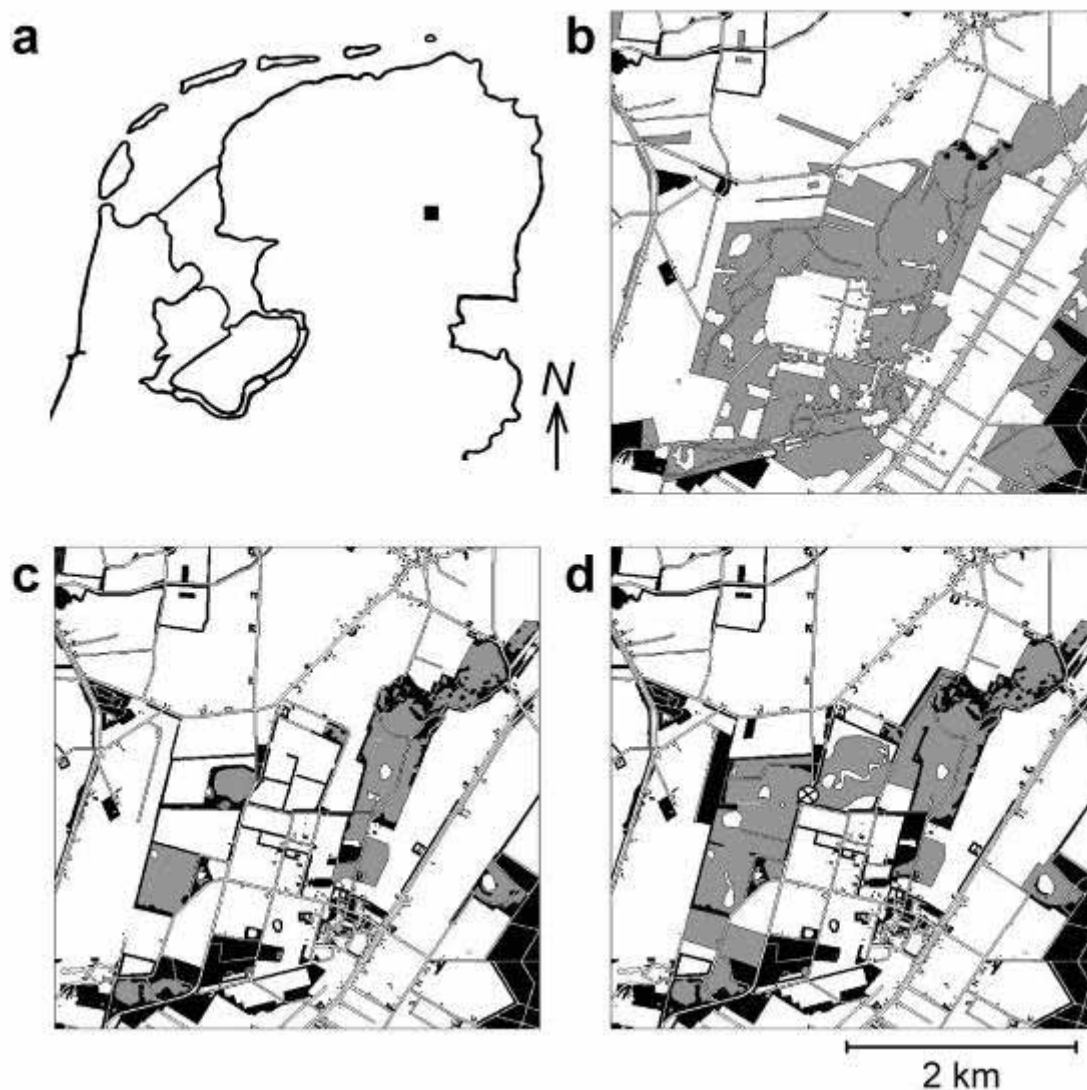
Previous research on the barrier effect of roads on ground beetle species has focussed on forest species (Mader 1984; Keller & Largiadèr 2003; Koivula & Vermeulen 2005). Mader *et al.* (1990) found that small paved field tracks already had some barrier effect on a mix of open area ground beetle species, but they did not discuss species specific results. In this paper, we study whether a road between two areas with relatively xeric and thermic habitats is a barrier to an eurytopic and a stenotopic ground beetle species. We measure if successful crossings, by walking or flying, do occur, and whether ground beetles are killed by traffic. We discuss whether or not the direction of movement of the two carabid species is affected by this road. If this is the case, this may hinder the free exchange of individuals or even species between the areas on the two sides of the road. Finally, we give some recommendations on how to deal with the road from a nature conservation perspective.



## Material and Methods

### *Location*

The provincial road (N317, Hooogeveenseweg), with 6.5 m wide asphalt pavement, was build around 1968 and connects the village Westerbork with the town Hoogeveen. The field site, 52°46'N–6°35'E, was located around a part of the road in the nature restoration area, that is bordered on the west side by a heathland area, the Hullenzand (Fig. 2), and on the east side by a formerly arable field, the Groote Veld. On average 2400 cars pass here daily (data Province Drenthe). On both sides of the road is a grassy verge. On the heathland side, about 2 m from the road, the verge and the heathland are separated by a dry ditch.



**Figure 1.** Location and development of the nature restoration area Mantingerveld. The studied provincial road runs through the middle of this area. White areas are arable fields, grey areas are heathlands and for figure d also formerly arable fields, and black areas are forests. A: Location of the Mantingerveld in the north of the Netherlands (■). B: Situation in 1954. C: Situation in 1990. D: Situation in 2004. The location of the road enclosure is indicated by a circle with a cross.



**Figure 2.** The heathland area Hullenzand; *Poecilus versicolor* and *Agonum sexpunctatum* are common here.

#### *The studied species*

We used *Poecilus versicolor* (Sturm, 1824) and *Agonum sexpunctatum* (L, 1758) to study walking behaviour close to the road. These species were selected, because they are common in the Mantingerveld and they are able to find a habitat in the oligotrophic formerly arable fields (Verhagen & Vermeulen 2005). *Poecilus versicolor* is an eurytopic species of open areas (Turin *et al.* 1991); it can be found in different types of open and low vegetation on various soil types. However, in the Netherlands *P. versicolor* has a preference for sandy soils and it is most abundant in heathlands (Turin 2000). It is a macropterous beetle and capable of flying, but only a small percentage of the population has the opportunity to develop wing muscles (Desender 1989). There are observations of *P. versicolor* in the formerly arable field Groote Veld, but in very low densities compared to the heathland Hullenzand (Verhagen & Vermeulen 2005). The second species, *Agonum sexpunctatum*, is in the Netherlands a stenotopic species of oligotrophic humid heathland areas (Turin *et al.* 1991), although it can occur in other types of habitats. The species is macropterous and capable of flying, but a proportion of the population has reduced wings (Desender 1989). *Agonum sexpunctatum* is common in the heathland Hullenzand, and was recently found in the formerly arable field Groote Veld (observation A. Spee).

### *Experimental enclosures*

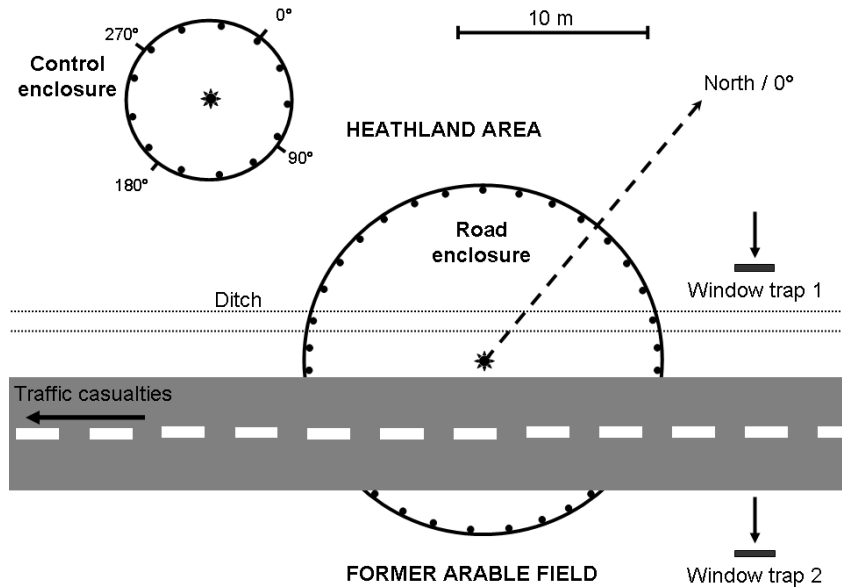
From hard board fences, we made a circular enclosure around the road and a circular control enclosure to test whether the presence of a road altered the direction of movement for the two ground beetle species (Fig. 3). The control enclosure was in the heathland area, about 30 m away from the road enclosure. The diameter of the road enclosure was 19.4 m and that of the control enclosure 8.4 m. Ground beetles were collected in the surrounding area and marked by placing small pits with a tiny soldering-iron in the elytra. In the road and control enclosure the marked individuals of *P. versicolor* and *A. sexpunctatum* were released at the centre. Within the enclosures against the fence, dry pitfall traps (diameter: 10 cm, depth: 9 cm) were placed at about 2 m from each other, all at the same distance from the release point (13 for the control and 27 for the road enclosure). In the road enclosure 1188 individuals of *P. versicolor* and 113 individuals of *A. sexpunctatum* were released. In the control enclosure these numbers were 342 and 39 individuals, respectively. We noted whether an individual was caught in one of the pitfalls.

In the enclosures, the north was set to the angle 0° and the pitfalls in the enclosures were clockwise given values between 0 and 360°. In the road enclosure the pitfalls between 295° and 345° were not considered during statistical analyses, to compensate for the gaps in the enclosure caused by the road. In this way an even distribution of sampling points is created, allowing calculation of directional preferences of the ground beetles. Directional preferences in both enclosures, expressed as mean vector length and mean angle, were calculated according to Batschelet (1981), using the number of recaptures in the different pitfalls. To study a possible bimodal directional preference, the data were transformed by multiplying the angle of each recaptured individual by two, and the mean vector and angle were recalculated (Batschelet 1981).

Significance of mean angles was analysed with a Rayleigh test for randomness (Batschelet 1981). Differences in distribution of walking preferences between the road and the control enclosure were analysed with Chi-squared tests, after pooling pitfalls in both enclosures in three parts.

### *Traffic casualties*

For nine weeks, from the 31<sup>st</sup> of March until the 3<sup>rd</sup> of June, we collected and identified carabids killed by traffic. The collection was done daily on weekdays, on two transects of 100 m over the whole paved part of the road including one meter of the verges on both sides. It took approximately 30 minutes to finish one transect. One transect was close to the road enclosure, in between the heathland and the formerly arable field. The second transect was located in between some patches of forest and an agricultural field.



**Figure 3.** Schematic representation of the experimental set-up. Indicated are the locations of the road and control enclosure, including all the pitfalls (●). Marked beetles were released at the centre of each enclosure (\*). The window traps and transects for collecting traffic casualties are indicated as well.

### Window traps

Close to the road enclosure, we placed two window traps to catch carabids, flying from the heathland area towards the formerly arable field. One trap was located on the heathland side of the road and the other one was located on the formerly arable field side of the road (Fig. 2). A plexiglass window was placed in a metal frame about one meter above ground level. The window was one by one m and a 15 cm broad gutter, filled with a formalin solution, was located under one side of the window to collect carabids that flew against the window from one direction. These traps were emptied weekly for a period of seven weeks; from the 15<sup>th</sup> of April until the 26<sup>th</sup> of May.

## Results

### Experimental enclosures

In the road enclosure the recapture rate for *P. versicolor* was 32% (380 individuals). Twenty-four of the 380 recaptured individuals had crossed the road. This is far less as would be expected by random movement of the beetles. *Poecilus versicolor* showed a significant movement perpendicular to the road: mean angle 298° ( $r = 23.0$ ,  $df = 331$ ,  $P < 0.001$ ) (Fig. 4a). In addition, an adapted Rayleigh test revealed a bimodal directional preference alongside the road and in the ditch ( $r = 79.7$ ,  $df = 331$ ,  $P < 0.001$ ).

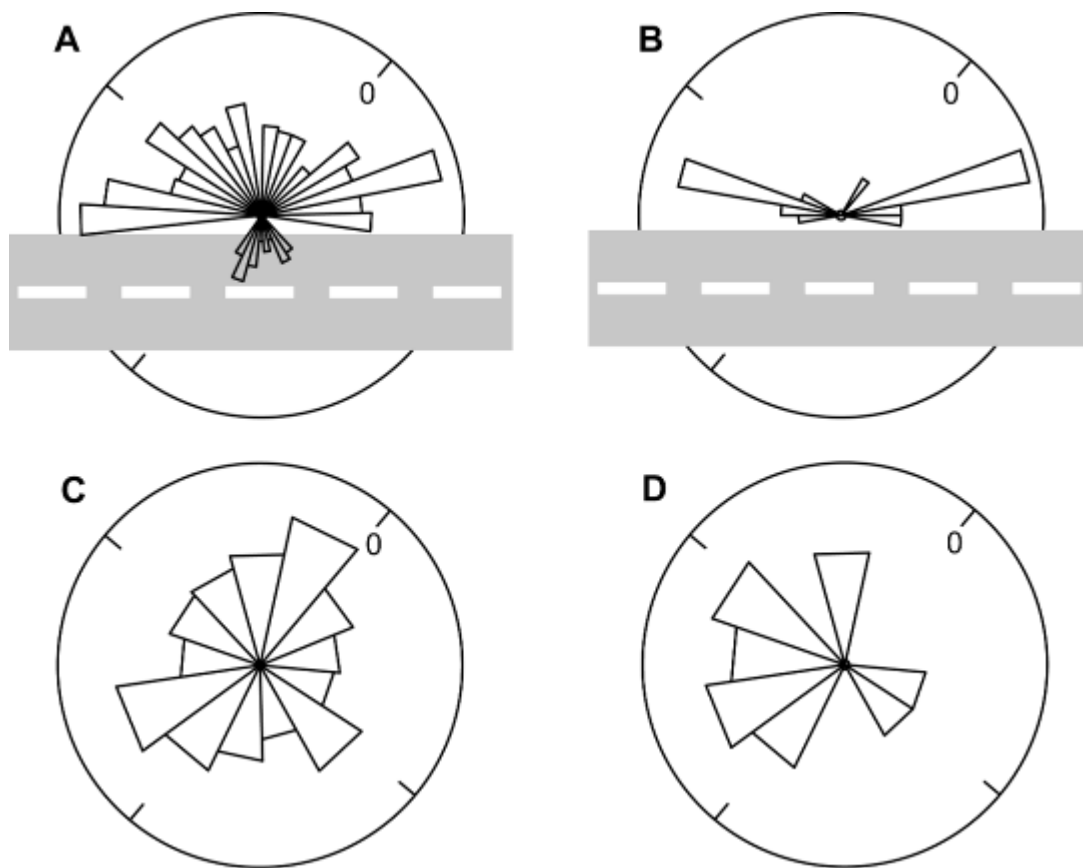
In the road enclosure the recapture rate for *A. sexpunctatum* was 39% (45 individuals). The barrier effect of the road for *A. sexpunctatum* was even stronger: not a single individual had crossed the road. But, no single directedness for this species could be revealed. The data gives a good explanation for this: we found a very strong bimodal directional preference alongside the road and especially in the ditch (Fig. 4b). An adapted Rayleigh test confirmed this ( $r = 0.88$ ,  $df = 44$ ,  $P < 0.001$ ).

In the control enclosure the recapture rates for *P. versicolor* and *A. sexpunctatum* were respectively 48% (164 individuals) and 33% (13 individuals). No directional preference was found for *P. versicolor* in the control enclosure (Fig. 4c). However, *A. sexpunctatum* exhibited a significant movement to the south-west; mean angle  $217^\circ$  ( $r = 0.50$ ,  $df = 14$ ,  $P = 0.027$ ) (Fig. 4d), which is probably due to the low number of recaptures.

When the distribution of the walking directions of *P. versicolor* and *A. sexpunctatum* in the road enclosure is directly compared to the control enclosure, there is a clear difference in direction of movement for both species ( $\chi^2 = 50.7$ ,  $df = 2$ ,  $P < 0.001$  for *P.v.* and  $\chi^2 = 22.9$ ,  $df = 2$ ,  $P < 0.001$  for *A.s.*).

#### Traffic casualties

We gathered 29 dead individuals of eight ground beetle species from the road (Appendix 1). These included seven individuals of *P. versicolor* and three individuals of the stenotopic heathland species *Carabus arvensis* Herbst.



**Figure 4.** Recapture results of the road and the control enclosure for both ground beetle species. The different triangles are in the direction of the pitfalls (attached to the fence) where the individuals were caught. The length of the triangles is proportional to the number of recaptures in that direction and not comparable between the circles. A. Walking pattern of *P. versicolor* in the road circle (380 individuals). B. Walking pattern of *A. sexpunctatum* in the road circle (45 ind.). C. Walking pattern of *P. versicolor* in the control circle (164 ind.). D. Walking pattern of *A. sexpunctatum* in the control circle (13 ind.).

*Window traps*

We collected 272 individuals of 18 ground beetle species from the window traps directed from the heathland towards the formerly arable field (Appendix 2). One individual of *A. sexpunctatum* was among these catches, but we found it in the window trap on the heathland side of the road. Besides *A. sexpunctatum*, we found no heathland or drift sand species in the window traps.

**Discussion***Effects of the road*

We found two effects of the road on the walking behaviour of the ground beetles. Firstly, the road prevents both species from moving freely between the areas on both sides of the road: the eurytopic species *P. versicolor* is reluctant to cross the road and has a significant movement away from the road and for the stenotopic species *A. sexpunctatum* we did not detect road crossings. For other ground beetles similar results had already been shown (Mader 1984; Koivula & Vermeulen 2005). Our experiment confirms that to the open area species of this experiment, roads are barriers in the landscape as well. Both insect species tested in this experiment are rather common and not particular vulnerable. We expect the road to be an even more prominent barrier for more stenotopic species, especially if these species are small and incapable of flying (see for example Bauer & Bauer 1990). The different heathland areas in the Mantingerveld are fragmentized by the road, resulting in divided populations on both sides for some species. This will also reduce the chance of colonisation for the formerly arable fields. Secondly, both species, and especially *A. sexpunctatum*, show a high tendency to walk alongside the road and particularly in the ditch. Mader *et al.* (1990) found similar reactions of ground beetles to roads and a railway track. This tendency might lead ground beetles away from their habitat and it might also increase the distance to move before they reach the next suitable site, with the risk that their energy supply will be exhausted before they reach it (Mader *et al.* 1990).

We found three individuals of *Carabus arvensis* killed by traffic. This is a stenotopic heathland species that is rare in the Netherlands (Turin 2000). Also some mammals, birds, amphibians and a reptile were found as traffic casualties (data not shown). This illustrates the direct effects of traffic on target species of heathland conservation. Especially when taking into consideration the discrepancy between the number of animals killed by traffic and the low number of individuals found during surveys (Slater 2002). The absence of specific heathland and drift sand ground beetle species flying close to the road (except for one individual of *A. sexpunctatum*), indicate the possibility that even to flying stenotopic species roads might be barriers (Askling & Bergman 2003; Bhattacharya *et al.* 2003; Laurance *et al.* 2004).

'Natuurmonumenten' aims to develop one coherent heathland, but the road prevents species from moving freely and puts their populations under pressure by causing death of individuals.

*Suggestions for reducing the barrier effect*

The best way to undo the barrier effect of the provincial road is to displace the road outside the nature restoration area, but this is probably not an option. A successful mitigation measure for the heathland species might be a wildlife overpass. Almost no literature exists on the use of wildlife overpasses by ground beetles, so the effectiveness of these structures is largely unknown. Only Rietze (2002) shows that several ground beetle species use wildlife overpasses to cross the road when the vegetation of the source area is similar to the vegetation on the overpass and habitat corridors towards the overpass are provided (see also Luell *et al.* 2003). However, for species of moist and wet habitats the use is improbable (Rietze 2002), underpasses seem to provide good mitigation measures for such species (Luell *et al.* 2003).

A broad overpass will function better than a small one and it would be best to make the overpass at the same level as the surrounding landscape. When the overpass is covered by the characteristic habitat of the target species of the Mantingerveld – a heathland mosaic – stenotopic species might be able to cross the road, and large or eurytopic animals can cross the road without being killed.

*Dealing with the bimodal walking behaviour*

The fact that *P. versicolor* and *A. sexpunctatum* have the tendency to keep walking alongside the road and in the ditch, shows that roads and accompanying structures, can lead ground beetles away from their habitat. This might be ameliorated by a good construction of the roadside verges. Verges and ditches through a certain area or habitat type should also end in the same area or habitat type. Roadside verges should be integrated in the nature reserves and should not lead species away to unsuitable habitats. On the other hand, roadside verges themselves can also provide a habitat for target species (e.g., Vermeulen 1993; Eversham & Telfer 1994).

The tendency of the ground beetles to walk alongside the road suggests that roadside verges can lead these insects towards a wildlife overpass, but also from one area to another area. This corridor function may be strengthened if the verges consist of the typical vegetation of the both areas to be connected, are not too long, and they also provide in opportunities for reproduction (CHAPTER 6; Getz *et al.* 1978; Vermeulen 1993). The usually unavoidable presence of roads and the accompanying verges might this way be turned into helpful connections between scattered nature reserves.

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## References

- Aerts R, Huiszoon A, van Oostrum JHA, van de Vijver CADM & Willems JH **1995**. The potential for heathland restoration on formerly arable land at a site in Drenthe, The Netherlands. *Journal of Applied Ecology* 32: 827-835.
- Askling J & Bergman K-O **2003**. Invertebrates - a forgotten group of animals in infrastructure planning? Butterflies as tools and model organisms in Sweden. *Proceedings of the International Conference on Ecology and Transportation*: 476-482.
- Batschelet E **1981**. *Circular statistics in biology (Mathematics in biology)*. Academic Press, London, UK.
- Baur A & Baur B **1990**. Are roads barriers to dispersal in the land snail *Arianta arbustorum*? *Canadian Journal of Zoology* 68: 613-617.
- Bhattacharya M, Primack RB & Gerwein J **2003**. Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area? *Biological Conservation* 109: 37-45.
- Desender K **1989**. Dispersievermogen en ecologie van loopkevers (Coleoptera, Carabidae) in België: een evolutionaire benadering. *Studiedocumenten van het Koninklijk Belgisch Instituut voor Natuurwetenschappen* 54: 1-136.
- Dyer SJ, O'Neill JP, Wasel SM & Boutin S **2002**. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. *Canadian Journal of Zoology* 80: 839-845.
- Eversham BC & Telfer MG **1994**. Conservation value of roadside verges for stenotopic heathland Carabidae: corridors or refugia? *Biodiversity and Conservation* 3: 538-545.
- Forman RTT & Alexander LE **1998**. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29: 207-231.
- Getz LL, Cole FR & Gates DL **1978**. Interstate roadsides as dispersal routes for *Microtus pennsylvanicus*. *Journal of Mammalogy* 59: 208-212.
- Keller I & Largiadèr CR **2003**. Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. *Proceedings of the Royal Society of London B* 270: 417-423.
- Koivula MJ & Vermeulen HJW **2005**. Highways and forest fragmentation - effects on carabid beetles (Coleoptera, Carabidae). *Landscape Ecology* 20: 911-926.
- Laurance SGW, Stouffer PC & Laurance WF **2004**. Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. *Conservation Biology* 18: 1099-1109.
- Luell B, Bekker GJ, Cuperus R, Dufek J, Fry G, Hicks C, Hlaváč V, Keller V, Rosell C, Sangwine T, Tørsløv N & le Maire-Wndall B **2003**. *Wildlife and Traffic: A European handbook for identifying conflicts and designing solutions*. KNNV publishers, Utrecht, the Netherlands.
- Mader HJ **1984**. Animal habitat isolation by roads and agricultural fields. *Biological Conservation* 29: 81-96.
- Mader HJ, Schell C & Kornacker P **1990**. Linear barriers to arthropod movements in the landscape. *Biological Conservation* 54: 209-222.
- Pulliam HR & Dunning JB **1997**. Demographic processes: population dynamics on heterogeneous landscapes. In: *Principles of conservation Biology, second edition* (Meffe GK & Carroll CR eds.): 203-232. Sinauer Associates Publishers, Sunderland, USA.



- Reh W & Seitz A **1990**. The influence of land use on the genetic structure of populations of the common frog *Rana temporaria*. *Biological Conservation* 54: 239-249.
- Rietze J **2002**. Wirksamkeit von Grünbrücken über Verkehrswege am Beispiel der Laufkäfer - Methoden, Erfahrungen und Ergebnisse. *Angewandte Carabidologie* 4-5: 63-93.
- Slater FM **2002**. An assessment of wildlife road casualties - the potential discrepancy between numbers counted and numbers killed. *Web Ecology* 3: 33-42.
- Spellerberg IF **2002**. *Ecological effects of roads*. The land reconstruction and management series, vol. 2. Science Publishers, Enfield, USA.
- Turin H **2000**. *De Nederlandse loopkevers - verspreiding en ecologie (Coleoptera: Carabidae)*. Nederlandse Fauna 3. Museum Naturalis, KNNV Uitgeverij, European Invertebrate Survey-Nederland, Leiden, the Netherlands.
- Turin H, Alders K, den Boer PJ, van Essen S, Heijerman Th, Laane W & Penterman E **1991**. Ecological characterization of carabid species (Coleoptera, Carabidae) in The Netherlands from thirty years of pitfall sampling. *Tijdschrift voor Entomologie* 134: 279-304.
- Verhagen R & Vermeulen R **2005**. *Loopkevers van het Mantingerveld. De effecten van habitatversnippering en maatregelen ter ontsnippering in beeld gebracht*. Stichting Willem Beijerinck Biologisch Station, Loon, the Netherlands.
- Vermeulen HJW **1993**. The composition of the carabid fauna on poor sandy road-side verges in relation with comparable open areas. *Biodiversity and Conservation* 2: 331-350.

**Appendix 1.** Carabid species that were found death on the road and in a small strip of both verges. Collection was done on two 100 m transects, transect 1 was located in between the heathland and the formerly arable field, transect 2 was in between some forest fragments and an agricultural field.

Species	transect 1	transect 2
<i>Amara nitida</i> Sturm	1	-
<i>Amara</i> sp.	1	2
<i>Calathus melanocephalus</i> (Linnaeus)	-	1
<i>Carabus arvensis</i> Herbst	3	-
<i>Carabus nemoralis</i> Müller	5	2
<i>Carabus problematicus</i> Herbst	-	2
<i>Harpalus affinis</i> (Schrank)	-	1
<i>Harpalus</i> sp.	1	1
<i>Poecilus versicolor</i> (Sturm)	2	5
<i>Pterostichus niger</i> (Schaller)	-	1
<i>Pterostichus oblongopunctatus</i> (Fabricius)	1	-

**Appendix 2.** Carabid species that were caught by two window traps. The window traps, placed close to the road, captured animals that were flying from the heathland towards the formerly arable field. Window trap 1 was located at the heathland side of the road and window trap 2 was located on the formerly arable field side of the road.

Species	trap 1	trap 2
<i>Acupalpus brunnipes</i> (Sturm)	7	-
<i>Agonum meulleri</i> (Herbst)	1	1
<i>Agonum sexpunctatum</i> (Linnaeus)	1	-
<i>Amara aenea</i> (Degeer)	16	9
<i>Amara anthobia</i> A. Villa & G.B. Villa	3	2
<i>Amara famelica</i> Zimmermann	15	13
<i>Amara lunicollis</i> Schioedte	31	13
<i>Amara nitida</i> Sturm	14	15
<i>Amara plebeja</i> (Gyllenhal)	1	-
<i>Amara similata</i> (Gyllenhal)	1	-
<i>Anchomenus dorsale</i> (Pontoppidan)	2	-
<i>Ansiodactylus binotatus</i> (Fabricius)	4	3
<i>Calathus melanocephalus</i> (Linnaeus)	21	34
<i>Harpalus rufipalpis</i> Sturm	11	16
<i>Harpalus affinis</i> (Schrank)	3	8
<i>Pterostichus strenuus</i> (Panzer)	1	1
<i>Pterostichus vernalis</i> (Panzer)	14	7
<i>Stenolophus teutonius</i> (Schrank)	-	4



8



# HOW ANTS FIND EACH OTHER; TEMPORAL AND SPATIAL PATTERNS IN NUPTIAL FLIGHTS

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**Summary.** Reproduction is a key factor in understanding population ecology and therefore species occurrence. However, patterns in reproductive behaviour for distinct ant species remain insufficiently understood. In this paper strategies in mate finding are studied for six ant species (*Lasius niger*, *Lasius umbratus*, *Temnothorax nylander*, *Myrmica rubra*, *Myrmica ruginodis*, *Stenamma debile*) in a forest - forest edge - agricultural field gradient. Using window traps, we studied whether these species had a restricted nuptial flight season, displayed swarming behaviour, and whether the alates aggregated at the forest edge. The flight season was limited to one month or less for *L. niger*, *T. nylander*, *M. rubra*, *M. ruginodis* and *S. debile*. Swarming behaviour occurred in all but one (*L. umbratus*) species. Although none of the six species seemed to have highest nest density at the forest edge, three of them, *M. rubra*, *M. ruginodis* and *S. debile*, showed male aggregations there, indicating this to be the main mating site. This last finding could be due to a more suitable micro-climate, but most likely, edges are conspicuous land marks which are used by ants to meet mates. The behavioural patterns of ant sexuals at forest edges can influence dispersal possibilities in fragmented landscapes, reproductive success and nest densities.

**Key words.** edge effects, flight phenology, Formicidae, mate finding, reproduction

## Introduction

Reproduction behaviour and phenology are key factors for any species and need to be documented to understand species occurrence and population characteristics (Tschinkel 1991; Kaspari *et al.* 2001a). For ants, with a relative sessile way of living, flight capable sexuals are of high importance to ensure outbreeding, the founding of new colonies and colonization of new areas (Kannowski 1963; Hölldobler & Wilson 1990; Mabelis 1994). For this reason, every year much energy is invested in the production of winged sexuals (Brian 1979). Due to its vital importance, reproductive behaviour is precise and constant in most species. With few exceptions, males and gynes have to rely on meeting each other for mating during nuptial flights. The existence of mechanisms that increase the chance of finding each other is therefore crucial.

Broadly speaking, two types of nuptial flight events can be recognized (Hölldobler & Bartz 1985; Boomsma *et al.* 2005): (1) female calling syndrome, where females stay at a certain site and try to attract males, (2) male aggregation syndrome, where males come together at certain sites waiting for and attracting females. Both types can exist in one species (e.g., Franks *et al.* 1991). The production of pheromones plays an important role to attract each other during these events (Ayasse *et al.* 2001). Mechanisms to enhance successful mating – especially in the male aggregation syndrome – are the production of large numbers of sexuals (Brian 1979; Hölldobler & Wilson 1990) and the synchronous release of winged individuals from the nests (Kannowski 1963; Hölldobler & Wilson 1990). A third mechanism is the aggregation of winged ants at certain sites (Chapman 1954; Marikovski 1961; Woychiechowski 1990). During nuptial flights a single or several of these strategies can be exploited and this can vary for different species.

The occurrence of these mechanisms remains fragmentary and poorly known at the species level (Hölldobler & Wilson 1990). In this paper, the temporal and spatial patterns of nuptial flights of six ant species are explored at a forest - forest edge - agricultural field transect. We studied whether the alates of these ant species (i) had a restricted flight season (time of year during which alates display nuptial flights), (ii) displayed swarming behaviour (many individuals occurring on the same moment), and (iii) aggregated at the forest edge. In this way, more insight is obtained in the differences in reproductive behaviour between several co-existing species and a better understanding is gained in the possible effects of landscape features on the occurrence of species.

## Material and Methods

### *Study location*

At a location near Wageningen (51°58'N–5°39'E, province Gelderland, the Netherlands), a forest, the bordering agricultural grassland and the transition between these habitats were sampled. Each of the three habitats will be referred to as a 'site' during the remainder of this paper.



**Figure 1.** The field location; some of the window traps in the ‘field’ and in the ‘forest edge’ are depicted.

The tree layer of the forest is approximately 20 m high and is dominated by *Quercus robur*. Other species occurring in the tree and shrub layer are: *Betula pendula*, *Corylus avellana*, *Sorbus aucuparia* and *Prunus serotina*. In the herb layer species like *Athyrium filix-femina*, *Dryopteris dilatata* and *Holcus lanatus* can be found. The forest edge is facing south by southeast and is situated around a ditch and consists of a row of *Alnus glutinosa* trees. This forest edge is sharp and straight and *Rubus caesius*, *Humulus lupulus*, *Arrhenatherum elatius* and *Holcus lanatus* are abundant. The agricultural grassland consists of a *Lolium multiflorum* monoculture with sparse occurrence of other plant species. This grassland was mowed three times during the study period, during two of which the window traps needed to be removed for several days. Manure was injected in early spring before sampling started and after each mowing event.

#### *Measuring ground activity of workers*

Ten pitfall traps were used at each of the three sites to measure worker activity. We assume that gradients in worker activity across the sites reflect underlying nest density. The traps were made of a test tube with a diameter of 15 mm and a depth of 120 mm (modified from the description in Majer 1978), filled with a raspberry/cherry wine (12% alcohol) to attract ants. The traps were placed in the ground at the forest edge (0.1 m into the edge vegetation), 15 m into the field, and 15 m into the forest. Within each site, the traps were spaced 8 m from each other and placed close to the window traps (see below). The test tube traps were open from August the 6th (9.00 AM) until August the 9th (9.00 AM) 2006.

#### *Measuring flight activity of alates*

Window traps were used to collect flying ants (Fig. 1, modified from the description in Duelli *et al.* 1999). The traps were placed with a distance of 8 m from each other in

each of the three sites: at the forest edge (0.5 m from the tree branches), 15 m into the field and 15 m into the forest. A trap consists of a wooden frame containing a transparent plexiglass pane of 80 by 60 cm, vertically fixed with its lower side 1 m above ground level. Below each pane, a plastic gutter was placed protruding 8.9 cm on each side. These gutters were half filled with a saturated salt solution. Both in the field and in the forest edge ten window traps were placed, alternately with a parallel and perpendicular orientation towards the forest edge (Fig. 1). In the forest, six alternately positioned window traps were operative. This lower number is due to the fact that the setup was initially intended for a study sampling field inhabiting flying ground beetles. In that study the window traps in the forest merely acted as a control to establish whether flying ground beetles entered the forest at all.

Field observations revealed that straight flying small insects were not always effectively intercepted by the window traps. These insects were sometimes able to land on the pane or simply fly off. Probably especially descending insects end up in the gutters, additionally directed by the panes. Males do often not fly away after mating, as gynes do to find possible nesting sites, but 'fall' down (Hölldobler 1976; Carlton & Goldman 1984; Hölldobler & Wilson 1990; P. Boer pers. obs.). Thus especially when the window trap catches are male dominated, we expect them to provide a reliable indication of the mating location of ants.

The gutters of the window traps were emptied daily from April the 19th until October the 10th 2006 at approximately 9.00 AM (during the nuptial flight season of the recorded species this coincided with UTC+2h). After October the 10th, the gutters were occasionally checked until December the 1st, but no more alates were found. Window trap catches from the same site were bulked and treated as one sample. All ants were identified to species level and their sex was noted. If more than 50% of the total number of collected alates was caught on only one or two days, the species was considered to display a synchronous release of sexuals. Species with an observed flight season of less than one month, are considered as having a restricted flight season (Kannowski 1963). The period between the first and the last catch of multiple sexuals on one day was considered the flight season, since the catches of single individuals might concern ants from other areas or decision errors of individuals (Kaspari *et al.* 2001b). From the 10th until the 17th of May and from the 22nd until the 26th of June, the window traps were temporarily removed during agricultural activities in the field.

#### *Micro-climate measurements*

To determine differences in micro-climate for the three sites, six data loggers (type: Hobo RH/T. H08-003-02) were attached on the frame of window traps; two per site. Every month, the data loggers were randomly redistributed among the traps. The data loggers measured relative humidity and temperature every 15 minutes. The average of both data loggers per site was used to determine temperature and relative humidity.



### Statistics

The spatial distribution of ant workers (differences between sites) was analysed using G-tests for goodness of fit (with Williams' correction), assuming even distributions of workers over the sites. The distribution of flying alates over the sites was tested against that of the workers (from the test tube traps), using logit analyses of proportions allowing for the difference in window trap number. For species not found in the test tube traps we used goodness of fit tests, assuming an even distribution over the sites. Two analyses were performed for species found in both the test tube traps and in the window traps. First, we analysed whether the relative number of alates (compared to worker density) differed between the species' nesting site (either forest or field) and the forest edge. Secondly the same test was done between the nesting site and the remaining opposite site (field or forest). Sex ratios were analysed using goodness of fit tests. Differences in temperature and relative humidity between the sites were analysed using Wilcoxon signed rank tests. In this analysis, only data from the actual period of nuptial flights were used, i.e., the 29th of May until the 1st of October.

## Results

### *Species composition and sex ratio*

A total of 19 ant species was collected in the window traps (Table 1). Six species were found in sufficiently high numbers in the window traps for analyses: *Lasius niger* (Fig. 2), *Lasius umbratus*, *Temnothorax nylanderi*, *Myrmica rubra*, *Myrmica ruginodis* and *Stenamma debile* (Table 1).

For these six species, sex ratios – number of ♂♂ divided by number of ♀♀ – were found to significantly deviate from 1, with the catches of *L. umbratus* and *T. nylanderi* dominated by gynes and the catches of the other species dominated by males (Table 2).

### *Temporal patterns of nuptial flight: restricted flight season and swarming behaviour*

The flight season of the six ant species fell from the end of June until the end of September (Fig. 2, disregarding days on which only one alate was caught). *Lasius umbratus* had a very long period in which nuptial flights occurred, it might even have been slightly longer, but from the 22nd until the 26th of June no observations could be made. Also *T. nylanderi* had a relatively long flight season. On the other hand, *L. niger* displayed a relatively short flight season of exactly one month. *Myrmica rubra*, *M. ruginodis* and *S. debile* showed a short peak, between 1 and 2 weeks, in alate emergence. These results are not caused by sampling artefacts, since *M. ruginodis* with a short flight season was caught with the most individuals and *T. nylanderi* with a long flight season was collected in the lowest abundance. The related *M. rubra* and *M. ruginodis* had a distinct non-overlapping flight season.

Within their flight season, for all species except for *L. umbratus*, more than 50% of the alates were caught on only one or two days (Fig. 2).



**Figure 2.** *Lasius niger* ants prior to a nuptial flight event. Several males, one gyne (the large ant in the middle) and one worker (un-winged ant just below the gyne) are depicted.

**Table 1.** All ant species caught using 30 test tube traps and 26 window traps, including the number of worker and alate individuals. The species dealt with in this paper (caught in sufficient numbers by the window traps) are given in bold.

	test tube traps (# workers)	window traps (# alates)
<i>Formica rufa</i> L., 1758	-	1
<i>Lasius brunneus</i> (Latreille, 1798)	-	1
<i>Lasius flavus</i> (Fabricius, 1782)	-	9
<i>Lasius fuliginosus</i> (Latreille, 1798)	-	4
<i>Lasius meridionalis</i> (Bondroit, 1920)	-	7
<i>Lasius mixtus</i> (Nylander, 1846)	-	1
<b><i>Lasius niger</i></b> (L., 1758)	<b>82</b>	<b>205</b>
<i>Lasius platythorax</i> Seifert, 1991	33	5
<b><i>Lasius umbratus</i></b> (Nylander, 1846)	-	<b>154</b>
<i>Myrmecina graminicola</i> (Latreille, 1802)	-	1
<b><i>Myrmica rubra</i></b> (L., 1758)	<b>351</b>	<b>33</b>
<b><i>Myrmica ruginodis</i></b> Nylander, 1846	<b>69</b>	<b>209</b>
<i>Myrmica rugulosa</i> Nylander, 1849	-	1
<i>Myrmica sabuleti</i> Meindert, 1861	8	4
<i>Myrmica scabrinodis</i> Nylander, 1846	-	9
<i>Ponera coarctata</i> (Latreille, 1802)	-	1
<b><i>Stenamma debile</i></b> (Förster, 1850)	-	<b>83</b>
<b><i>Temnothorax nylanderi</i></b> (Förster, 1850)	<b>24</b>	<b>53</b>
<i>Tetramorium caespitum</i> (L., 1758)	-	1

*Worker activity*

Six ant species were collected in the test tube traps (Table 1). In total, four species were sampled in the forest (352 individuals), four at the forest edge (126 individuals), and three in the field (89 individuals). In the forest *M. rubra* and *M. ruginodis* were the most abundant species. In the edge the samples were dominated by *M. rubra*. In the field *L. niger* was very dominant, with only a few individuals of two other species.

In Figure 3 (grey symbols) the relative amount of collected workers is given across the field - edge - forest transect. Of the six collected species in the test tube traps, four concerned workers of the six studied species: *L. niger*, *T. nylanderii*, *M. rubra* and *M. ruginodis*. Of all four species the occurrence of workers over the sites deviated highly significantly from an even distribution (all  $df = 2$ ,  $P < 0.001$ ).

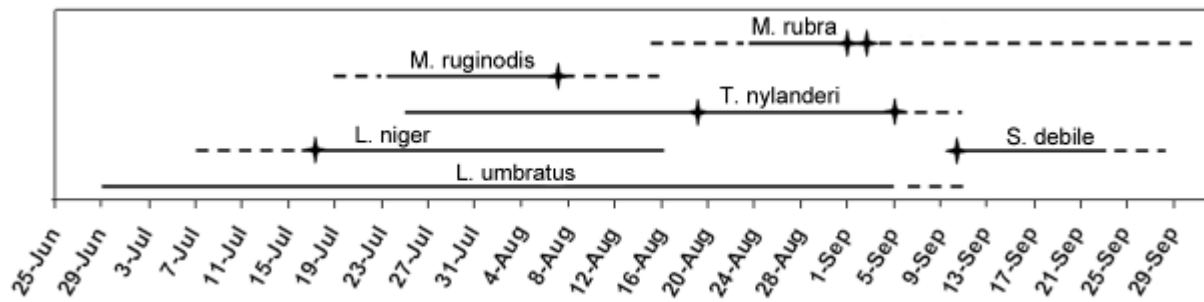
Two of the six species were not found in the test tube traps: *S. debile* and *L. umbratus*. In the Netherlands, *S. debile* is a forest species (van Loon 2004), so we may assume the nests of this species to be most abundant in the forest site. *Lasius umbratus* is a social parasite in nests of *Lasius* s.s. species (Dekoninck *et al.* 2004). At our location possible hosts are *L. niger* (highest worker activity density in the field) and *L. platythorax* (highest worker activity density in the forest, data not shown). From this, *L. umbratus* might be expected to have the lowest nest abundance in the forest edge.

*Spatial pattern of nuptial flights: Aggregation at the forest edge*

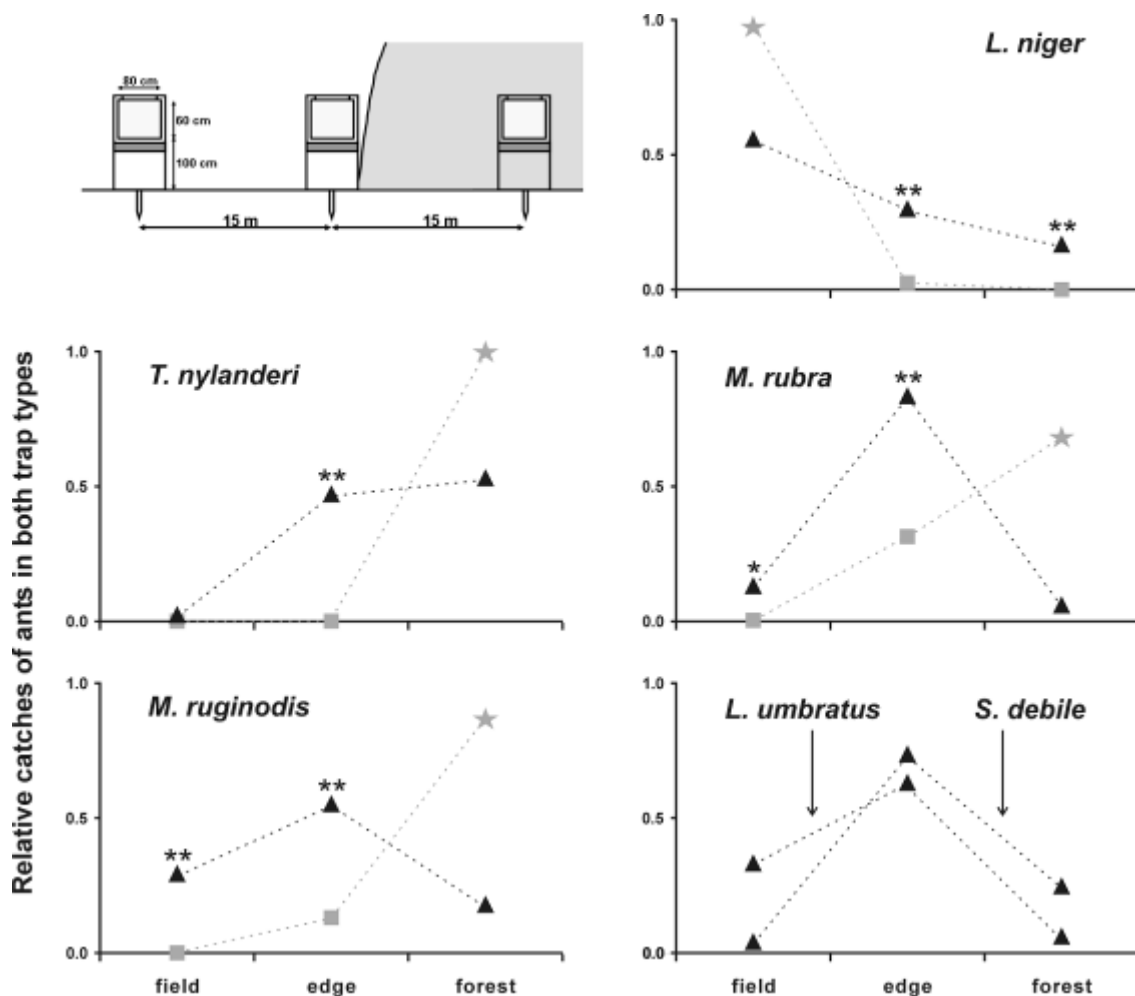
For four out of the six studied species, highest alate abundance was found at the forest edge (Fig. 3, black symbols). All four species of which workers were caught showed a occurrence of alates over the sites that differed significantly from the worker distribution ( $df = 2$ ,  $P < 0.001$  for all species). Each of these showed a significantly higher alate abundance at the forest edge than would be expected from the occurrence of workers (Fig. 3): *L. niger* (log-odds ratio = 3.05,  $P < 0.001$ ), *T. nylanderii* (log-odds ratio = 3.70,  $P < 0.001$ ), *M. rubra* (log-odds ratio = 3.57,  $P < 0.001$ ) and *M. ruginodis* (log-odds ratio = 3.06,  $P < 0.001$ ). For three of these, alates were also found in significantly higher relative abundances in the habitat 'opposite' to their nesting habitat: *L. niger* in the forest (log-odds ratio = 3.81,  $P < 0.001$ ), and *M. rubra* (log-odds ratio = 3.58,  $P = 0.009$ ) and *M. ruginodis* (log-odds ratio = 4.25,  $P < 0.001$ ) both in the field (Fig. 3). *Temnothorax nylanderii* did not have a high relative alate number in its 'opposite' habitat (log-odds ratio = 0.94,  $P = 0.64$ ).

**Table 2.** Observed sex ratios for alates caught by the window traps.

	♂	♀	sex-ratio (♂/♀)	Significance ( $df = 1$ )
<i>L. niger</i>	176	29	6.06	$G = 116.79$ , $P < 0.001$
<i>L. umbratus</i>	29	125	0.23	$G = 64.28$ , $P < 0.001$
<i>T. nylanderii</i>	2	51	0.04	$G = 55.91$ , $P < 0.001$
<i>M. rubra</i>	31	2	15.50	$G = 30.20$ , $P < 0.001$
<i>M. ruginodis</i>	177	32	3.66	$G = 51.37$ , $P < 0.001$
<i>S. debile</i>	65	18	3.61	$G = 28.09$ , $P < 0.001$



**Figure 2.** The occurrence of alates of the six ant species at the sampled location in 2006. Dashed lines represent the period in between the first catch of one individual and the first catch of several individuals or between the last catch of several individuals and the last catch of one individual. The solid lines, considered here as the flight season, represent the period between the first and the last catch of several individuals. The vertical marks represent the day on which >50% of the alates was found, when two marks are given these days make together >50%.



**Figure 3.** Results from the window trap and test tube trap catches. In the upper left corner a schematically representation of the experimental set-up; the window traps, test tube traps, forest, and relevant distances and sizes are depicted. The other graphs show the relative distribution of the species over the test tube traps (grey symbols) and the window traps (black symbols). The main nesting habitat of the species is indicated by a grey star. Dotted lines between the data points are only placed to emphasize the patterns. Significance asterisks indicate that in that particular habitat more alates were observed than would be expected from the workers (always tested against the main nesting habitat). \*:  $P < 0.01$ , \*\*:  $P < 0.001$ .

The alates of the two species of which no workers were caught, *S. debile* (a forest species) and *L. umbratus* (highest nest density most likely not in the forest edge), were not distributed evenly over the sites ( $G = 63.54$  and  $G = 74.48$  resp., both  $df = 2$ ,  $P < 0.001$ , Fig. 3). Both species showed a higher abundance of alates at the forest edge when compared to both the forest (*L. umbratus*:  $G = 61.62$ ; *S. debile*:  $G = 17.37$ ; both  $df = 1$ ,  $P < 0.001$ ) and the field (*L. umbratus*:  $G = 15.03$ ; *S. debile*:  $G = 71.76$ ; both  $df = 1$ ,  $P < 0.001$ ) (Fig. 3).

#### *Micro-climatic conditions*

As expected, temperature was lower in the forest compared to the edge ( $Z = -26.55$ ,  $P < 0.001$ ) and the field ( $Z = -30.16$ ,  $P < 0.001$ ). Also, temperature at the forest edge was higher than that in the field ( $Z = -7.885$ ,  $P < 0.001$ ). Expected patterns were found for relative humidity as well: in the forest it was higher than at the edge ( $Z = -46.49$ ,  $P < 0.001$ ) and in the field ( $Z = -45.20$ ,  $P < 0.001$ ). The edge had higher relative humidity than the field ( $Z = -2.978$ ,  $P = 0.003$ ).

## **Discussion**

#### *Sampling methods*

Whether test tube traps are appropriate for sampling sufficient numbers of species and individuals, largely depends on the aim of the study. They seem very satisfactory for rapid biodiversity assessments, as they collect all abundant species with ground active workers (Majer 1997; Borgelt & New 2006). In our study this proved to be the case: all species with ground active workers that were abundant in the window traps, were also sufficiently caught by the test tube traps. Of the two species that were not collected in the test tubes, the workers of *L. umbratus* live entirely subterranean in symbiosis with root aphids (Czechowski & Rotkiewicz 1997) and *S. debile* forages mostly underground or in the litter layer with a small home range (Buschinger 1999). More intensive sampling with pitfall traps would most likely not have changed the results. In contrast, window traps are suitable to sample abundant species in the airspace around the traps including sexuals of subterranean species.

#### *Types of nuptial flight and sex-ratio*

For species with a male aggregation syndrome, the sex ratio is male biased at the reproduction sites. After mating, females fly off to possible nest sites (Seifert 2007), males however do not move away from these sites (Hölldobler & Wilson 1990) and therefore have a higher chance of ending up in traps if these are located on the reproduction site (Woyciechowski 1987, 1990, 1992). Species caught with significantly more males at the study location most likely mate there. The catches of *M. rubra*, *M. ruginodis*, *L. niger* and *S. debile* were all male biased and for the first three species the male aggregation syndrome is known (Brian & Brian 1955; Boomsma & Leusink

1981; Woyciechowski 1990, 1992; P. Boer pers. obs.). For *S. debile* the type of nuptial flight is not easy to describe. Buschinger (1999) found young queens in the nest with their mother; suggesting female calling behaviour, since it is unlikely that a gyne can find her home nest after swarming. Although swarming seems to be uncommon for *S. debile* (Buschinger & Heinze 2001; Seifert 2007), on the 10th and the 11th of September 47 and 18 alates respectively were found in the window traps (50 males and 15 females), indicating that the male aggregation syndrome occurs in this species as well.

The catches of *T. nylanderi* and *L. umbratus* were gyne dominated. This could be expected for *T. nylanderi*, since in this genus female calling behaviour is known to occur (Buschinger & Buschinger 2003). Mating occurs around the nests in the forest, and afterwards only gynes fly off to find suitable nesting places. In other words, there are no 'falling' males to end up in the window traps. However, gyne dominated catches are not expected for *L. umbratus* which typically displays male swarming behaviour, and for which sex ratio's of flying alates are mostly male dominated (P. Boer pers. obs.). This species is known to have meeting places high in the air, and possibly only gynes on their way to new nesting sites were intercepted by the window traps.

#### *Temporal patterns in nuptial flight*

Four out of six ant species, *L. niger*, *M. rubra*, *M. ruginodis* and *S. debile*, had a short flight season, which is in agreement with the statement of Kanno (1963) that local populations in temperate regions have flight seasons of approximately one month (but see Dunn *et al.* 2007). The relatively long flight season of the other two species, *L. umbratus* and *T. nylanderi*, seems to contrast with this. The synchronous flights of *T. nylanderi* alates circumvents the disadvantages of a long flight season and may even turn it into an advantage. The combination of a long possible flight season but a synchronous alate emergence gives the ants a better opportunity to wait for the optimal circumstances for nuptial flights. The alates caught outside the swarming events might have made decision errors or might originate from other areas and will have a lower possibility to mate (Kaspari *et al.* 2001b). The length of the flight season of alates appears to be partly determined by geography (latitude: Kaspari *et al.* 2001b; elevation: Dunn *et al.* 2007) and further studies of regional effects on flight season and other life-history traits are needed to gain understanding of this pattern. The non-overlapping flight seasons of *M. rubra* and *M. ruginodis* are interesting and might be evolved to avoid hybridisation. Other sites where both species co-exist should be investigated on this phenomenon.

A synchronous release of sexuals from different colonies is a very efficient way to promote outbreeding. Five out of the six species showed this synchronous release pattern, but none of these events coincided for the different species. This means that flight seasons and swarming events are initially dependant on the species in question. The flight season is affected by species' life-history traits and physiology, for example the period of production of sexuals, the moment of alate emergence from

pupal cases, the time needed to create nest openings, and the size of the alates (Kannowski 1963; Boomsma & Leusink 1981). In the second place, specific meteorological conditions might trigger alate releases from the nest, most likely a combination of high soil temperature and warm and calm above ground conditions (Boomsma & Leusink 1981; Depa 2006). Analyses of our data on the occurrence of alates and prevailing meteorological circumstances indicate that most of the here presented species reacted to similar triggers (unpublished data).

#### *Spatial patterns in nuptial flight*

Although none of the species seem to have the highest worker activity at the sharp forest edge, four out of the six species showed here the highest abundance of sexuals. Alates of the opportunistic species *L. niger* were found in higher numbers than would be expected from the workers both at the edge and in the forest, so no aggregation at the forest edge could be proven for this species. For *L. umbratus* no swarming events and male aggregations could be found. The higher abundance of this species at the forest edge therefore need not be the result of nuptial flight aggregations. *Lasius* species are known to reach altitudes of 50 m or higher during nuptial flights (Duelli *et al.* 1989; P. Boer pers. obs.), so the forest edge is too low to have influence on the nuptial flights of *L. niger* and *L. umbratus*. The observed abundance of *L. umbratus* at the forest edge is possibly caused by gynes on their way to find new nesting places (see Wilson & Hunt 1966; Goodisman *et al.* 2000).

*Temnothorax nylanderii* alates were not found with highest abundance at the edge, but the number of alates was higher there than would be expected from the worker presence. This might be due to an 'indirect' effect: *T. nylanderii* alates were abundant inside the forest (the nesting site), and if these alates simply fly in a random way through the forest, there might be accumulation at the forest edge of individuals that are reluctant to leave their habitat. Alates of the other forest species, *S. debile*, had very low occurrence in the field site as well. This reluctance of gynes to enter non-nesting habitat has also been observed in other species (Wilson & Hunt 1966).

For the other three species, *M. rubra*, *M. ruginodis* and *S. debile*, the combination of male dominated swarms and the high abundances at the forest edge indicates these species would seem to purposely aggregate here. Mating at aggregation sites is well known for other insects, both for other Hymenoptera (e.g., Alcock & Carey 1988), as for other insect orders, e.g., Lepidoptera, Ephemeroptera and Diptera (Downes 1969; Allan & Flecker 1989; Brown & Alcock 1990).

There is an obvious reason for aggregation behaviour in ants: it enhances the chance of mate finding and is an appropriate way to avoid kin-mating (Woyciechowski 1987; Seifert 2007). Brian and Brian (1955) reported mating of *M. rubra* at the conjunction of an elevated structure and bare ground; males fly towards the structure and wait for females at the ground. All kinds of structures might provide in aggregation sites (e.g., Donisthorpe 1927; Michener 1960; Woyciechowski 1990; Buschinger & Buschinger 2003). However, it still is unclear how ants 'choose'

places for aggregations. Kanno (1963) observed that alates of day flying species often flew towards places with highest light intensity, and for the forest dwelling species this could explain the establishment of meeting sites at the southerly exposed forest edge. It has also been suggested ants can distinguish prominent features in the landscape and fly towards it (Collingwood 1958; Seifert 2007). As the results of the micro-climatologically data have shown, the temperature at the edge was highest and the edge had a higher relative humidity than the field, so this site could also provide more attractive conditions for nuptial flights (Boomsma & Leusink 1981; Depa 2006). On the other hand, it is also possible that the observed aggregations are simply directed by accumulations of ants, and consequently pheromones, due to the effects of a physical transition (also influencing wind direction, turbulence, etc.).

## Conclusion

With the exception of *L. umbratus*, we could establish at least one behavioural strategy for the species at our study location to increase the chance of finding a mate (Table 3). Especially the behavioural deviations at the forest edge will affect species distributions. First, this implicates that for ants not only the quality of nesting biotope is important for the completion of life-cycles, but the physical structure of the area as well. Secondly, the reluctance of the sexuals of *S. debile* and *T. nylanderii* to leave their habitat, indicates that habitat fragmentation will lead to dispersal and colonisation limitations for these forest ants. Thirdly, the aggregations at the forest edge might explain differences in nest densities in heterogeneous habitats. The closer a place is to an aggregation site, the higher the chance fertilized females will land here and try to initiate a colony after a nuptial flight. These findings are important for distribution, population and conservation studies on ants.

**Table 3.** Observed strategies in alate nuptial flight for the studied species: restricted flight season ( $\leq$  one month), swarming behaviour (synchronous occurrence of  $>50\%$  of the alates during one or two days), and aggregation at the forest edge.

	restricted flight season	swarming behaviour	aggregations
<i>L. niger</i>	+	+	
<i>L. umbratus</i>			
<i>T. nylanderii</i>		+	
<i>M. rubra</i>	+	+	+
<i>M. ruginodis</i>	+	+	+
<i>S. debile</i>	+	+	+

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## References

- Alcock J & Carey M **1988**. Hilltopping behaviour and mating success of the tarantula hawk wasp, *Hemipepsis ustulata* (Hymenoptera: Pompilidae), at a high elevation peak. *Journal of Natural History* 22: 1173-1178.
- Allan JD & Flecker AS **1989**. The mating biology of a mass-swarming mayfly. *Animal Behaviour* 37: 361-371.
- Ayasse M, Paxton RJ & Tengö J **2001**. Mating behavior and chemical communication in the order Hymenoptera. *Annual Review of Entomology* 46: 31-78.
- Boomsma JJ & Leusink A **1981**. Weather conditions during nuptial flights of four European ant species. *Oecologia* 50: 236-241.
- Boomsma JJ, Baer B & Heinze J **2005**. The evolution of male traits in social insects. *Annual Review of Entomology* 50: 395-420.
- Borgelt A & New TR **2006**. Pitfall trapping for ants (Hymenoptera, Formicidae) in mesic Australia: what is the best trapping period? *Journal of Insects Conservation* 10: 75-77.
- Brian MV **1979**. Habitat differences in sexual production by two co-existent ants. *Journal of Animal Ecology* 48: 943-953.
- Brian MV & Brian AD **1955**. On the two forms macrogyna and microgyna of the ant *Myrmica rubra* L. *Evolution* 9: 280-290.
- Brown WD & Alcock J **1990**. Hilltopping by the red admiral butterfly: mate searching alongside congeners. *Journal of Research on the Lepidoptera* 29: 1-10.
- Buschinger A **1999**. *Stenamma debile* (Hymenoptera, Formicidae): Facultative polygyny, and an extreme 1997 sex ratio. *Insectes Sociaux* 46: 53-57.
- Buschinger A & Buschinger R **2003**. Schwarmverhalten von *Leptothorax tuberum* (Fabricius, 1775) im Freiland (Hymenoptera: Formicidae). *Myrmecologische Nachrichten* 5: 7-9.
- Buschinger A & Heinze J **2001**. *Stenamma debile* (Hymenoptera, Formicidae): Productivity and sex allocation across three years. *Insectes Sociaux* 48: 110-117.
- Carlton RG & Goldman CR **1984**. Effects of a massive swarm of ants on ammonium concentrations in a subalpine lake. *Hydrobiologia* 111: 113-117.
- Chapman JA **1954**. Swarming of ants on western United States mountain summits. *Pan-Pacific Entomologist* 30: 93-102.
- Collingwood CA **1958**. Summit ant swarms. *Entomologist's Record* 70: 65-67.
- Czechowski W & Rotkiewicz W **1997**. Common activities of female sexuals of *Lasius umbratus* (Nyl.) and *Formica sanguinea* Latr. or *Polyergus rufescens* (Latr.) on nests of the dulotic species (Hymenoptera, Formicidae). *Annales Zoologici (Warsaw)* 47: 465-467.
- Dekoninck W, Boer P & Maelfait J-P **2004**. *Lasius platythorax* Seifert, 1991 as a host of several *Chthonolasius* species, with remarks on the colony foundation of the parasites (Hymenoptera: Formicidae). *Myrmecologische Nachrichten* 6: 5-8.
- Depa Ł **2006**. Weather conditions during nuptial flight of *Manica rubida* (Latreille, 1802) (Hymenoptera: Formicidae) in southern Poland. *Myrmecologische Nachrichten* 9: 27-32..
- Donisthorpe HStJK **1927**. *British ants, their life-history and classification* (2<sup>nd</sup> Edition). George Routledge & Son, London, UK.
- Downes JA **1969**. The swarming and mating flight of Diptera. *Annual Review Entomology* 14: 271-298.
- Duelli P, Näf W & Baroni-Urbani C **1989**. Flughöhen verschiedener Ameisenarten in der Hochrheinebene. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 62: 29-35.

- Duelli P, Obrist MK & Schmatz DR **1999**. Biodiversity evaluation in agricultural landscapes: above-ground insects. *Agriculture, Ecosystems and Environment* 74: 33-64.
- Dunn RR, Parker CR, Gerarghty M & Sanders NJ **2007**. Reproductive phenologies in a diverse temperate ant fauna. *Ecological Entomology* 32: 135-141.
- Franks NR, Sendova-Franks AB, Sendova-Vassileva M & Vassilev L **1991**. Nuptial flights and calling behaviour in the ant *Leptothorax acervorum* (Fabr.). *Insectes Sociaux* 38: 327-330.
- Goodisman MAD, DeHeer C & Ross KG **2000**. Unusual behavior of polygyne fire ant queens on nuptial flights. *Journal of Insect Behavior* 13: 455-468.
- Hölldobler B **1976**. The behavioral ecology of mating in harvester ants (Hymenoptera: Formicidae: *Pogonomyrmex*). *Behavioral Ecology and Sociobiology* 1: 405-423.
- Hölldobler B & Bartz SH **1985**. Sociobiology of reproduction in ants. *Fortschritte der Zoologie* 31: 237-257.
- Hölldobler B & Wilson EO **1990**. *The ants*. Belknap Press of Harvard University, Cambridge, Massachusetts, USA.
- Kannowski PB **1963**. The flight activities of formicine ants. *Symposia Genetica et Biologica Italica* 12: 74-102.
- Kaspari M, Pickering J, Longino JT & Windsor D **2001a**. The phenology of a neotropical ant assemblage: evidence for continuous and overlapping reproduction. *Behavioral Ecology Sociobiology* 50: 382-390.
- Kaspari M, Pickering J & Windsor D **2001b**. The reproductive flight phenology of a neotropical ant assemblage. *Ecological Entomology* 26: 245-257.
- van Loon AJ **2004**. Formicidae - mieren. In: *De wespen en mieren van Nederland (Hymenoptera: Aculeata)*. Nederlandse Fauna 6 (Reemer M, van Loon AJ & Peeters TMJ eds.): 227-263. NNMN, KNNV and EIS-Nederland, Leiden, the Netherlands.
- Mabelis AA **1994**. Flying as a survival strategy for wood ants in a fragmented landscape (Hymenoptera, Formicidae). *Memorabilia Zoologica (Warsaw)* 48: 147-170.
- Majer JD **1978**. An improved pitfall trap for sampling ants and other epigaeic invertebrates. *Journal of the Australian Entomological Society* 17: 261-262.
- Majer JD **1997**. The use of pitfall traps for sampling ants - a critique. *Memoirs of the Museum of Victoria* 56: 323-329.
- Marikovski PI **1961**. Material on sexual biology of the ant *Formica rufa* L. *Insectes Sociaux* 8: 23-30.
- Michener CD **1960**. Treetop mating aggregations of *Pogonomyrmex* (Hymenoptera: Formicidae). *Journal of the Kansas Entomological Society* 33: 46.
- Seifert B **2007**. *Die Ameisen Mittel- und Nordeuropas*. Lutra Verlags- und Vertriebsgesellschaft, Tauer, Germany.
- Tschinkel WR **1991**. Insect sociometry: a field in search of data. *Insectes Sociaux* 38: 77-82
- Wilson EO & Hunt GL **1966**. Habitat selection by the queens of two field-dwelling species of ants. *Ecology* 47: 485-487
- Woychiechowski M **1987**. The phenology of nuptial flights of ants (Hymenoptera, Formicidae). *Acta Zoologica Cracoviensia* 30: 137-140.
- Woychiechowski M **1990**. Nuptial flights in several ant species and their aerial aggregations (Hymenoptera, Formicidae). *Acta Zoologica Cracoviensia* 33: 555-564.
- Woychiechowski M **1992**. Nuptial flights of ants (Hymenoptera, Formicidae) and their aerial aggregations. *Biology and Evolution of social insects* (Billen J ed.): 41-45. University Press, Leuven, Belgium.



# 9



Foto: Dick Kuiper

# GENERAL DISCUSSION

## ARTHROPODS IN LINEAR ELEMENTS – OCCURRENCE, BEHAVIOUR AND CONSERVATION MANAGEMENT

### **Biodiversity conservation in roadside verges**

In the Netherlands all habitats are created or highly influenced by men, which entails that for their maintenance they are almost all dependent on human interference (e.g., Stumpel 2004). Absence of management often leads to a decline in biodiversity, largely due to two factors: (i) In human-dominated landscapes most natural disturbances – often drivers for biodiversity (e.g., Hastings 1980; Wilson 1994; Lambeets 2009) – have been lost, (ii) All habitats suffer from high atmospheric deposition of nitrogenous compounds – originating predominately from bio-industry (MNP 2007) – boosting vegetation succession towards densely covered and species-poor situations (Bobbink *et al.* 1998; Schaffers *et al.* 1998). Conservation management aimed at the preservation of biodiversity is therefore necessary to counteract these negative aspects. In addition, a substantial part of our country is covered by agricultural and urban areas, which are highly unsuitable biotopes for many species. In these areas, the conservation of biodiversity in all sorts of small, semi-natural landscape elements has become increasingly urgent as they represent refuges for many plants and animals in a largely hostile environment (Novacek & Cleland 2001).

This thesis deals with the conservation of arthropods (mainly) in roadside verges. Arthropods are highly abundant in small landscape elements, comprise the majority of our biodiversity, provide many essential ecosystem services, and are often seriously threatened. We were able to prove that roadside verges offer various opportunities for arthropod conservation, as many species were found in these landscape elements (CHAPTER 2). For various groups, a substantial part of the species indigenous in the Netherlands appeared to be present in the roadside biotopes sampled for our studies. Although the majority might be generalist species, several threatened, protected and rare (CHAPTER 2; Fig. 1; Table 1) and many specialist species were found here as well (CHAPTER 5 & 6). Strong indications exist that many insects and spiders can also fulfil their entire life-cycle here (e.g., Wynhoff *et al.* 2005; Noordijk 2008), because feeding resources were present (CHAPTER 4), nesting sites were discovered (Noordijk & Boer 2007), and reproduction and overwintering occurred here (CHAPTER 6; Raemakers *et al.* in prep.). The importance of roadside verges for arthropod diversity seems a general phenomenon in countries with large areas of urban and agricultural lands (CHAPTER 2).



**Figure 1.** The extremely rare ground beetle *Cylindera germanica* (L.) is found only at one location in the Netherlands, where its habitat partly occurs on substantial stretches of roadside verges.

Three research questions were formulated regarding the conservation of arthropods in roadside verges.

- (i) Since roadside verges covered with grassland need to be regularly mown to secure traffic safety and to maintain or promote diverse plant communities, we tested which mowing regime would be most beneficial for arthropod diversity.
- (ii) As sandy roadside verges often contain well-developed open, warm and dry plant communities, we tested whether such verges act as valuable additional arthropod habitats and whether they can function as ecological corridors in a highly fragmented heathland and drift sand landscape.
- (iii) Because roadside verges are prone to edge effects due to their small and linear outline, we explored how typical edge biotopes affect insect behaviour.

### **Arthropods in grassland verges**

In the Netherlands, many roadside verges have hay-meadow characteristics (Sýkora *et al.* 1993; Schaffers 2000). At present, such plant communities have become rare because traditional agricultural activities have ceased. Hay-meadows are important for botanical diversity and rare plants (Schaminée *et al.* 1996). We performed experiments in three grassland verges under hay-making management and found several spiders, ants, ground beetles and weevils with a very restricted national occurrence, including one weevil species new to the Dutch fauna (Table 1), illustrating the importance of managed grassland verges to arthropods.

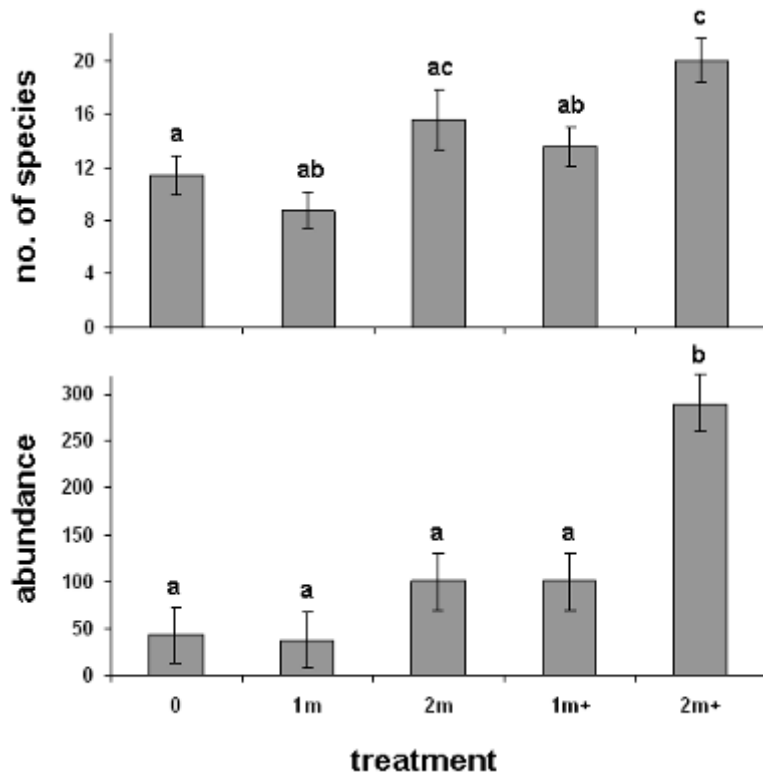
The main purpose of management in roadside grasslands is to secure traffic safety by keeping the verges open and preventing tree and shrub establishment, but an important secondary aim is to stimulate diverse plant communities. In roadside verges with relatively high productivity, the general applied management of mowing for hay twice a year appear necessary to maintain high plant species-richness. This activity replaces more natural disturbances and counteracts the negative impacts of atmospheric deposition of nitrogenous compounds (Schaffers *et al.* 1998; Keizer *et al.* 2006). Mowing is therefore applied in many grassland verges. However, little was known on the effects of mowing regimes on arthropods. To examine which mowing regime would be most appropriate from the arthropod-conservation point of view, the effects of different mowing treatments on insect and spider diversity was investigated. In CHAPTER 3 we could prove that in relatively high-productive grassland verges mowing twice a year with removal of the cuttings resulted in the most attractive situation for epigeic arthropods. This can be explained by the fact that many ground-dwelling animals prefer open vegetation to move freely and need sunlit soils for a favourable micro-climate. Mowing twice per year with removal of the cuttings also provided best feeding opportunities for flower-visiting insects, as was shown in CHAPTER 4. Apparently, a management aiming at diverse plant communities, results in high flower abundances (and fewer grasses), and is therefore also favourable for flower-visiting insects. In addition, the early-summer cut caused many plants to flower again later in the season and this attracted also many insects. Cutting twice per year with hay-removal thus appears the most appropriate management not only for the vegetation, but also for epigeic arthropods and flower visiting insects. In low-productive verges a less intensive management can be applied without harming plant and insect biodiversity (CHAPTER 3). In medium to high-productive verges, however, a less intensive management will result in a rapid decrease in diversity of ground-dwelling arthropods, flower-visiting insects and plant species (CHAPTER 3 & 4).

To support these results that were obtained by studying actively moving animals, we performed an inventory on weevils in the experimental plots of the medium-productive verge (close to the city Heerlen; Heijerman & Noordijk in prep). The entire plots were sampled with a sweeping net (on 20.v.2008, after four years of management treatments), assuring that the catches truly reflect actual presence. All weevils were identified and counted. Again, the plots receiving hay-making twice a year harboured highest species number and in particular abundance (Fig. 2). For these herbivorous insects (often specialised) this is probably caused by the highest plant species richness found in these plots. As weevils have their adult stage mainly in spring, it is expected that the first cut in early summer would not harm these insects; by then, their eggs or larvae are situated in the soil.

The three experiments all indicate that the generally applied mowing regime that aims at maintaining diverse plant communities coincides for a significant part with management aiming at arthropod diversity. Arthropods might further benefit from a rotational management that leaves small patches of vegetation intact during

**Table 1.** Rare arthropod species found in the three studied roadside locations (described in CHAPTER 3); the number between square brackets indicate the number of localities in national databases.

Species [no. localities]	Roadside location
<b>ARANEAE - Spiders</b>	
<i>Aulonia albimana</i> (Walckenaer) [10]	medium-productive
<i>Callilepis nocturna</i> (L.) [4]	medium-productive
<i>Ozyptila sanctuaria</i> (O. P.-Cambridge) [5]	medium-productive
<i>Pardosa proxima</i> (C.L. Koch) [10]	medium-productive
<i>Xysticus acerbus</i> Thorell [6]	medium-productive
<b>FORMICIDAE - Ants</b>	
<i>Lasius distinguendus</i> Emery [9]	low-productive
<i>Lasius sabularum</i> (Bondroit) [20]	medium & high-productive
<b>CARABIDAE - Ground beetles</b>	
<i>Amara montivaga</i> Sturm [20]	medium-productive
<i>Harpalus attenuatus</i> Steph. [21]	low-productive
<i>Parophonus maculicornis</i> (Duft.) [13]	medium-productive
<i>Pterostichus ovoideus</i> (Sturm) [10]	medium-productive
<i>Paratachys bistriatus</i> (Duft.) [9]	high-productive
<b>CURCULIONIDAE - Weevils</b>	
<i>Apion</i> s.l. f. nov. spec. [2]	medium-productive
<i>Diplapion stolidum</i> (Germ.) [25]	medium-productive
<i>Sitona waterhousei</i> Walt. [22]	medium-productive



**Figure 2.** Weevil diversity (above) and abundance (below) in the sweeping net samples from the experimental plots in the medium-productive verge. Means ( $\pm$  s.e.) not sharing the same letter are significantly different (ANOVA with LSD post-hoc tests  $P < 0.05$ ). 0 = no mowing, 1M = mowing once a year without hay removal, 1M+ = mowing once a year with hay removal, 2M = mowing twice a year without hay removal, 2M+ = mowing twice a year with hay removal.



mowing (e.g., Morris *et al.* 2005). Although the primary aim of this thesis was to make the first step towards a general management to promote arthropods, CHAPTER 3 and 4 provide some indications on how to implement a more detailed and fine-tuned management. In CHAPTER 3 overall diversity increments were observed in the low-productive site, possibly caused by the 'rotational' mowing scheme created by the variation in experimental plots. On the other hand, diversity decreased significantly in the high-productive site during the course of the experiment, even in the plots still receiving hay-making twice a year. Most likely, the plots receiving a less intensive management negatively affected the entire verge. These results indicate that in low-productive roadside verges best opportunities exist for a rotational management and that caution should be taken that in high-productive verges vegetation refuges remain small so that they do not affect the important hay-meadow characteristics of the entire verge. Furthermore, in CHAPTER 4 results indicate that in the plots receiving hay-making twice a year, flower abundance is higher than under the other treatments already 2–4 weeks after the mowing event in early-summer. This indicates that mowing verges in two parts with only a small time-shift would already secure feeding resources throughout the season for flower-visiting insects.

### **Arthropods in open sandy verges**

In the Veluwe region, four highways were constructed between 1950 en 1980. Because these roads and accompanying verges were constructed on the original low-productive sandy soils, little management was needed for a considerable time. In these habitats, mosaics of nutrient-poor grasslands, heathlands, grey hair-grass vegetation, trees and shrubs developed. These verges are usually bordered by a strip of slightly richer soil with grassy vegetation right next to the asphalt and by forest on the other side. It has often been suggested that highway verges on the Veluwe could function as ecological corridors (Jansen 1992; Vermeulen 1994a; Smeenge *et al.* 2005; Keizer *et al.* 2006). When uninterrupted stretches of suitable vegetation are present in roadside verges between separate nature reserves, corridor functions seem very plausible (Beier & Noss 1998; Ries *et al.* 2001; Anderson & Jenkins 2006). Unfortunately, since approximately twenty years, open and warm plant communities have largely disappeared through vegetation succession; restoration seems thus urgently needed on a large scale (Fig. 3; Noordijk *et al.* 2005, 2008).

The presence of xero- and thermophilic ground beetle and spider species as discussed in CHAPTER 5 and 6 indicate that entomological values of sandy highway verges can be high. The sites studied in these chapters were selected on the presence of low-productive vegetation patches of relatively high quality. Although these sites are no longer representative for most roadside locations in the Veluwe region, as low-productive vegetation has been disappearing, our results prove that highway verges do not bear intrinsic characteristics that make them unsuitable for a wide array of specialized species of heathland situations (see also Vermeulen 1995). However – as was shown in CHAPTER 5 – arthropod species composition in these remaining grey hair-grass vegetation patches in highway verges does differ from that



**Figure 3.** Habitats for xero- and thermophilic species have disappeared at many locations in roadside verges on the Veluwe, mostly due to the encroaching pine trees almost reaching the asphalt.

in nearby nature reserves: some carabids and spiders occurring in the reserves are lacking. The results indicate that the vegetation in the verges is of lower quality, i.e., the sward is denser, places with bare sand are missing and the vegetation patches are too small (see also Angold 1997).

In CHAPTER 6 we conclude that in sandy roadside verges reproduction takes place for many ‘target’ ground beetle species. The characteristics of the studied verges indicate that potentially all highway verges on the Veluwe can be restored to nutrient-poor and open habitat areas. If such verges would stretch between separate nature reserves they will function as habitat corridors for target species of heathlands. In addition, we showed that recently created linear forest clearings between nature reserves and roadside verges worked efficiently to guide target ground beetles through forest barriers, indicating movement corridor functions.

For sandy regions with scattered heathlands our results imply that roadside verges can help to counteract fragmentation of the area. Since roads are one of the main causes of fragmentation of the landscape (CHAPTER 7), it seems wise to construct and manage the accompanying verges to counteract fragmentation effects (Verkaar & Bekker 1991; Luell *et al.* 2003). Creating an ecological network seems well possible; roadside verges are abundant, span long distances and, after restoration and under right management, can harbour many characteristic species. Probably not all target species will be able to benefit from such corridors (CHAPTER 5). An important condition is that the entire stretch of verge between two nature reserves should be

managed as habitat for xero- and thermophilic arthropod species as interruptions with high vegetation or with closed swards can act as barriers for some habitat specialists (Vermeulen 1994b). Also, simple forest clearings can bridge short distances to facilitate species to move between the separate units of such a network, e.g., a nature reserve and close-by roadside verge.

### **Arthropods in edge biotopes**

Due to the linear outline of roadside habitats, ecological patterns and processes in roadsides differ from habitats with more extensive vegetation patches. Borderlines are long, often with hard and straight edges (Fig. 4). In CHAPTER 7 we showed that verges are bordered by a straight asphalt barrier, hindering ground beetles to move freely. If we extrapolate the results from ground beetles to animals with a less mobile life-style, e.g., snails (Bauer & Bauer 1990), it is clear that roads can really isolate animal populations. Due to the sharp boundary and strong difference between the vegetation and the asphalt, animals tend to walk along this edge. Moreover, we have strong indications that straight forest edges can direct flying ground beetles (CHAPTER 6; unpubl. data). Straight forest edges also proved to be important for the reproductive behaviour of ant species, as here the winged ants meet for mating (CHAPTER 8).

These results imply that, although roads are one of the main causes of fragmentation, if the accompanying verges are rightly designed, constructed and managed using ecological knowledge, fragmentation effects can be mitigated. Our observations on walking and flying ground beetles imply that these animals can be intentionally directed to certain areas by linear elements. This gives an extra indication that roadsides can be designed or managed as ecological corridors. Sharp vegetation edges, like the studied forest edge in CHAPTER 8, can be important parts of the landscape and are abundant in roadside biotopes. The fact that ants meet at such borders to mate, might be an explanation why roadside verges in the Veluwe, often bordered by forests, are so rich in ant species (Noordijk & Boer 2007).



**Figure 4.** Roadside verges have straight and hard edges with the surroundings; the asphalt on one side and different biotopes – a forest edge in this case – on the other side.

### Managing for arthropod diversity

When management is applied according to ecological principles, valuable conditions for arthropods can be sustained or developed in roadside verges. Unfortunately, nature conservation considerations are becoming increasingly less important for road owning authorities: targeted regimes are replaced by general directives and work by contractors is only rarely inspected. Moreover, due to atmospheric deposition many verges are slowly being enriched with nutrients; for some locations even mowing for hay twice per year is insufficient to stabilize plant productivity (van de Haterd *et al.* 2009). Not surprising, standardized plant surveys in roadside verges have shown a decrease in target vegetation types and threatened species (Sýkora *et al.* 2002; Bakker & Bijkerk 2008). Considering the importance of roadside verges for species-rich semi-natural habitats, a re-evaluation and adaptation of the general management following ecological guidelines seem necessary if biodiversity targets are to be maintained and increased.

Our results provide general baseline recommendations for arthropod conservation in roadside verges. In grassland verges, making hay twice per year provides best overall results for arthropods. Sandy verges should contain broad stretches of open and warm plant communities, so they can function as additional habitat and habitat corridors in a landscape context. A major challenge remains to fine-tune this management by incorporating arthropod specific small-scale measures. Targeted experiments on the importance of small additional habitat features and on forms of rotational management that enhance arthropod survival, but maintain the characteristic habitat, should be the subject of future studies.

There is still a lot to be learned about efficient conservation of arthropod habitats. As these species are mobile and have different life-stages, ecological requirements vary in time and place. Home range size and level of specialism of the species are major determinants in this. The habitat of many arthropods comprises different vegetation types or physical structures, indicating that a conservation scheme based on maintaining only one certain vegetation type or high plant diversity might not always be appropriate in conserving broad arthropod communities (Panzer & Schwartz 1998; Dennis *et al.* 2007). Moreover, the countless number of arthropod species, each with specific demands, makes a general beneficial conservation strategy practically impossible. A promising conservation strategy is therefore the protection of landscapes with mosaics of distinct biotopes. Within these mosaics many arthropods depend on the presence of particular features, like dead wood, micro-relief, small water bodies, heaps of decaying plant material, stones, and patches of bare sand, all of which are of no special interest for plant and vertebrate species and the conservation of which tends to be neglected. A broad landscape approach, supplemented by fine-tuned small-scale measures, will most likely produce best results for the conservation of arthropods (Koster 1988; Ellis 1989; Jansen 1992; Kirby 1992; New 1995; van Turnhout *et al.* 2001; Samways 2005, 2007; Haslett 2007).

A biotope mosaic approach as mentioned above seems hard to realise within roadside verges that comprise almost by definition small surfaces, although roadsides can play an important part in such a landscape mosaic approach. But also within roadsides, when interpreting our results as the baseline management recommendations and adding some additional small-scale measures at selected sites, great benefits for arthropod conservation can be realised. Our most important recommendations will be discussed below.

#### *Grassland verges*

Mowing for hay in early summer and autumn proved very beneficial for epigeic arthropods, for a group of herbivorous insects and for the feeding opportunities of flower-visiting insects (CHAPTER 3 & 4). This regime should be applied in the largest parts of grassland verges, which is fortunately already done at most places. On the other hand, if verges are completely mown, many resources needed for arthropod survival are suddenly and completely removed. There are many arthropods that will not be able to thrive under such an intensive form of mowing: obvious examples are web-building spiders, herbivorous insects having their adult or low-mobile nymph stage in early summer, arthropods overwintering in dead plant remains, etc. (e.g., Morris 1979; Bell *et al.* 2001; Di Giulio *et al.* 2001). At selected sites – e.g., in roadside verges on low-productive soils, in wide verges where more space is available or where verges border other semi-natural areas – good opportunities exist to supplement the general management by additional measures. At sites like these, small parts of the verge could be mown less frequently or in a different period; preferably each year a different fraction of the verge could be left unmown, allowing for feeding resources throughout the year (CHAPTER 4) and overwintering sites. When possible, rotational mowing between the verge and adjacent ditches can be implemented as well. The creation of small water bodies, steep edges of bare sand, and piles of mown grass, tree trunks or branches can also be realised easily when larger areas are available.

#### *Heathland verges*

Based on the results in this thesis, key-factors for the increase in presence of xero- and thermophilic species in heathland verges are extension of the total surface of suitable open vegetation, increasing the openness of the sward and cover of bare sand, and the prevention of encroachment by tall herbs, grass, trees or shrubs (CHAPTER 5). This management should be performed over entire roadside verge stretches if they are to function as ecological corridors (CHAPTER 6). To obtain such verges, an initial extensive restoration of the open and sandy situations is necessary. Encroaching trees and shrubs should be removed over the full width and length of the verges and in large parts of the verges the topsoil should be removed exposing bare sand where vegetation succession can start again. Patches that still contain open low-productive vegetation should be left intact. Here, arthropod species can survive the restoration practices and thereafter colonize other parts of the verges.

### Box: Protected species in roadside verges



The Dutch Flora and Fauna Act regulates the protection of several plants and animals living in the wild (see [www.minlnv.nl](http://www.minlnv.nl)). It comprises those parts of the Habitats Directive and Wild Birds Directive dealing with species protection, and the Convention on International Trade in Endangered Species of Wild Fauna and Flora. The Act includes many vertebrates and vascular plants. However, only a limited number of invertebrates is protected, and these consist to a considerable extent of butterflies. Under this Act, activities that may be damaging to protected species are essentially prohibited, i.e., it is generally not allowed to kill or disturb the listed species and to disturb their roosts or habitats.

It is often possible to stray from the prohibitions if doing so does not unfavourably affect the preservation status of the species. For management or constructions in roadside verges a dispensation or exemption from the Act is required if protected species are present (see [www.minlnv.nl](http://www.minlnv.nl)). For the common protected species ('table 1 species' according the Dutch Species protection Act), road managing authorities have a general dispensation (e.g., for depicted Southern wood ant *Formica rufa* L., Bee orchid *Ophrys apifera* Huds. and Tuberous Pea *Lathyrus tuberosus* L.). Other species are more thoroughly protected; when management is necessary a dispensation is given when a strict conduct of behaviour is applied or one has to apply for an exemption, which may be issued after a careful test (e.g., for the depicted Natterjack toad *Bufo calamita* Laurenti and Sand lizard *Lacerta agilis* (L.)). Detailed inventories of roadside habitats are therefore necessary before management works take place.



Connections between low-productive vegetation in nature reserves and the adjacent verges should be created, if necessary by creating linear forest clearings. This way, verges can act as extensions of existing nutrient-poor habitat and at the same time function as ecological corridors between nature reserves. Subsequent periodical management should aim at maintaining the open and sparsely vegetated area as large as possible, using relatively small-scale measures phased over both time and location. Each year, encroaching trees, shrubs, herbs and grasses should be removed in a different part of the total area of highway verge in such a way that all sites receive this treatment once every eight to ten years. The management cycle can be restarted after this period. Again, patches of bare sand should be created occasionally, where vegetation succession can restart. The more productive grassy vegetation close to the asphalt should be mown more often – preferably every autumn – and the cuttings need to be removed. Additional small-scale measures to create additional arthropod habitats can be undertaken at selected sites where ample surface is present. Examples of such measures are: creating small water bodies, steep edges of bare sand, and piles of tree trunks or branches.

Following these approaches, a species-rich and highly characteristic arthropod fauna, including protected and threatened species, may be preserved and stimulated. When planning restoration measures, locations should first be inventoried on protected species that may possibly require tailored management (BOX; CHAPTER 2; Zuiderwijk 1989; Keizer *et al.* 2006; Noordijk & Boer 2007). Regular monitoring of the effects of management on biodiversity or target species should be common practices, not only for plants (see Bakker & Bijkerk 2008 for existing monitoring scheme), but for arthropods as well (see Noordijk *et al.* 2008).

### Concluding remarks

Compared to nature reserves, roadside verges are distinctive biotopes that are strongly influenced by edge effects and anthropogenic disturbances. Direct effects of traffic and indirect effects of its pollution will, in addition to fragmentation and the small size of the verges, have negative influences on arthropods. However, in this thesis a number of positive aspects of these omnipresent and unavoidable linear elements have also been identified. Roadside verges harbour arthropod communities of conservation interest and can be used to create ecological networks, their straight edges can guide dispersing insects and are favoured as mating sites, and the right mowing scheme preserves favourable circumstances for valuable arthropod communities. With management based on ecological principles, roadside verges are well suited to conserve or develop valuable conditions for arthropods.

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## References

- Anderson AB & Jenkins CN **2006**. *Applying Nature's design, corridors as a strategy for biodiversity conservation*. Columbia University Press, New York, USA.
- Angold PG **1997**. The impact of a road upon adjacent heathland vegetation: effects on plant species composition. *Journal of Applied Ecology* 34: 409-417.
- Bakker R & Bijkerk W **2008**. *Meetnet bermflora rijkswegen, analyserapport 2004-2007*. Altenburg & Wymenga Ecologisch Onderzoek, Rapport 1074.
- Baur A & Baur B **1990**. Are roads barriers to dispersal in the land snail *Arianta arbustorum*? *Canadian Journal of Zoology* 68: 613-617.
- Beier P & Noss RF **1998**. Do habitat corridors provide connectivity? *Conservation Biology* 12: 1241-1252.
- Bell JR, Wheeler CP & Cullen WR **2001**. The implications of grassland and heathland management for the conservation of spider communities: A review. *Journal of Zoology* 255: 377-387.
- Bobbink R, Hornung M & Roelofs JGM **1998**. Essay review: The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural vegetation. *Journal of Ecology* 86: 717-738.
- Dennis RLH, Shreeve TG & Sheppard DA **2007**. Species conservation and landscape management: a habitat perspective. In: *Insect conservation biology* (Stewart AJA, New TR & Lewis OT eds.): 92-126. CABI, Wallingford, UK.
- Di Giulio M, Edwards PJ & Meister E **2001**. Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *Journal of Applied Ecology* 38: 310-319.
- Ellis WN (ed.) **1989**. *Insektenfauna en natuurbeheer*. Wetenschappelijke Mededeling KNNV nr. 192. KNNV Uitgeverij, Utrecht, the Netherlands.
- Haslett JR **2007**. *European strategy for the conservation of invertebrates*. Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention). Nature and environment, no. 145. Council of Europe Publishing, Strasbourg, France.
- Hastings, A. **1980**. Disturbance, coexistence, history, and competition for space. *Theoretical Population Biology* 18: 363-373.
- Jansen GW (ed.) **1992**. *Insektenvriendelijk beheer van wegbermen*. Rijkswaterstaat, Dienst Weg- en Waterbouwkunde, Delft, the Netherlands.
- Keizer PJ, van den Hengel LC & Groshart C **2006**. *Leidraad beheer groenvoorzieningen*. Rijkswaterstaat, Dienst Weg- en Waterbouwkunde Delft, the Netherlands.
- Kirby P **1992**. *Habitat management for invertebrates: a practical handbook*. Sandy, Bedfordshire, United Kingdom.
- Koster A **1988**. *Insektenbeheer*. Wetenschappelijke Mededeling KNNV nr. 187. KNNV Uitgeverij, Utrecht, the Netherlands.
- Lambeets K **2009**. *The effects of flooding disturbance on the distribution and behaviour of riparian arthropods along a lowland gravel river*. PhD thesis, Ghent University, Belgium.
- Luell N, Bekker GJ, Cuperus R, Dufek J, Fry G, Hicks C, Hlaváč V, Keller V, Rosell C, Sangwine T, Tørsløv N & le Maire Wandall **2003**. *Habitat fragmentation due to transportation infrastructure. Wildlife and Traffic: A European handbook for identifying conflicts and designing solutions*. COST 341. KNNV Publishers, Utrecht, the Netherlands.
- MNP – Milieu en Natuurplanbureau **2007**. *Natuurbalans 2007*. MNP-publicatienummer 500402005, Bilthoven, the Netherlands.



- Morris MG **1979**. Responses of grassland invertebrates to management by cutting 2. Heteroptera. *Journal of Applied Ecology* 16: 417-432.
- Morris MG, Clarke RT & Rispin WE **2005**. The success of a rotational grazing system in conserving the diversity of chalk grassland Auchenorrhyncha. *Journal of Insect Conservation* 9: 363-374.
- New T **1995**. *An introduction to invertebrate conservation biology*. Oxford University Press, United Kingdom.
- Noordijk J **2008**. De fenologie van *Arctosa perita* (Araneae, Lycosidae). *Nieuwsbrief Spined* 25: 30-33.
- Noordijk J & Boer P **2007**. Mieren in Veluwebermen: soortenrijkdom en aanbevelingen voor beheer (Hymenoptera: Formicidae). *Nederlandse Faunistische Mededelingen* 27: 23-50.
- Noordijk J, Vermeulen R & Heijerman Th **2005**. Loopkevers in veranderende Veluwebermen. *De Levende Natuur* 106: 255-258.
- Noordijk J, Sýkora KV & Schaffers AP **2008**. Conservation value of sandy roadside verges for arthropods – implications for management. *Proceedings of the Netherlands Entomological Society Meeting* 19: 75-93.
- Novacek MJ & Cleland EE **2001**. The current biodiversity extinction event: scenarios for mitigating and recovery. *Proceedings of the National Academy of Sciences of the United States of America* 98: 5466-5470.
- Panzer R & Schwartz MW **1998**. Effectiveness of a vegetation-based approach to insect conservation. *Conservation Biology* 12: 693-702.
- Ries L, Debinski DM & Wieland ML **2001**. Conservation value of roadside prairie restoration to butterfly communities. *Conservation Biology* 15: 401-411.
- Samways MJ **2005**. *Insect diversity conservation*. Cambridge University Press, Cambridge, United Kingdom.
- Samways MJ **2007**. Insect conservation: a synthetic management approach. *Annual Review of Entomology* 52: 465-487.
- Schaffers AP **2000**. *Ecology of roadside plant communities*. PhD-thesis, Wageningen University, the Netherlands.
- Schaffers AP, Vesseur MC & Sýkora KV **1998**. Effects of delayed hay removal on the nutrient balance of roadside plant communities. *Journal of Applied Ecology* 35: 349-364.
- Schaminée JHJ, Stortelder AHF & Weeda EJ **1996**. *De vegetatie van Nederland. Deel 3. Plantengemeenschappen van graslanden, zomen en droge heiden*. Opulus Press, Uppsala, Sweden.
- Smeenge H, Vlottes H & Meus D **2007**. *Natuurplan Rijksweg A50, tracé Valburg-Grijsoord*. Dienst Landelijk Gebied – Regio Oost, Team Natuur, Zwolle, the Netherlands.
- Stumpel AHP **2004**. *Natuurbeheer voor reptielen en amfibieën*. Alterra Scientific Contribution 13 / PhD thesis Wageningen University, the Netherlands.
- Sýkora KV, de Nijs LJ & Pelsma TAHM **1993**. *Plantengemeenschappen van Nederlandse wegbermen*. Stichting Uitgeverij KNNV, Utrecht, the Netherlands.
- Sýkora KV, Kalwij JM & Keizer P-J **2002**. A phytosociological and floristic evaluation of 15-year ecological management of roadside verges in the Netherlands. *Preslia* 74: 421-436.
- van de Haterd RJW, van den Hengel B & Keizer PJ **2009**. Lange termijn effecten van maaibeheer in wegbermen. *De Levende Natuur* 110: 88-94.
- van Turnhout C, Stuijzand S & Esselink H **2001**. Is het huidige herstelbeheer toereikend voor de heidefauna? *De Levende Natuur* 102: 183-188.

- Verkaar HJ & Bekker GJ **1991**. The significance of migration to the ecological quality of civil engineering works and their surroundings. In: *Nature engineering and civil engineering works* (van Bohemen HD, Buizer DAG & Little A eds.): 44-61. Pudoc, Wageningen, the Netherlands.
- Vermeulen HJW **1994a**. Corridor function of a road verge for dispersal of stenotopic heathland ground beetles (Carabidae). *Biological Conservation* 69: 339-349.
- Vermeulen R **1994b**. The effects of different vegetation structures on the dispersal of carabid beetles from poor sandy heaths and grasslands. In: *Carabid beetles: ecology and evolution* (Desender K, Dufrêne M, Loureau M, Luff M & Maelfait J-P eds.): 387-392. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Vermeulen HJW **1995**. *Road-side verges: habitat and corridor for carabid beetles of poor sandy and open areas*. PhD thesis, Landbouwwuniversiteit Wageningen.
- Wilson JB **1994**. The 'intermediate disturbance hypothesis' of species coexistence is based on patch dynamics. *New Zealand Journal of Ecology* 18: 176-181.
- Wynhoff I, van Swaay C & Boeren J **2005**. Overleven in de wegberm: het Donker Pimpernelblauwtje in Limburg. *Natuurhistorisch Maandblad* 94: 145-149.
- Zuiderwijk A **1989**. *Reptielen in wegbermen; een analyse van 106 locaties*. Instituut voor Taxonomisch Zoölogie, UvA, Amsterdam / RWS-DWW, Delft, the Netherlands.





## SUMMARY

Intensification of agriculture and urbanisation have caused large-scale destruction and fragmentation of natural and semi-natural areas in the Netherlands with great loss of biodiversity. As a consequence, the conservation of the biodiversity of the remaining small landscape elements has become increasingly urgent. We carried out ecological studies on the insects and spiders in (mainly) roadside verges. Our inventories showed that these linear landscape elements house a wide variety of arthropod species. For several groups, more than half of the indigenous species were found, among them several rare and threatened species, as well as many specialised species. Moreover, considering that we only covered a small fraction of the vast network of roadside verges, the number of species found is remarkably high. However, up till now, the conservation of arthropods in roadside verges has hardly ever been considered; our results show this neglect is clearly undeserved.

We studied the effect of mowing management of grassland verges on the presence of arthropods. We also compared the occurrence of arthropods in sandy roadside verges with similar biotopes in the surrounding landscape. In addition, we examined the behaviour of insects in edge biotopes. The aim of all these studies was to obtain a better understanding of the arthropods in roadside verges, in order to enable us to recommend appropriate measures for the conservation of the arthropod assemblages found there.

Roadside verges have become an important location of species-rich grasslands, which are now otherwise rare in the Netherlands. To conserve their biodiversity, such grasslands need to be mown in order to prevent plant succession. More so, because succession is accelerated by atmospheric nitrogen deposition. We carried out two studies on the effect of a mowing management on grassy verges. Over a five-year period, we studied ground beetles, weevils, ants and epigeic spiders with pitfall traps in experimental plots with five different mowing treatments. These treatments represented neglect and common forms of management: no mowing; and mowing once a year in autumn with and without removal of cuttings; and mowing twice a year with and without removal of cuttings. The plots were located in three verges representing a plant productivity gradient, comprising a low-productive, medium-productive and high-productive grassland verge. At the low-productive site, management only resulted in a higher arthropod abundance in plots that were mown twice a year and the cuttings removed. At the medium-productive and high-productive site, this type of management not only resulted in highest abundance of arthropods, but also in the highest species diversity. Mowing twice a year without removal of cuttings and mowing only once but with removal of cuttings resulted in intermediate values for arthropod abundance and diversity. Mowing once a year without hay removal as well as a management of no mowing resulted both in low arthropod abundance and low species diversity.

In the medium-productive verge, we also studied the effect of the different management types on the visitation of flowers by insects. During an entire growing

season, in the third year of the experimental period, we counted the number of species of flowering plants, the number of inflorescences, as well as recording the abundance of insects, and the number of visits to flowers. In the plots that had been mown twice a year with removal of the cuttings, the values for all measured variables were the highest and this persisted throughout the growing season. The effect of the early summer cut proved to be very important for insect feeding opportunities due to the re-flowering of plants later in the summer. Abundance of flowers correlated highly with both plant species-richness and the number of insect visits.

Therefore, in medium-productive to high-productive grassland verges, mowing twice a year with the removal of cuttings promotes epigeic arthropods as well as the feeding opportunities for flower-visiting insects. Fortunately, this type of mowing is already applied at many locations. However, under this management regime, most arthropod resources will be absent just after mowing for a short time. For this reason, a rotational management leaving another small part of the verge unmown and intact can thus be expected to further enhance arthropod survival. However, such vegetation refuges should not become too large, nor be at exactly the same place for several years, as ruderalisation will decrease its suitability for grassland arthropods. In low-productive grassland locations, a more extensive management, like described below, may be applied as yearly mowing seems not necessary to retain high species diversity.

In the sandy Veluwe region, roadside verges used to be covered by heathland or by dry, sandy, open vegetation. Such sites are of major importance for xerophilic and thermophilic arthropods. Unfortunately, vegetation succession has caused these biotopes to largely disappear. Intervention is necessary to preserve both the rare and the characteristic species assemblages. In this context, we compared the occurrence of ground beetles and spiders in pitfall traps in grey hair-grass (*Corynephorus canescens*) vegetation on six motorway verges and in adjacent nature reserves. The total number of species in the verges was similar to those in nearby nature reserves, but ground beetles tended to be more abundant in the reserves. Many stenotopic species (specialist species with a narrow ecological amplitude) were present in the verges, confirming the substantial conservation value of this sandy, open habitat. However, compared to the nature reserves, there were fewer species of stenotopic ground beetles, and stenotopic spiders were less abundant. Most likely, this difference is due to a difference in 'habitat quality'. Species preferring bare sand and individuals of large ground beetle species were scarcer in the roadside verges. This suggests that the sward of the roadside verges was too dense and that patches of suitable vegetation were too small to sustain healthy populations of some of the stenotopic species. Habitat analyses supported this idea: compared to the nature reserves, the verges had proportionally less bare sand, more herb and tree cover and the patches of grey hair-grass vegetation were smaller.

In addition, we investigated whether roadside verges and forest clearings could be used to reduce the negative effect of landscape fragmentation for ground

beetles. We compared the catches from three open sandy roadside verges and three newly-created linear forest clearings with the catches from heathland nature reserves and nearby forests. We had made these clearings in order to connect the roadside verges with the nature reserves. Using pitfall and window traps, we looked at the species composition and abundance of ground beetles, and could show that both before and after the creation of the forest clearings, the species composition in the roadside verges differed from that in the nature reserves. However, the occurrence of teneral individuals and flightless species indicated that the verges do provide a valuable habitat where reproduction takes place, implying that they can act as habitat corridors. Forest seems to act as a barrier for both walking and flying individuals of most target species of ground beetles. In contrast, in the forest clearings, the pitfall traps sampled similar numbers of target species to those found in the nature reserves and on roadside verges. Teneral, though, were only found for two species. In the forest clearings, flying ground beetles, caught in the window traps, were very abundant; far more individuals were caught here than in the nature reserves and on roadside verges. This indicates that these linear clearings are used particularly by dispersing ground beetles, and as such they can act as movement corridors.

In order to make conditions more suitable for xerophilic and thermophilic species on roadside verges, we suggest removing encroaching trees and shrubs from the verges and recreating pioneer conditions thereby expanding the nutrient-poor zone. Subsequently, management should be carried out regularly, e.g., the selective removal of encroaching vegetation every 8-10 years, aiming to maintain the road verges as a sustainable warm and open habitat. When such a management is implemented over large distances, it is likely that roadside verges will act as habitat corridors for target species. In addition, simple forest clearings can bridge short distances to facilitate the movement of species between the separate sites with warm and open vegetation, for example, from nature reserves to nearby roadside verges. Both roadside verges and forest clearings can be used to create an ecological network in the highly fragmented heathland landscape.

Roadside habitats can often be classified as edge biotopes and as such they are subject to many so-called edge effects, namely, specific ecological processes and patterns due to the influence of other biotopes in the vicinity. We studied the behaviour of several insect species in edge situations. First, we studied the effect of the abrupt change from vegetation to asphalt on the direction of movement of two ground beetle species, *Poecilus versicolor* and *Agonum sexpunctatum*. Using mark-recapture experiments, we noted the number of times the beetles crossed the road and deviations in walking direction caused by its presence. This revealed two effects of the road on walking behaviour: (i). It acts as a barrier: *P. versicolor* showed a clear resistance to cross the road and we did not detect any road crossings by *A. sexpunctatum*. (ii) The presence of a road induces strong movements parallel to it in the adjacent verge and in the ditch. This applied for both species, but particularly for *A. sexpunctatum*. The animals tend to stray along the sharp boundary between the

asphalt and the vegetation. A related result was obtained in the (previously described) linear forest clearings where we found a high abundance of flying ground beetles; probably they unintentionally, or maybe intentionally, follow the forest edge when dispersing. Both studies point to the possibility that linear biotopes in roadside verges form structures that direct animal dispersion. Again, this indicates that roadsides can be constructed to act as potential ecological corridors. In addition, we used window traps to study the behaviour of flying ants at a sharply defined forest edge in relation to the location of their nests. Although none of the six species studied had the highest nest density at the forest edge, three of them showed aggregations of males here, indicating that the forest edge is the main mating site. This last finding could be due to a more suitable micro-climate, but it is more likely that the edge acts as a conspicuous landmark used by ants for meeting mates. Our results proved that the edge situations characteristic of roadside verges may also have other positive effects on arthropods than guiding dispersal, such as providing a location for mating.

All these studies have clearly shown that roadside verges can provide valuable arthropod habitats. All kinds of anthropogenic disturbances and edge effects may have a negative effect on the arthropods living on verges. However, the road network is an inherent and inevitable part of the intensely populated Netherlands, and therefore we wanted to emphasise the positive aspects of these linear elements with semi-natural vegetation. It appeared that arthropod communities of high conservation value occur in roadside verges, that the road network can form the basis for an ecological network, that straight biotope edges in roadside verges can guide dispersing insects and are favoured as mating sites, and that a regular applied mowing scheme provides valuable conditions for arthropods.



## SAMENVATTING

Zowel verstedelijking als de intensivering van de landbouw hebben geleid tot grootschalige vernietiging en versnippering van de (half-)natuurlijke gebieden in Nederland. Allerlei kleine landschapselementen worden hierdoor steeds belangrijker voor het behoud van onze biodiversiteit. Dit proefschrift behandelt de bescherming van geleedpotigen, insecten en spinnen, in (voornamelijk) wegbermen. Met onze inventarisaties konden we aantonen dat er erg veel geleedpotigen in wegbermen voorkomen. Voor enkele groepen werd zelfs meer dan de helft van het totaal aantal inheemse soorten gevonden, waaronder veel karakteristieke en enkele zeldzame en beschermde soorten. Aangezien we slechts een klein deel van het totale wegbermareaal hebben bemonsterd zijn de aangetroffen soortsaantallen verrassend hoog. Tot nu toe bestond er weinig aandacht voor de bescherming van geleedpotigen in wegbermen; gezien de hoge diversiteit is dat onterecht.

Wij onderzochten het effect van maaien in grazige bermen op de geleedpotige fauna. Daarnaast vergeleken we de soorten die voorkomen in zandige bermen met andere leefgebieden in de omgeving. Bovendien bestudeerden we insectengedrag in 'randbiotopen'. Ons onderzoek is vaak toepassingsgericht, waarbij het formuleren van praktische beheeraanbevelingen voor het behoud en bevordering van de ongewerveldendiversiteit een belangrijk doel is.

Soortenrijke graslanden zijn zeldzaam geworden in Nederland en wegbermen vormen belangrijke wijkplaatsen voor dit biotoop. Om de soortenrijkdom in graslanden in stand te houden moeten ze gemaaid worden, gebeurt dit niet dan verruigt de vegetatie; een proces dat door atmosferische stikstofdepositie aanzienlijk wordt versneld. Wij deden twee experimenten in grazige bermen. In een periode van vijf jaar werd met bodemvallen het effect van vijf maairegimes in proefvlakken onderzocht op de aanwezigheid van loopkevers, snuitkevers, mieren en grondbewondende spinnen. Het ging hierbij om gangbare vormen van bermbeheer en verwaarlozing: niet maaien, en één keer per jaar maaien in het najaar met en zonder afvoer van het maaisel, en twee keer per jaar maaien, in de vroege zomer en het najaar, eveneens zowel met als zonder ruimen van het maaisel. De proefvlakken lagen op drie locaties: in een laag-, middel- en hoog-productieve grazige berm. In de laag-productieve berm was het effect van beheer beperkt; wel bleek de abundantie van geleedpotigen het grootst in de proefvlakken waar twee keer per jaar gemaaid werd met afvoer. Op de middel- en hoog-productieve locaties leverde dit type beheer niet alleen duidelijk de hoogste abundantie, maar ook de hoogste diversiteit aan geleedpotigen op. Twee keer per jaar maaien zonder afvoer en slechts één keer maaien met afvoer resulteerde in tussenliggende waarden. Eén keer maaien zonder maaiselafvoer en met name het beheer van niks doen gaf een lage diversiteit en abundantie van geleedpotigen.

Een tweede experiment werd uitgevoerd in de middel-productieve berm; hier bestudeerden we het effect van de verschillende beheerstypen (gedurende het derde jaar waarin ze werden toegepast) op bloembezoekende insecten. Tijdens het

groeiseizoen werden zowel aantal bloeiende plantensoort en bloemen geteld, als de abundantie aan insecten en de daadwerkelijke bloembezoeken. Twee keer per jaar maaien met afvoer van maaisel had de hoogste waarden voor alle deze variabelen en dit was constant over het groeiseizoen. De maaibeurt in de vroege zomer zorgde voor een herbloei van planten later in het seizoen en dit bleek was belangrijk voor de foerageermogelijkheden voor insecten. We vonden duidelijke correlaties tussen de hoeveelheid bloemen met zowel het aantal plantensoorten en het aantal bloembezoeken door insecten.

Een beheer waarbij de berm twee keer per jaar gemaaid wordt en het maaisel wordt afgevoerd is in middel- tot hoog-productieve grazige bermen dus aan te bevelen om groundbewonende geleedpotigen en foerageermogelijkheden voor bloembezoekende insecten te bevorderen. Gelukkig wordt deze vorm van maaien op veel plekken al toegepast. Hierbij zal in de berm echter gedurende een bepaalde korte tijd na het maaien een groot gebrek zijn aan allerlei bestaansbronnen voor geleedpotigen. Een manier van gefaseerd maaien, waarbij kleine plekken van de vegetatie mogen blijven staan, zal de overlevingskansen van deze dieren daarom waarschijnlijk bevorderen. Dergelijke ongemaaide plekken mogen echter niet te groot zijn of jaren achter elkaar op dezelfde plek liggen, omdat de aantrekkelijkheid voor geleedpotigen van graslanden er flink zal afnemen. Op laag-productieve locaties is een extensievere vorm van beheer, die meer lijkt op de manier zoals hieronder besproken wordt, mogelijk.

Op de zandgronden van de Veluwe werden wegbermen veelal gekenmerkt door de aanwezigheid van heide, zandige droge schrale graslanden en zandige pioniervegetaties. Voor droogte- en warmteminnende geleedpotigen zijn dit belangrijke vegetaties. In de bermen op de Veluwe verdwijnen deze leefgebieden echter steeds meer door vegetatiesuccessie. Voor het behoud van de karakteristieke en zeldzame soorten zijn gerichte beheeringrepen dan ook noodzakelijk. Met behulp van bodemvallen in buntgrasvegetatie vergeleken wij de loopkevers en spinnen van zes snelwegbermen met die in nabijgelegen natuurgebieden. De totale soortenrijkdom in de bermen was gelijk aan die in de natuurgebieden, maar er werden minder loopkeverindividuen aangetroffen. In de bermen werden ook veel stenotop soorten (specialistische soorten met een smalle ecologische amplitude) gevonden, wat de grote natuurbeschermingswaarde van de zandige Veluwebermen bevestigt. In vergelijking met de natuurgebieden, waren er in de bermen echter minder stenotop loopkeversoorten en stenotop spinnenindividuen. Waarschijnlijk zijn de verschillen tussen de bermen en natuurgebieden te wijten aan verschillen in 'habitatkwaliteit'. Vooral soorten met een voorkeur voor kale plekken zand en de grotere loopkevers waren in de bermen minder algemeen. Dit suggereert dat voor sommige stenotop soorten de vegetatie te dicht is en de geschikte leefgebieden te klein zijn geworden. Dit is in overeenstemming met een habitatanalyse: vergeleken met de natuurreservaten hadden de bermen minder kaal zand, een hogere kruid- en boombedekking en de plekken met buntgrasvegetatie waren kleiner.

Vervolgens is onderzocht of in het heidelandschap de versnippering van loopkeverpopulaties tegengegaan kan worden door het gebruik van corridors. We vergeleken de aanwezigheid van loopkevers in drie bermen met warme schrale vegetatie en in drie nieuw gemaakte lijnvormige kapvlaktes, met de loopkeverfauna in grote heideterreinen en bossen. De lijnvormige kapvlakten werden daarbij tijdens het experiment aangelegd tussen de onderzochte bermen en natuurgebieden. De soortensamenstelling in de wegbermen bleek zowel voor en na aanleg van de kapvlaktes af te wijken van die in de natuurreservaten. De aanwezigheid van niet-vliegende en nog niet uitgeharde loopkevers (individueen die net uit de pop komen) bewees dat de bermen waardevol reproductiegebieden zijn. Bossen bleken barrières te vormen voor zowel lopende als vliegende individuen van vrijwel alle doelsoorten. In de lijnvormige kapvlaktes werden lopende doelsoorten in dezelfde aantallen aangetroffen als in de natuurterreinen en bermen, maar slechts van twee soorten werden nog niet uitgeharde kevers aangetroffen. Vliegende kevers waren echter zeer talrijk in de kapvlaktes; hiervan werden veel meer individuen aangetroffen dan in de natuurgebieden en bermen. Dit betekent dat de lineaire kapvlaktes in hoge mate gebruikt worden door dispergerende loopkevers.

Om de voor heide karakteristieke geleedpotigen te bevorderen in wegbermen moeten eerst bosjes en boomopslag verwijderd worden en weer pionieromstandigheden gecreëerd worden. Vervolgens moet een regelmatig beheer waarbij ongeveer elke 8-10 jaar selectief vegetatieopslag wordt verwijderd, de warme schrale omstandigheden in stand houden. Als zo'n beheer over grote afstanden wordt toegepast, kunnen bermen echt als habitatcorridors dienen. Daarbij kunnen lineaire kapvlaktes dienen als bewegingscorridors om korte afstanden te overbruggen, bijvoorbeeld tussen natuurterreinen en dichtbijzijnde bermen.

Leefgebieden in bermen kunnen vaak gezien worden als randbiotopen, waardoor er allerlei randeffecten optreden; specifieke ecologische processen en patronen onder invloed van andere biotopen in de nabijheid. Wij onderzochten het gedrag van enkele insecten in 'randsituaties'. Ten eerste keken we naar het effect van de plotselinge overgang tussen vegetatie en het asfalt van een weg op de looprichting van de loopkevers *Poecilus versicolor* en *Agonum sexpunctatum*. Door een merktugvangexperiment bepaalden we het loopgedrag. Er konden twee effecten worden aangetoond: (i) De weg vormt een barrière voor beide soorten. Van *Poecilus versicolor* werden weinig en van *A. sexpunctatum* géén overstekende individuen waargenomen. (ii) Er bestaat een duidelijke neiging om langs de weg en vooral in de daar liggende greppel te lopen. Dit patroon was met namen voor *A. sexpunctatum* duidelijk. Door het scherpe contrast tussen de vegetatie en het asfalt blijkt de looprichting van de dieren dus beïnvloed te worden; ze volgen de weg in parallelle richting. Een vergelijkbaar resultaat lieten vliegende loopkevers in de (hierboven beschreven) kapvlaktes zien. In deze lineaire elementen werden zeer veel vliegende individuen aangetroffen, waarschijnlijk omdat loopkevers tijdens dispersie al dan niet doelgericht bosranden volgen. Beide studies tonen aan dat allerlei lineaire biotopen in wegbermen richting kunnen geven aan de dispersie van insecten. Dit

vormt weer een duidelijke aanwijzing dat wegbermen als ecologische corridors kunnen worden ingericht.

Vervolgens werd ook het gedrag van gevleugelde geslachtsdieren van mieren in relatie tot een scherpe bosrand en hun nestlocaties onderzocht met behulp van raamvallen. Hoewel geen van de zes onderzochte mierensoorten de hoogste nestdichtheid had aan de bosrand, kwamen hier wel aggregaties voor van de mannetjes van drie soorten. Dit duidt erop dat juist hier de paring plaatsvindt. Dit kan komen doordat het micro-klimaat aan de bosrand aantrekkelijk is, maar waarschijnlijk vormen bosranden opvallende randobjecten die door mieren bewust gekozen worden om een partner te ontmoeten. Deze resultaten bewijzen dat de vaak in bermen aanwezige randsituaties ook andere substantiële effecten op insectenpopulaties kunnen hebben namelijk het voorzien in geschikte paringslocaties.

Uit ons onderzoek blijkt dat wegbermen waardevolle leefgebieden voor geleedpotigen kunnen zijn. Er treden hier echter wel veel menselijke verstoringen en randeffecten op die een negatieve invloed kunnen hebben op de aanwezige geleedpotigen. Maar omdat in onze moderne samenleving wegen overal aanwezig en niet te vermijden zijn, hebben we in dit proefschrift juist de positieve aspecten van deze begroeide stroken benadrukt. Uit ons onderzoek blijkt dat in wegbermen geleedpotigengemeenschappen van groot natuurbeschermingsbelang kunnen voorkomen, dat bermen gebruikt kunnen worden om ecologische netwerken aan te leggen, dat lineaire biotoopranden in bermen dispersie van insecten kunnen geleiden en ook in trek zijn als paringslocatie, en dat een veelvuldig toegepast maaibeheer voor een waardevolle vegetatie voor geleedpotigen zorgt.





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Foto: Elly Morriën

## CURRICULUM VITAE

Jinze (Albertus Johan) Noordijk zag het levenslicht op 27 Oktober 1977 in Amsterdam, waarna hij al snel naar de karaktervolle Zaanstreek verhuisde. Een VWO-opleiding aan het Pascal College in Zaandam werd afgerond in 1996. In datzelfde jaar begon hij met de studie Biologie aan de Vrije Universiteit in Amsterdam. Hier heeft hij een scriptie voltooid naar de effecten van UV-b op de chemische samenstelling van stuifmeelkorrels en mogelijkheden om hiermee de ozonlaagdikte in het verleden te reconstrueren. Daarna werd de vakgroep Dieroecologie gekozen om drie afstudeervakken te volbrengen. Hij begon met de bestudering van geleedpotigen op vierhonderd plataanstammen. Vervolgens ging hij naar Zuid-Frankrijk waar hij een flora- en fauna-inventarisatie deed van en een beheerplan schreef voor het beekdal van de Liort. Een derde stage werd uitgevoerd op het oosten van Java, Indonesië, waar uitvoerig de (afwezigheid van een) macro-evertebratengemeenschap in een rivier van vulkanische origine werd bestudeerd. In 2003 begon hij met het promotie-onderzoek aan de Wageningen Universiteit naar het voorkomen van en beheer voor insecten en spinnen in wegbermen waar dit boek het resultaat van is. In 2008 ontving hij de Uyttenboogaart-Eliasen Stimuleringsprijs voor zijn onderzoek in de Veluwebermen. Na het werk in Wageningen was hij zeven maanden post-doc onderzoeker naar de ecologische effecten van en sociale motivaties voor beheersovereenkomsten in het agrarisch gebied bij het Centrum voor Milieukunde Leiden, van de universiteit aldaar. Daarnaast heeft hij voor verschillende ecologische adviesbureaus inventariseer- en rapporteerwerk gedaan. Op het moment is Jinze hoofdredacteur van het tijdschrift Entomologische Berichten, ecooloog bij bureau Viridis in Culemborg en medewerker bij het European Invertebrate Survey - Nederland in Leiden.

## PUBLICATIONS

### *Scientific and international articles*

- Rozema J, Noordijk J, Broekman RA, van Beem A, Meijkamp NV, de Bakker NV, van de Staaij WM, Stroetenga M, Bohncke SJP, Konert M, Kars S, Peat H, Smith RIL & Convey P **2001**. (Poly)phenolic compounds in pollen and spores of plants as indicators of solar UV-B: a new proxy for the reconstruction of past solar UV-B? *Plant Ecology* 154: 9-26.
- Noordijk J **2004**. Les Rhopalocères de la vallée du Liort (Aveyron, Midi-Pyrénées) et leur lien vis-à-vis de la qualité de l'environnement (Lepidoptera: Papilionoidea et Hesperioidea). *Alexanor* 23: 119-126.
- Boer P & Noordijk J **2005**. *Myrmica schenckioides* nov. sp., a new socially parasitic ant species (Hymenoptera, Formicidae). *Entomologische Berichten* 65: 120-123.
- Löhr AJ, Noordijk J, Lrianto K, van Gestel CAM & van Straalen NM **2006**. Leaf decomposition in an extremely acidic river of volcanic origin in Indonesia. *Hydrobiologia* 560: 51-61.
- Noordijk J, Prins D, de Jonge M & Vermeulen R **2006**. Impact of a road on the movements of two ground beetle species (Coleoptera: Carabidae). *Entomologica Fennica* 17 (*Proceedings of the XII European Carabidologists' Meeting*): 276-283.
- Noordijk J, Schaffers AP & Sýkora KV **2008**. Diversity of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) in roadside verges with grey hair-grass vegetation. *European Journal of Entomology* 105: 257-265.
- Noordijk J, Morssinkhof R, Boer P, Schaffers AP, Heijerman Th & Sýkora KV **2008**. How ants find each other: spatial and temporal patterns in nuptial flights. *Insectes Sociaux* 55: 266-273.
- Noordijk J, Sýkora KV & Schaffers AP **2008**. The conservation value of sandy highway verges for arthropods – implications for management. *Proceedings of the Netherlands Entomological Society Meeting* 19: 75-93.
- Noordijk J & de With N **2008**. Les Odonates de la vallée du Liort - avec quelques notes sur la gestion conservatoire (département de l'Aveyron). *Martinia* 24: 143-150.
- Vermeulen R, Turin H, den Boer PJ, Noordijk J, van der Laaken K **2008**. The European Carabidologist Meeting after 40 years back in the Netherlands. *Baltic Journal of Coleopterology* 8: 169-172.
- Noordijk J, Raemakers IP, Schaffers AP & Sýkora KV **2009**. Arthropod richness in roadside verges in the Netherlands. *Terrestrial Arthropod Reviews* 2: 63-76.
- Noordijk J, van Dijk J, Lokhorst AM, Musters CJM, Staats H & de Snoo GR **2009**. Boeren over weidevogelbescherming. *Landschap* 26: 83-90.
- Noordijk J, Delille K, Schaffers AP & Sýkora KV **2009**. Optimizing grassland management for flower-visiting insects in roadside verges. *Biological Conservation* 142: 2097-2103.
- Noordijk J, Schaffers AP, Heijerman Th & Sýkora KV **submitted**. Habitat and movement corridors to improve landscape connectivity for heathland carabids.
- Noordijk J, van Dijk J, Musters CJM & de Snoo GR **submitted**. Invertebrates in field margins; taxonomic group diversity and functional group abundance in relation to age.
- Noordijk J, Musters CJM, van Dijk J & de Snoo GR **submitted**. Vegetation development in sown field margins and on adjacent ditch banks.
- Noordijk J, Schaffers AP, Heijerman Th, Boer P, Gleichman M & Sýkora KV **submitted**. Effects of vegetation management by mowing on epigeic arthropods.

## Other publications

- Noordijk J **2000**. Broedvogelinventarisatie Kalverpolder 2000. *De Kieft* 24(4): 18-21.
- Berg MP, Noordijk J, Bongers M, Schakel A **2001**. De springstaart *Isotomurus maculatus* nieuw voor de fauna van Nederland (Parainsecta: Collembola: Entomobryomorpha). *Nederlandse Faunistische Mededelingen* 15: 79-85.
- Noordijk J & Berg MP **2001**. De corticole fauna van platanen I: Arachniden (Arachnida: Aranea, Pseudoscorpiones, Acari). *Nederlandse Faunistische Mededelingen* 15: 13-31.
- Noordijk J & Berg MP **2002**. De corticole fauna van platanen II: Insecten (Insecta: Collembola, Psocoptera, Coleoptera; Carabidae). *Nederlandse Faunistische Mededelingen* 17: 41-56.
- Boer P & Noordijk J **2004**. De Ruige gaststeekmier (*Myrmica hirsuta*) nieuw voor Nederland (Hymenoptera: Formicidae). *Nederlandse Faunistische Mededelingen* 20: 25-32.
- Noordijk J & Thijsen W **2004**. Weidevogeldichtheden in de Wijde Wormer aan de hand van twee telmethoden. *De Kieft* 28(3): 17-19.
- Noordijk J, Vermeulen R & Heijerman Th **2005**. Loopkevers in veranderende Veluwebermen. *De Levende Natuur* 106: 255-258.
- Noordijk J **2005**. Spinnen van bermen op de Veluwe (Arachnida: Araneae). *Nieuwsbrief Spined* 20: 29-34.
- Noordijk J, Raemakers IP, Schaffers AP, de Nijs LJ, Gleichman M & Sýkora KV **2006**. Kansen voor geleedpotigen in bermen, acht jaar onderzoek langs de weg. *Entomologische Berichten* 66: 166-173.
- Noordijk J **2006**. Broedvogels in de Kalverpolder van 2002 tot en met 2005. *De Kieft* 30(1): 16-18.
- Noordijk J & Wijnhoven H **2006**. De hooiwagen *Dicranopalpus ramosus* in Noord-Holland. *Tussen Duin en Dijk* 5(3): 10-11.
- Noordijk J **2006**. *Callilepus nocturna* (L.), *Xysticus acerbus* Thorrell en *Pardosa proxima* (C.L. Koch) gevonden bij Heerlen (Araneae: Gnaphosidae, Thomisidae, Lycosidae). *Nieuwsbrief Spined* 22: 19-22.
- Noordijk J & Ballintijn K **2006**. Stadse juffers en andere libellen van Purmerend en Zaanstad. *Tussen Duin en Dijk* 5(4): 18-22.
- Prins D, de Jonge M, Noordijk J & Vermeulen R **2006**. Effecten van de Hoogeveense weg op loopkevers. *De Levende Natuur* 107: 218-222.
- Verdonschot RCM, Noordijk J, Sýkora KV & Schaffers AP **2007**. Het voorkomen van loopkevers (Coleoptera, Carabidae) langs een vegetatiegradiënt in de Millingerwaard. *Entomologische Berichten* 67: 82-91.
- Noordijk J, Heijerman Th & Turin H **2007**. Recente waarnemingen van *Harpalus griseus*: is er een trend (Coleoptera: Carabidae)? *Nederlandse Faunistische Mededelingen* 26: 43-50.
- Noordijk J, Wijnhoven H & Cuppen J **2007**. The distribution of the invasive harvestman *Dicranopalpus ramosus* in the Netherlands (Arachnida: Opiliones). *Nederlandse Faunistische Mededelingen* 26: 65-68.
- Noordijk J & Boer P **2007**. Mieren in Veluwebermen: soortenrijkdom en aanbevelingen voor beheer. *Nederlandse Faunistische Mededelingen* 27: 23-50.
- Kohler F, van Klink R, Noordijk J & Kleijn D **2007**. De invloed van natuurgebieden op zweefvliegen en bijen in agrarische gebieden (Diptera: Syrphidae & Hymenoptera: Apidae s.l.). *Entomologische Berichten* 67: 187-192.
- Noordijk J & van Helsdingen PJ **2007**. Spinnen in akkers - biologie en plaagbestrijding (Arachnida: Araneae). *Entomologische Berichten* 67: 249-252.

- Noordijk J, Bruin J & van Rijn P **2007**. Agrobiodiversity - conservation and functionality. *Entomologische Berichten* 67: 278-283.
- Noordijk J **2007**. De gestreepte muisspin *Haplodrassus dalmatensis* is niet zeldzaam op de Veluwe (Araneae: Gnaphosidae). *Nieuwsbrief Spined* 23: 2-3.
- Noordijk J, Sýkora KV & Schaffers AP **2008**. Snelwegbermen als leefgebied voor plant en dier. *Land + Water* 6/7: 26-27.
- Noordijk J, Boer P & Morssinkhof R **2008**. Miereninventarisatie universiteitsterrein 'De Born' in Wageningen 2006. *Forum Formicidarum* 7(1): 6-10.
- Noordijk J, Boer P, Wijnhoven H, Smits J & Raemakers IP **2008**. De staafmier *Ponera coarctata* in Nederland. *Entomologische Berichten* 68: 78-82.
- Vermeulen R, Turin H, den Boer PJ & Noordijk J **2008**. Loopkevercongres jubileert in Nederland. *Entomologische Berichten* 68: 227-230
- Noordijk J & Boer P **2008**. Mieren in lineaire elementen. *Forum Formicidarum* 7(2): 2-5.
- Noordijk J, Boer P, Gleichman M & Morssinkhof R **2008**. Mieren van het Hulshorsterzand: resultaten van een inventarisatie met potvallen en raamvallen. *Forum Formicidarum* 7(3): 9-16.
- Noordijk J **2008**. De fenologie van *Arctosa perita* (Araneae: Lycosidae). *Nieuwsbrief Spined* 25: 30-33.
- Noordijk J & Berg MP **2009**. Een vondst van de mierenpissebed *Platyarthrus hoffmannseggii* bij de oprolmier *Myrmecina graminicola*. *Forum Formicidarum* 8(3): 2-5.
- Noordijk J & Wijnhoven H **2009**. Hooiwagenwaarnemingen uit Zeeuwse akkerranden. *Entomologische Berichten* 69: 78-82.
- Noordijk J, Verdonschot RCM & Sýkora KV **2009**. Wolfspinnen in een vegetatiegradiënt in de Millingerwaard. *De Levende Natuur* 110: 199-205.
- Noordijk J, van 't Veer R & Jonker K **2009**. De avifauna van de Enge Wormer 1. de broedvogels. *De Kieft* 33(2): 26-27.
- Noordijk J, Klut A & Belier J **2009**. De avifauna van de Enge Wormer 2. de wintergasten. *De Kieft* 33(3): 20-21.
- Hengeveld R, Noordijk J, Opsteeg T, Turin H & Vermeulen HJW (eds.) **2009**. *Book of abstracts - XIV European carabidologists meeting*. Willem Bijerinck Biologisch Station, Loon.
- Noordijk J, Berg MP & Ooms C **2009**. Loopkeverinventarisatie van een veenmosrietland in de Kalverpolder. *Tussen Duin en Dijk* 8(4): in druk.
- Noordijk J, Verdonschot RCM & van Helsdingen PJ **2009**. Spinnen en hooiwagens van verschillende leefgebieden in de Millingerwaard (Arachnida: Araneae & Opiliones). *Nieuwsbrief Spined* 27: in druk.
- Noordijk J **2009**. De Hooiwagenfauna van de Gelderse Vallei (provincie Utrecht). *Opilionieuws* 4: in druk.
- Noordijk J, Musters CJM & de Snoo GR **ingediend**. Neemt de biodiversiteit toe als ingezaaide akkerranden ouder worden? *De Levende Natuur*.
- Noordijk J & de Jong Th **ingediend**. Water- en terreinbeheer voor de Noordse woelmuis op de Makkumerwaard. *Zoogdier*.

## Reports

- Noordijk J, Foulquier R, Beaudouin P & Rol H **2005**. *Ecosystème d'un ruisseau, inventaire de flore et faune de la vallée du Liort*. Rapport Les Amis du Moulin de Liort, La Salvétat Peyrales.

- Boer P & Noordijk J **2005**. *Het effect van chopperen van kraaiheiden op de bodemfauna op Texel*. Onderzoeksverslag Staatbosbeheer, Regio west, Beheerseenheid Texel. Rapportnummer 2005-2.
- Jungerius PD, Ketner-Oostra R, van den Acker H, Aptroot A, Boer P, Keizer P-J, Koopmans G, Noordijk J, Raaijmakers H, Riksen M, Struijk R, Verkerk L **2006**. *Onderzoek voor de toepassing van effectgerichte maatregelen in het stuifzandlandschap van het Hulshorster Zand*. Stichting Geomorfologie & Landschap, Ede.
- Werkgroep Kalverpolder & Enge Wormer **2007**. *Beheerplan Kalverpolder*. Vogelbeschermingswacht "Zaanstreek", Wormer, Zaandam & Wageningen.
- Noordijk J, Ballintijn K, de With N, Hellmann F, Hillebrand H, Morriën E **2008**. *Aanvullende inventarisatie van het Liortdal, 2-9 augustus 2007*. Rapport Les Amis du Moulin de Liort, La Salvat Peyralès.
- Noordijk J & Vermeulen R **2008**. *Loopkevers in Drenthe. Bestudering en interpretatie van beschikbare loopkevergegevens voor de actualisering van het achtergronddocument "Natuur in Drenthe"*. Rapport Stichting Willem Bijerinck Biologisch Station, Loon.
- Noordijk J & Vermeulen R **2008**. *Zandloopkevers in Noord-Brabant - het voorkomen op basis van literatuurgegevens en veldinventarisaties in 2008*. Rapport Stichting Willem Bijerinck Biologisch Station, Loon.
- Bouwman JH, de Vries HH, Reemer M, Kalkman VJ, Noordijk J, Vermeulen R **2008**. *Bedreigde insecten van Noord-Brabantse stuifzanden*. Rapport VS2008.034. De Vlinderstichting, Wageningen.
- Noordijk J & de Jong Th **2009**. *De Noordse woelmuis in buitendijkse gebieden in het IJsselmeer*. Rapportnummer 2009-21. Bureau Viridis, Culemborg.
- de Jong Th & Noordijk J **2009**. *Ecologisch kwetsbare wateren in het beheersgebied van het Hoogheemraadschap De Stichtse Rijnlanden*. Rapportnummer 2009-22. Bureau Viridis, Culemborg.







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## CERTIFICATE

The Netherlands Research School for the  
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(SENSE), declares that

*Jinze Noordijk*

Born on: *27 October 1977* at: *Amsterdam, The Netherlands*

has successfully fulfilled all requirements of the  
Educational Programme of SENSE.

Place: *Wageningen* Date: *3 November 2009*

the Chairman of the  
SENSE board

Prof. dr. R. Leemans

the SENSE Director  
of Education

Dr. A. van Dommelen



The SENSE Research School declares that Mr. Jinze Noordijk has successfully fulfilled all requirements of the Educational PhD Programme of SENSE with a work load of 47 ECTS, including the following activities:

SENSE PhD courses:

- Environmental research in context
- Research context activity: Research communication on 'Possibilities to expand arthropod habitat using roadside verges'
- Restoration ecology of low productive ecosystems

Other courses:

- Natuurbeheer in het agrarisch landschap
- Numerieke methoden voor de verwerking van ecologische gegevens
- Techniques for writing & presenting scientific papers
- Information literacy
- Multivar

Research and Management Skills:

- Training in identifying carabid beetles
- Editor of the professional journal *Entomologische Berichten*
- Member of the Scientific Advisory Committee for the 14th European Carabidologists Meeting
- Special feature editor of a theme issue of *Entomologische Berichten*: 'Agrobiodiversiteit - nut en natuur'
- Writing several popular-scientific papers and papers for engineers

Presentations:

- Poster Presentation: Effects of isolation on carabids and spiders in heathy roadside verges, XII European Carabidologist Meeting, 21 September 2005, University of Murcia, Spain
- Oral Presentation: Conservation value of roadside verges in a highly fragmented landscape, European Section of the Society for Conservation Biology, 23 August 2006, Eger, Hungary
- Poster Presentation: The Conservation value of sandy highway verges for arthropods - implications for management, Meeting of the Section Experimental and Applied Entomology of the Netherlands Entomological Society, 17 December 2007, Ede, The Netherlands
- Oral Presentation: Bescherming van insecten en spinnen in snelwegbermen op de Veluwe, 67th Autumn Meeting of the Netherlands Entomological Society, 8 November 2008, Leiden, The Netherlands

Mr. J. Feenstra  
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