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Diversity of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) in roadside verges with grey hair-grass vegetation

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Abstract. 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 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 (re-)create pioneer conditions. Subsequent management should aim at further improving the road verges as extensions of nutrient-poor habitat.

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 outside the urban areas, around 1.8 km/km^2, 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; Noordijk et al., 2006). 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; Raemakers et al., 2001; Spellenberg, 2002; Saarinen et al., 2005). 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-Corynephoretum*), 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 epigaeic ground beetles and spiders were sampled in highway verges and nearby nature reserves, using

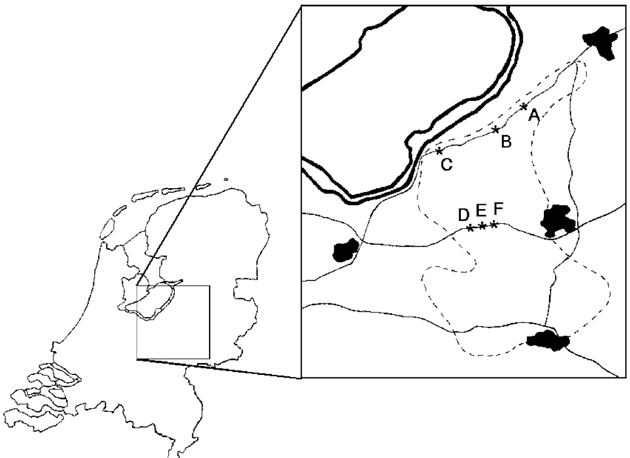

Fig. 1. Sampling locations in the Veluwe. The inset shows highways and towns. The dashed line delineates the sandy soils of the Veluwe. The letters indicate the six locations where both roadside verges and the adjacent nature reserves were sampled. The locations are named after the nature reserves, A: "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.

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 high diversity of stenotopic species, with a potential species pools.

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 pers. observ.). 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 an area of 16 m^2 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 (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^2 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 (Maguran, 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 vs. 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 (4999 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.

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

TABLE 1. The stenotopic ground beetles and non-webbuilding spiders of heath/drift sand areas, and the number of individuals caught in pitfall traps at the six locations. For the non-stenotopic species see Appendices 1 and 2.

Location	Hulshorster zand		Caitwicker zand		De Haere		Beekhuizer zand		N. Milligsche zand		Bremmert	
Species	reserve	verge	reserve	verge	reserve	verge	reserve	verge	reserve	verge	reserve	verge
CARABIDAE												
Amara consularis (Duftschmid)	.	.	.	.	.	.	4	.	1	3	.	.
Amara equestris (Duftschmid)	.	8	5	3	1	.	3	3	.	.	5	2
Broscus cephalotus (L.)	1	.	.	.	.	.	1	.	.	.	.	.
Calathus ambiguus (Paykull)	3	.	206	.	.	.	31	.	3	3	192	.
Cicindela campestris L.	2	2	1	.	10	.	.	.	.	1	1	.
Cicindela hybrida L.	2	.	.	.	1	.	3	.	.	.	15	.
Cicindela sylvatica L.	.	.	.	.	4	.	.	.	.	.	.	.
Cymindis macularis Mannerheim	5	.	.	.	.	.	.	.	.	.	.	.
Harpalus anxius (Duftschmid)	11	16	20	50	6	5	4	.	6	42	14	12
Harpalus latus (L.)	.	1	.	.	.	.	.	2	1	.	.	.
Harpalus neglectus Serville	3	.	.	.	.	1	32	.	3	6	2	.
Harpalus rufipalpis Sturm	.	27	.	10	2	6	4	37	7	96	2	9
Harpalus servus (Duftschmid)	2	.	5	.	1	.	13	.	.	.	1	.
Harpalus smaragdinus (Duftschmid)	1	6	1	1	1	.	3	.	3	39	5	2
Harpalus solitaris Dejean	.	2	.	.	.	.	16	.	.	.	.	4
Masoreus wetterhallii (Gyllenhal)	.	9	.	3	.	.	.	1	5	1	.	1
Notiophilus germinyi Fauvel	77	.	.	30	25	59	6	16	1	4	4	24
Olisthopus rotundatus (Paykull)	.	3	.	.	2	4	.	.	1	6	1	2
Poecilus lepidus (Leske)	31	41	18	9	12	4	4	16	64	43	34	37
ARANEAE												
Aelurillus v-insignitus (Simon)	1	.	.	.	10	1	.	.	1	.	3	2
Agelena labyrinthica (Clerck)	.	.	1	.	.	.	.	.	.	.	.	.
Agroeca proxima (O.P.-Cambridge)	2	.	.	.	1	.	.	.	.	.	.	.
Alopecosa barbipes (Sundevall)	6	.	40	6	16	37	21	21	2	3	12	21
Alopecosa fabrilis (Clerck)	17	22	18	.	15	23	3	.	1	3	14	19
Arctosa perita (Latreille)	6	.	.	.	.	.	12	.	.	.	1	.
Atypus affinis Eichwald	1	1	1	24	4	.	2	1	.	.	.	.
Cheiracanthium erraticum (Walckenaer)	.	.	.	2	.	.	.	1	.	.	.	.
Cheiracanthium virescens (Sundevall)	.	2	.	.	.	.	.	.	.	2	.	2
Drassodes cupreus (Blackwall)	.	.	.	.	1	4	.	4	.	.	1	1
Haplodrassus dalmatensis (L. Koch)	14	.	.	.	.	.	.	.	.	.	.	.
Haplodrassus signifer (C.L. Koch)	2	3	9	8	6	6	2	4	6	15	9	16
Micaria dives (Lucas)	1	.	.	.	4	1	.	.	.	.	.	.
Micaria fulgens (Walckenaer)	.	.	.	.	.	.	2	.	.	.	.	1
Micaria silesiaca L. Koch	.	.	.	.	1	.	.	.	1	1	9	21
Ozyptilla scabricula (Westring)	.	.	.	.	.	2	.	.	.	.	.	.
Pardosa monticola (Clerck)	26	27	62	9	3	3	17	8	389	202	112	29
Pellenes tripunctatus (Walckenaer)	2	1	.	2	.	2	.	.	5	1	1	1
Phaeocedus braccatus (L. Koch)	.	3	.	3	.	.	.	2	.	.	.	1
Phlegra fasciata (Hahn)	1	1	.	.	.	1	.	4	1	.	.	.
Sitticus distinguendus (Simon)	.	.	.	.	1	.	1	.	.	.	.	.
Sitticus saltator (O.P.-Cambridge)	8	.	.	.	.	.	.	.	.	.	.	.
Steatoda albomaculata (De Geer)	.	.	1	.	.	.	3	.	.	.	3	1
Talavera aequipes (O.P.-Cambridge)	.	.	.	.	1	.	.	.	.	.	.	.
Talavera petrensis (C. L. Koch)	8	.	5	.	2	.	2	.	.	1	4	2
Tegenaria agrestis (Walckenaer)	6	1	4	2	1	.	9	2	.	1	2	4
Thanatus formicinus (Clerck)	.	.	.	2	.	.	.	.	.	.	.	.
Xysticus ninnii Thorell	.	.	.	.	3	.	.	.	.	.	1	.
Zelotes electus (C.L. Koch)	6	4	.	.	5	17	5	9	4	1	.	5
Zelotes longipes (L. Koch)	57	16	61	3	30	38	28	40	45	45	66	106

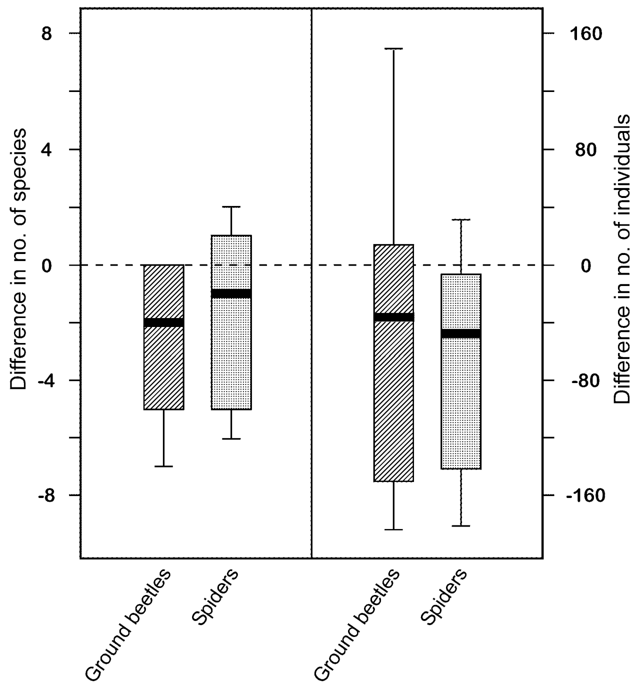

Fig. 2. Box-and-Whisker plot of pair-wise differences in species number (left) and abundance (right) of stenotopic ground beetles (crosshatched bars) and spiders (stippled bars) in six roadside verges, with the adjacent nature reserves as a reference (horizontal dotted line).

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.

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.

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

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, $P = 0.01$).

Only seven of the stenotopic ground beetle species recorded were poor dispersers, i.e. have never been observed in flight: *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.

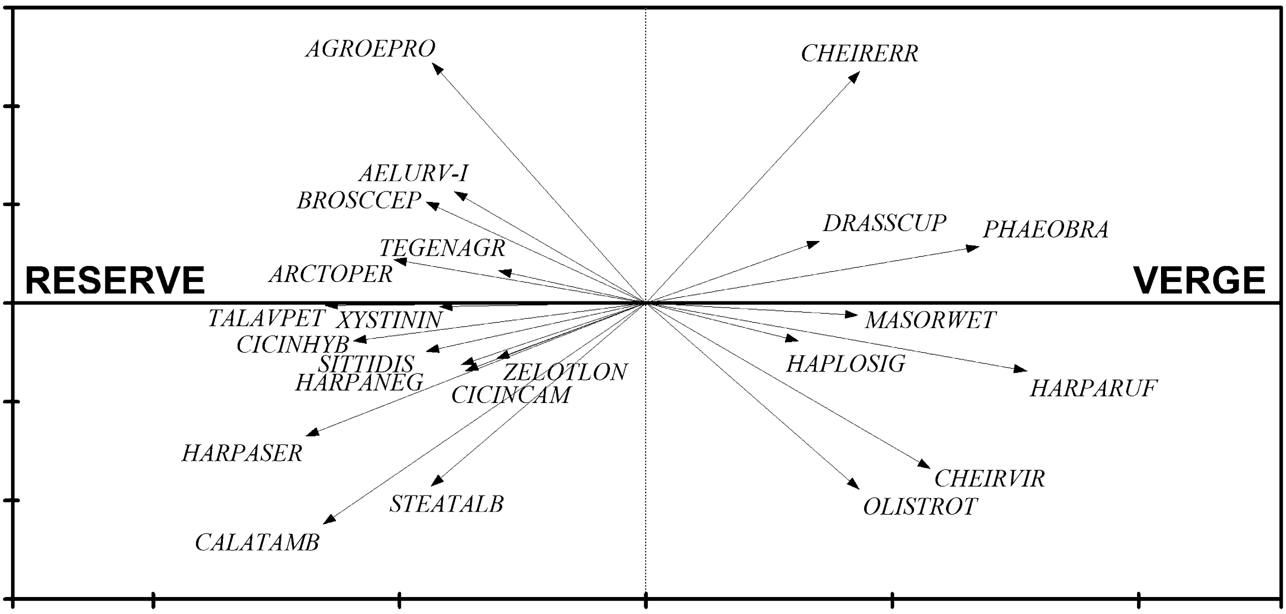

Fig. 3. RDA ordination of the stenotopic species, with nature reserve / roadside verge as the explanatory variable and location as a covariable. Only species with a clear preference for nature reserves or roadside verges are shown (> 9% fit on the first axis and occurring in more than one location). AELURV-I: *Aelurrilus 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*, ZELOTLON: *Zelotes longipes*.

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, there 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 very abundant when large patches of homogeneous and moss-rich grey hair-grass vegetation are present (e.g. Van Essen, 1993).

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 in the verges: examples are *Amara equestris*, *Harpalus anxius*, *H. smaragdinus*, *H. solitaris*, *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*

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 effec ts of location).

	Transformation	Nature reserves	Roadside verges		
Sand cover (%)	Ln(x+1)	20.33	4.21	df = 1, F = 28.54	$P < 0.001$
Litter cover (%)	Ln(x+1)	9.04	9.67	df = 1, F = 3.56	$P = 0.07$
Moss cover (%)	–Ln[100–(x–1)]	70.38	71.29	df = 1, F = 0.04	$P = 0.85$
Herb cover (%)	Ln	14.69	24.42	df = 1, F = 10.49	$P < 0.01$
Distance to nearest tree (m)	Ln	11.25	4.15	df = 1, F = 31.65	$P < 0.001$

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 *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 (Tscharntke 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., 2000; 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 nutrient-poor habitats for stenotopic arthropods, and thus function as ecological corridors connecting heathland and/or drift sand areas (for more details see Noordijk et al., 2008).

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 P.G. 1997: The impact of a road upon adjacent heathland vegetation: effects on plant species composition. *J. Appl. Ecol.* **34**: 409–417.

Barkman J.J., Doing H. & Segal S. 1964: Kritische Bemerkungen und Vorschläge zur quantitativen Vegetationsanalyse. *Acta Bot. Neerl.* **13**: 394–419 [in German, English abstr.].

Bauchhenss E. 1990: Central European xerotherm habitats and their epigaeic spider fauna – an autecological approach. *Abh. Naturw. Ver. Hamburg* **31/32**: 153–162 [in German, English abstr.].

Biedermann R. 2003: Body size and area-incidence relationships: is there a general pattern. *Global Ecol. Biogeogr.* **12**: 381–387.

Boeken M., Desender K., Drost B., Van Gijzen T., Koese B., Muilwijk J., Turin H. & Vermeulen R. 2002: *The Ground Beetles of the Netherlands and Flanders (Coleoptera: Carabidae)*. Stichting Jeugdbondsuitgeverij, Utrecht, 212 pp. [in Dutch].

Bonte D., Baert L. & Maelfait J.-P. 2002: Spider assemblage structure and stability in a heterogeneous coastal dune system (Belgium). *J. Arachnol.* **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. *J. Biogeogr.* **30**: 901–911.

De Bonte A.J., Hazebroek E., Van den Hengel L.C., Keijzer P.-J., Sýkora K.V. & Schaminée J.H.J. 1997: *Botanical Quality of Roadside Verges in the Agricultural Landscape*. Rijkswaterstaat, Dienst Weg en Waterbouw, Delft. Report no. W-DWW-97-092, 160 pp. [in Dutch, English abstr.].

Delgado García J.D., Arévalo J.R. & Fernández-Palacios J.M. 2007: Road effects on the abundance of the lizard Gallotia gallotia (Sauria: Lacertidae) in two Canary Islands forests. *Biodivers. Conserv.* **16**: 2949–2963.

Den Boer P.J. 1990: The survival value of dispersal in terrestrial arthropods. *Biol. Conserv.* **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). *Biol. Conserv.* **48**: 277–294.

De Vries H.H., Den Boer P.J. & Van Dijk T.S. 1996: Ground beetle species in heathland fragments in relation to survival, dispersal, and habitat preference. *Oecologia* **107**: 332–342.

Eversham B.C. & Telfer M.G. 1994: Conservation value of roadside verges for stenotopic heathland Carabidae: corridors or refugia? *Biodivers. Conserv.* **3**: 538–545.

Forman R.T.T. & Alexander L.E. 1998: Roads and their major ecological effects. *Annu. Rev. Ecol. Syst.* **29**: 207–231.

Gelbard J.L. & Harrison S. 2003: Roadless habitats as refuges for native grasslands: interactions with soil, aspect, and grazing. *Ecol. Appl.* **13**: 404–415.

Getz L.L., Cole F.R. & Gates D.L. 1978: Interstate roadsides as dispersal routes for Microtus pennsylvanicus. *J. Mamm.* **59**: 208–212.

Halaj J., Ross D.W. & Moldenk A.R. 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, 460 pp. [in German / English].

Hopkins P.J. & Webb N.R. 1984: The composition of the beetle and spider faunas on fragmented heathlands. *J. Appl. Ecol.* **21**: 935–946.

Keals N. & Majer J.D. 1991: The conservation status of ant communities along the Wubin-Perenjori Corridor. In Saunders D.A. & Hobbs R.J. (eds): *Nature Conservation 2: The Role of Corridors*. Surrey Beatty, Sydney, pp. 387–393.

Ketner-Oostra R., Van der Peijl M.J. & Sýkora K.V. 2006: Restoration of lichen diversity in grass-dominated vegetation of coastal dunes after wildfire. *J. Veg. Sci* **17**: 147–156.

Mader H.J., Schell C. & Kornacker P. 1990: Linear barriers to arthropod movements in the landscape. *Biol. Conserv.* **54**: 209–222.

Maguran A.E. 2004: *Measuring Biological Diversity*. Blackwell, Malden, 256 pp.

Major R.E., Smith D., Cassis G., Gray M. & Colgan D.J. 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. *Aust. J. Zool.* **47**: 611–624.

Noordijk J. & Boer P. 2007: Ants in roadside verges on the Veluwe: species richness and recommendations for management (Hymenoptera: Formicidae). *Nederl. Faunist. Mededel.* **27**: 23–50 [in Dutch, English abstr.].

Noordijk J., Vermeulen R. & Heijerman T. 2005: Ground beetles in changing roadside verges. *De Levende Natuur* **106**: 255–258 [in Dutch, English abstr.].

Noordijk J., Prins D., De Jonge M. & Vermeulen R. 2006: Impact of a road on carabid movements. *Entomol. Fenn.* **17**: 276–283.

Noordijk J., Sýkora K.V. & Schaffers A.P. 2008. The conservation value of sandy highway verges for arthropods – implications for management. *Proc. Neth. Entomol. Soc. Meet.* **19**: 75–93.

Norris K.C. 1999: Quantifying change through time in spider assemblages: sampling methods, indices and sources of error. *J. Insect Conserv.* **3**: 309–325.

Platnick N.I. 2006: *World Spider Catalog, Version 7.0*. available at: http://research.amnh.org/entomology/spiders/catalog/INTRO1.html. Visited on 23.xi.2006.

Raemakers I.P., Schaffers A.P., Sýkora K.V. & Heijerman T. 2001: The importance of plant communities in road verges as a habitat for insects. *Proc. Exp. Appl. Entomol. (Amsterdam)* **12**: 101–106.

Riksen M., Ketner-Oostra R., Van Turnhout C., Nijssen M., Goossens D., Jungerius P.D. & 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. *Landsc. Ecol.* **21**: 431–447.

Roberts M.J. 1998: *Spider Identification Guide* (translation and adaptation for the Netherlands by Noordam A.P.). Tirion Publishers, Baarn, 397 pp. [in Dutch].

Rypstra A.L., Carter P.E., Balfour R.A & Mrshall S.D. 1999: Architectural features of agricultural habitats and their impact on the spider inhabitants. *J. Arachnol.* **27**: 371–377.

Saarinen K., Valtonen A., Jantunen J. & Saarnio S. 2005: Butterflies and diurnal moths along road verges: does road type affect diversity and abundances? *Biol. Conserv.* **123**: 403–412.

Schaffers A.P. 2000: *Ecology of Roadside Plant Communities*. Ph.D. Thesis, Wageningen University, 303 pp.

Schaffers A.P. & Sýkora K.V. 2002: Synecology of species-rich plant communities on roadside verges in the Netherlands. *Phytocoenologia* **32**: 29–83.

Small E.C., Sadler J.P. & Telfer M.G. 2003: Carabid assemblages on urban derelict sites in Birmingham, UK. *J. Insect Conserv.* **6**: 233–246.

Southwood R. & Henderson P.A. 2000: *Ecological Methods*. Blackwell Science, Oxford, 590 pp.

Spellenberg I.F. 2002: *Ecological Effects of Roads. Land Reconstruction and Management. Vol. 2*. Science Publisher, Enfield, 251 pp.

Ter Braak C.J.F & 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, 351 pp.

Tikka P.M., Högmander H. & Koski P.S. 2001: Road and railway verges serve as dispersal corridors for grassland plants. *Landsc. Ecol.* **16**: 659–666.

TSCHARNTKE T., STEFFAN-DEWENTER I., KREUSS A. & THIES C. 2002: Characteristics of insect populations on habitat fragments: A mini review. *Ecol. Res.* **17**: 229–239.

TURIN H. 2000: *Dutch Fauna 3. The Ground Beetles from the Netherlands: Distribution and Ecology. (Coleoptera: Carabidae)*. Nationaal Natuurhistorisch Museum Naturalis. KNNV Uitgeverij, European Invertebrate Survey-Nederland, Leiden, 666 pp. [in Dutch, English abstr.].

TURIN H., ALDERS K., DEN BOER P.J., 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. *Tijd. Entomol.* **134**: 279–303.

VAN ESSEN S. 1993: *Ground Beetle Inventory Dwingelderveld 1991*. Staatsbosbeheer, Biologisch Station Wijster, Natuurmonumenten, 97 pp. [in Dutch].

VERMEULEN H.J.W. 1993: The composition of the carabid fauna on poor sandy road-side verges in relation with comparable open areas. *Biodivers. Conserv.* **2**: 331–350.

VERMEULEN H.J.W. & OPDAM P.F.M. 1995: Effectiveness of roadside verges as dispersal corridors for small ground-dwelling animals: a simulation study. *Landsc. Urban Plan.* **31**: 233–248.

WEEDA E.J., DOING H. & SCHAMINÉE J.H.J. 1996. *Koelerio-Corynephoreta*. In Schaminée J.H.J., Stortelder A.H.F. & Weeda E.J. (eds): *The Vegetation of the Netherlands 3*. Opulus Press, Leiden, pp. 61–144 [in Dutch].

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

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

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

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