Road-side verges:
habitat and corridor for carabid beetles of poor sandy and open areas.

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Proefschrift

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Stellingen

behorende bij het proefschrift

"Road-side verges: habitat and corridor for carabid beetles of poor sandy and open areas."

1. De verbreiding van bodembewonende evertebraten verloopt in een groot aaneengesloten gebied aanzienlijk sneller dan in verbreidingscorridoren.(dit proefschrift)

2. Voor random bewegende bodembewonende evertebraten geldt: "hoe breder de ecologische verbindingszones des te langer de afstanden waarover ze effectief zijn." (dit proefschrift)

3. Wil men in het NBP wegbermen de functie van verbindingszone laten vervullen, dan moeten de meeste wegbermen sterk verbreed worden, obstakels opgeruimd worden en aansluitingen met natuurgebieden gemaakt worden. (dit proefschrift)

4. Aansluiting van heideterreinen op brede schrale wegbermen betekent een vergroting van de totale oppervlakte beschikbaar schraal habitat. (dit proefschrift)

5. Meer samenwerking tussen de verschillende natuur- en terreinbeheerders kan leiden tot betere resultaten in het natuurbehoud (dit proefschrift)

6. Simulatiemodellen kunnen behulpzaam zijn bij het verkrijgen van inzicht in ecologische processen, ze kunnen echter nooit precies voorspellen hoe organismen zullen reageren. (dit proefschrift)

7. De negatieve invloeden van snelwegen op de natuur is voornamelijk bekend van de vele publicaties over enkele hogere vertebraten soorten; er zijn echter ook vertebraten soorten die juist profiteren van deze situatie.

8. Als toppredator van bodemsystemen lijken loopkevers goede indicatoren van de kwaliteit van de bodemfauna en dus de bodemprocessen. (Szyszko, pers. comm.)

9. De beperking van aantallen in dierpopulaties wordt niet in de eerste plaats bepaald door de hoeveelheid beschikbare energie maar door hoeveelheid geschikte stikstofverbindingen. (White, T.C.R., 1993. The Inadequate Environment. Nitrogen and abundance of animals. Springer-Verlag Berlin)

10. De overlevingskans van een populatie wordt meer bepaald door het patroon van de aantalsfluctuaties dan door het aantalsniveau. (den Boer, P.J., 1985. Fluctuations of density and survival of carabid beetles. Oecologia 67, Springer-Verlag, Berl., 322-330)

11. Het heeft zin om onderscheid te maken tussen metapopulaties en veeldelige (multipartite) populaties, daar enkele van de subpopulaties van een metapopulatie veeldelige populaties kunnen zijn.

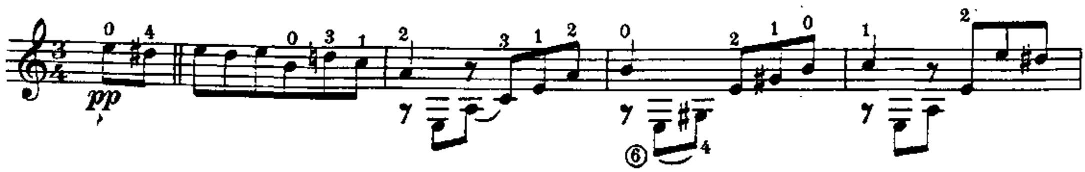
12. Verbindingen tussen tuinen van biologen en natuurgebieden kunnen in vele gevallen leiden tot verhoging van de biodiversiteit in de laatst genoemde gebieden.

13. Als wegbermen van snelwegen beschouwd kunnen worden als natuurreservaten, dan is dit het meest gepasseerde natuurschoon van Nederland.

14. Er zijn geen problemen, alleen maar situaties.

H.J.W. Vermeulen
Road-side verges: habitat and corridor for carabid beetles of poor sandy and open areas.
promotie op 12 juni 1995 in de aula van de Landbouwuniversiteit Wageningen.

Aan mijn moeder, Saskia en



Much of our own highly managed landscape is still interlaced with a wonderful network of hedgerows and roadside verges. These long winding strips of habitat by the road and lane and field margins are the last really big remaining nature reserves we have in Britain, except for the wild moors and lakes of our northern mountains and seas around us. (Elton, 1958)

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ABSTRACT

This research deals with the question whether or not heathy strips, like poor sandy and open road-side verges, can direct dispersal movements of stenotopic carabid beetles from one heathland fragment towards another, and under what conditions.

First by placing pitfall traps at ten heathy road-side verges in the north-eastern part of the Netherlands it was established that beetles of poor sandy and open habitats do not avoid road verges. A relation was found for the species occurring at the verge with both distance to a heathland fragment and width of the heathy strip at the verge. In a heathy verge connected to a fragment of heathland more heathland species and in higher numbers were present close to the fragment than farther away. At broad verges the occurrence of these species persisted at longer distances.

Mark/recapture experiments with three different carabid species showed that dispersal takes place randomly. Despite of these random movements, entrance of habitat areas of another kind, like dense grass vegetations or forest, surrounding the heathy corridor hardly occurred. This means that beetles stay in their corridor by the avoidance of the bordering areas. These experiments showed also that most individuals disperse not more than 50 m per year at verges of a width of 12 m, and at more narrow verges even less. Only occasionally a few individuals bridged distances of 150 m or more. Therefore, to bridge distances longer than 100 m a verge needs to be habitat as well, so that a new generation can continue dispersal along the corridor.

Distances walked per day in different kinds of habitat and chances of entering different kinds of habitat were accumulated in a simulation programme. With this programme it was possible to calculate the effects of differently sized corridors on the dispersal distances of the three beetle species tested for a time period of more than ten years. From these results recommendation for the creation and management of dispersal corridors, like heathy road-side verges, could be formulated.

keywords: *carabid beetles, dispersal corridor, heathy habitat, road verges, fragmentation, stenotopic, dispersal programme, metapopulation.*

CONTENTS

VOORWOORD

Mijn interesse voor alles wat groeit en bloeit werd al vroeg gewekt door mijn moeder, die tijdens de vele wandelingen in de natuur over een fabuleuze plantenkennis bleek te beschikken. Het systeem van haar opa, om de kleinkinderen een halve cent te geven voor ieder plantje of diertje dat ze kenden, had kennelijk gewerkt. Zo ook bij haar broer, mijn oom Henk Evenhuis, die mij wegwijs maakte in de insektenwereld. Mijn motivatie om een project als dit af te willen ronden werd indertijd sterk geprikkeld door mijn vader en mijn eerste vriendin.

Samen met Sjouke van Essen ben ik destijds begonnen met de studie biologie in Groningen. We wilden graag aan insekten gaan werken, hetgeen bij dierecologie op het Biologisch Centrum in Haren niet mogelijk was. Daarom werden we doorverwezen naar het Biologisch Station in Wijster, alwaar we kennis maakten met het onderzoek van Theo van Dijk en Piet den Boer. Hier kon aan loopkevers gewerkt worden. Na een druk sociaal leven in Groningen beviel mij het geografisch geïsoleerde Wijster goed. Zo goed zelfs dat Piet mij, op eigen verzoek, voor onderzoek doorverwees naar het nog meer geïsoleerde Tuczno in Polen. Onder bezielende begeleiding van Jan Szyszko en mede dankzij de gastvrijheid van familie Andrzejewski werd ook hier een loopkeveronderzoek met goed gevolg afgerond. Inmiddels hadden de theorieën van Piet den Boer ook wortel geschoten bij het Rijks Instituut voor Natuurbeheer (het tegenwoordige IBN). Op verzoek van en in samenwerking met RWS-DWW werd er een project voorgesteld om na te gaan of wegbermen als verbindingsbanen zouden kunnen functioneren tussen versnipperde natuurgebieden. Daar Piet altijd loopkevers als onderzoekssoorten had gebruikt, werden deze diertjes ook nu weer als proefkonijn uitverkoren. Ondanks het gebrek aan een rijbewijs rolde ik in dit onderzoek.

Veel dank ben ik verschuldigd aan Bram Mabelis, Dick Verkaar, Geesje Veenbaas en Paul Opdam voor de hulp bij de opzet van dit onderzoek en de verdere begeleiding. Mede dankzij Paul, die gedurende dit hele onderzoek als een soort waakhond op de tijd heeft gezeten, is dit proefschrift redelijk snel klaar gekomen. Ook was Paul nooit te beroerd om allerlei kleine en grote problemen bij het uitvoeren van het werk op te lossen. Dit ging zelfs eens zover dat hij een helikopter van het leger voor luchtfoto's probeerde te regelen. Het werd uiteindelijk een ultra light. Snel en efficiënt was ook zijn controle op de geschreven artikelen, zodat de hoofdstukken uit dit proefschrift thans bijna allemaal gepubliceerd of geaccepteerd zijn.

Gedurende mijn veldwerk, dat in het eerste jaar voornamelijk bestond uit rondes langs de snelwegen van noord-oost Nederland, heb ik vaak een onderkomen kunnen vinden bij locale wegbeheerders. De koffie stond bij hen altijd klaar. Tijdens het onderzoek op het Caitwickerzand was SBB-Garderen zelfs bereid om mij gedurende twee jaar werkruimte en gezelligheid te bieden op hun zolder. Ook schepte een van de medewerkers aldaar, Hans Snel, er een genoegen in om regelmatig de helpende hand toe te steken en om rondritjes te verzorgen door hun boswachterij.

In de wintermaanden werd het veldwerk verruild voor het warme Biologisch Station om de administratie bij te werken of een rapport of artikel te schrijven. Onder het genot van een kopje koffie of in de wandelgangen heb ik daar aan mijn collega's veel inspiratie ontleend. Met name Henk de Vries en Theo van Dijk waren nooit te beroerd om eens stevig met je van gedachten te wisselen over de meest uiteenlopende theorieën. Verder bleken Arnold Spee, Hans Turin en Taco van Huizen altijd bereid mijn determinaties te controleren en was Arnold ook vaak bereid om geheel vrijwillig stukjes van mijn proeven uit te voeren.

Speciale dank ben ik verschuldigd aan Piet den Boer en Tim Opsteeg. Tim wist feilloos mijn verbreidingsgedachten voor loopkevers om te zetten in computertaal. Het aldus geconstrueerde simulatieprogramma heeft hem minstens een jaar aan vrije avondjes gekost en mij bespaard. Piet heeft zich steeds met een nimmer aflatend enthousiasme door mijn stukken proza heen geworsteld, hetgeen gezien het matige engels in het begin zeker een hele kluif moet zijn geweest. Dankzij zijn correcties zijn er nog hele redelijke stukken uitgekomen. Ook onze discussies over dit project hebben hem heel wat avondjes en flessen wijn gekost.

Verder wil ik graag mijn promotor Claus Stortenbeker bedanken voor het promoten van dit project. Met name in de aller laatste fase van dit proefschrift heeft hij heel wat van zichzelf moeten vergen om de zaken voor deze promotie toch nog op tijd rond te krijgen.

Er is echter een persoon zonder wie ik dit project nooit had kunnen afronden: mijn vriendin en inmiddels mijn vrouw Saskia. Niet alleen had zij het benodigde rijbewijs voor het maken van rondes langs de snelwegen van Nederland maar ook had zij het geduld en uithoudingsvermogen om mij tot 's avonds laat ook in de weekends te assisteren zodat er ook nog wat vrije tijd voor ons samen over bleef.

SAMENVATTING

De versnippering van de vroegere "woeste gronden" wordt in Nederland als een probleem ervaren voor het langdurig overleven van bepaalde loopkeverpopulaties. Met name de aan het schrale biotoop gebonden loopkeversoorten met een gering verbreidingsvermogen blijken langzaam maar zeker uit de veelal kleine habitatsnippers te verdwijnen. Vermoed wordt dat het verdwijnen van populaties in kleine snippers eerder verband houdt met het uitsterven van kleine populaties als natuurlijk stochastisch proces dan met de ongeschiktheid van de snippers als leefgebied. Doordat de omliggende, ontgonnen terreinen van de snippers voor de bovengenoemde soorten als leefgebied ongeschikt zijn, is de kans op herkolonisatie van de geïsoleerde snippers vrijwel nihil. Om de kans op herkolonisatie te bevorderen worden dan ook door de overheid verbindingsbanen tussen de snippers voorgesteld (Natuurbeleidsplan). Herkolonisatie van leeggevallen snippers zou dan via dergelijke verbindingsbanen kunnen optreden en op regionaal niveau zouden soorten dan kunnen overleven in een soort metapopulatiestructuur.

Het onderzoek richtte zich op de geschiktheid van dergelijke verbindingsbanen voor stenotope loopkeversoorten van schrale graslandvegetaties met een gering verbreidingsvermogen. Hoewel dergelijke schrale verbindingsbanen tussen heidesnippers vooralsnog in Nederland niet bestaan, bestaan er wel lintvormige heidestructuren in Noord en Oost Nederland die als zodanig zouden kunnen functioneren n.l. schrale wegbermen.

In de eerste fase van het onderzoek werd nagegaan of de bedoelde loopkeversoorten wel voorkomen in zulke bermen, d.m.v. een inventarisatie met bodemvallen van 10 schrale wegbermen. Dit bleek inderdaad het geval te zijn en via een multivariate analyse werd verder aannemelijk gemaakt dat er een verband bestaat tussen het voorkomen van bepaalde soorten in bermen en de aanwezigheid van een met de berm verbonden heideterrein (hoofdstuk 2).

Voor een drietal soorten met een verschillende verspreiding over de wegberm, nl. a. in ongeveer gelijke frequentie aanwezig over de gehele berm (*Pterostichus lepidus*), b. in een hogere frequentie aanwezig op de berm dichter bij het belendende heideterrein (*Harpalus servus*) en c. alleen op de berm aanwezig binnen 100m. van het heideterrein (*Cymindis macularis*), is via merk- en terugvang proeven het verbreidingsproces bestudeerd (hoofdstuk 3). Van alle drie soorten bleken zich individuen vanuit het heideterrein naar de wegberm te bewegen en vice versa. Ook verbreiding langs de berm werd geconstateerd, hoewel de meeste individuen niet verder kwamen dan 25 - 50m per jaar. De afstanden afgelegd in een gewoon, niet-lintvormig heideterrein waren het grootst en in smalle wegbermen het kleinst. Soort c. bleek hierop een uitzondering. De snelle verplaatsing in de berm en de plotselinge verdwijning van alle individuen uit de berm doet denken aan een vluchtgedrag in een als habitat minder geschikt terrein.

Voor alle soorten bleek verder dat de terugvangstfrequentie per val met gelijke vangkans groter is in de berm dan in het open veld, een kans die toenam naarmate de berm smaller werd. Kennelijk had de corridorstructuur een vertragende werking op de verbreiding van deze loopkeversoorten maar dwingt deze structuur de kevers ook in de corridor te blijven. Dit werd nader onderzocht door kevers in enclosures met een straal van 4m los te laten op de grenzen van de corridorstructuur in verschillende vegetaties. Door een dagelijkse controle

gedurende de activiteitsperiode konden de loopsnelheden van de kevers in de verschillende vegetaties worden bepaald alsmede een frequentieverdeling van de kansen dat kevers de corridor verlaten en in het naburig habitat terecht komen en de kans dat ze hier weer in terugkeren (hoofdstuk 4). Voor loopkevers van schrale graslandvegetaties bleken zowel dichte grasvegetaties als bos vertragend effect te hebben op de loopsnelheid. Ook bleken deze vegetaties de kevers "terug te kaatsen". Slechts enkele individuen betraden deze vegetaties. De individuen die dit deden hadden voorts een sterke neiging om weer terug te lopen naar de schrale middenstrook van de berm. Dus de vegetaties die de berm omringen hebben een zodanige barrièrewerking, dat de random bewegende loopkevers gedwongen worden in de corridorstructuur te blijven. Verder lijken de overgangsvegetaties (veelal dichter wordende grasvegetaties) de verbreidingsnelheid van de kevers af te remmen. Daar de kever geen lengterichting van de berm kan onderscheiden verbreidt deze zich bij toeval in de lengterichting van de berm, waarbij er steeds een kans bestaat op teruglopen. Ook dit zal vertragend werken.

In de laatste fase van het onderzoek werd een simulatiemodel ontwikkeld, dat de reacties van loopkevers in een landschap accumuleert. Op basis van frequentieverdelingen van individuele reacties op habitatgrenzen en loopsnelheden van de verschillende soorten in verschillende vegetaties, gemeten in het enclosure-experiment, kan met dit model de effectiviteit worden geschat van verschillende soorten verbreidingscorridors. Bij toetsing van dit model met de resultaten van het merk-terugvang experiment, welke onafhankelijk zijn van de veldresultaten gebruikt in het model, bleek dat slechts 1 op 50 simulaties een significante afwijking gaf van de terugvangstverdeling in het veld (hoofdstuk 5). Als terugkoppeling naar het oorspronkelijk probleem werden nu verschillende soorten verbindingsbanen getoetst op hun effectiviteit als verbreidingsbaan. Uit de simulaties, gedaan voor 10.000 individuen per soort per simulatie over 1 jaar, blijken de gemiddelde verbreidingsafstanden slechts gering te zijn. De maximale loopafstanden zijn hooguit enkele honderden meters. Naarmate meer individuen deelnemen aan het verbreidingsproces blijkt de kans op een grote dispersieafstand toe te nemen. Dus verbindingsbanen verbonden met gebieden met een hoge populatiedichtheid zullen effectiever zijn dan die verbonden met gebieden met een lage populatiedichtheid. Naarmate de verbindingsbaan breder is, worden de gemiddelde dispersieafstanden langer. Bij versmallingen in de verbindingsbaan blijken individuen zich op te hopen, waardoor de kans op grote verbreidingsafstanden geringer wordt. Dit geldt ook voor vergraste plekken in de verbindingsbaan, omdat hier de verbreiding in het grassige stuk wordt vertraagd. Individuen van soorten die langer dan 1 jaar leven, zoals die van *P. lepidus* en *H. servus*, blijken in een tweede jaar maar een fractie verder te komen dan de afstanden afgelegd in het eerste jaar.

In een tweede reeks simulaties werden ook de netto-reproductie-waarden, ontleend aan jarenlange metingen in het Dwingelderveld, betrokken. Hiermee werd het mogelijk om simulaties over meerdere jaren uit te voeren (hoofdstuk 6). Deze simulaties, steeds gedaan voor 1000 individuen over 10 jaar, laten zien dat de geaccumuleerde verliezen aan de, als leefgebied ongeschikte omgeving van de verbindingsbaan, op de lange duur een grote rol spelen. Naarmate de kevers vaker met deze grenzen worden geconfronteerd wordt het verlies van individuen groter. Dit is vaker het geval bij smalle verbindingsbanen dan bij brede. Ook bij versmallingen in verbindingsbanen treedt door de opeenhoping van individuen voor de versmalling een grotere verlieskans van individuen op. Door grenzen te introduceren waar kevers scherp op reageren kan het verlies aan individuen naar de omgeving beperkt worden.

Een goede verbindingsbaan zou tevens ook een goed habitat moeten zijn zodat via een hoge reproductie de verliezen kunnen worden gecompenseerd. Alleen dan kan een berm over afstanden langer dan enkele honderden meters als verbindingsbaan functioneren. Voor een soort als *P. lepidus* lijken de bestaande wegbermen al als zodanig geschikt te zijn.

Als eindconclusie geeft deze studie aan dat schrale wegbermen verbreidingsbanen kunnen vormen voor loopkevers uit schrale habitats. Naarmate de verbindingsbaan smaller is, zullen de te verbinden habitatsnippers dichter bij elkaar moeten liggen. Iedere onderbreking, in de vorm van versmallingen en/of andere vegetaties zullen leiden tot vertragingen in de verbreidingsnelheid en verlies aan individuen. Verkeerde verbindingsbanen (te lang, te smal, te veel onderbrekingen of te vage grenzen) kunnen leiden tot een verhoogde uitsterfkans in de habitatsnipper, daar individuen uit het habitat via de verbindingsbaan worden weggeleid zonder aan een levensvatbare populatie bij te dragen. De beste verbindingsbaan lijkt vooralsnog die waar ook (sub)populaties in opgebouwd kunnen worden, zodat deze onderdeel wordt van de metapopulatie. Zulke verbindingsbanen kunnen dan ook refugia worden. De betekenis van een verbindingsbaan verschilt echter van soort tot soort. Het lijkt daarom raadzaam voor de meest gevoelige soort een verbindingsbaan te creëren, in de hoop dat minder gevoelige soorten er ook van profiteren. Bij het inschalen van verbindingsbanen lijkt het ontwikkelde simulatiemodel een behulpzaam instrument. Waarschijnlijk kan het ook voor andere organismen worden gebruikt en blijkt het tevens geschikt om netwerkstructuren te toetsen op hun bijdrage aan het overleven van (meta)populaties.

SUMMARY

In the Netherlands the fragmentation of the formerly so-called "wastelands" is regarded as a problem for the long term survival of certain ground beetle populations. Especially the species characteristic for poor sandy and open habitats with low powers of dispersal seem to disappear gradually from the usually small habitat remnants. It is supposed that the disappearance of populations from those small habitat fragments is more connected with stochastic processes normally occurring in nature than with the unsuitability of the fragments as a habitat. Because the cultivated areas, surrounding the remnants, certainly are unsuitable as a habitat for the above mentioned species, the chance of recolonization will be close to zero. To increase the chance of recolonization of isolated heathy habitat patches, the Dutch government proposes to establish dispersal corridors between fragments (Plan of Nature management). Recolonization of patches which lost their populations would be facilitated by these corridors, and at a regional level a species could survive in a kind of metapopulation.

The study presented here focused on the suitability of such dispersal corridors for stenotopic carabid beetles of poor sandy, open habitats with low powers of dispersal. Although such dispersal corridors between heathy habitat patches do not exist in the Netherlands yet, heath-like and ribbon-shaped structures do occur: poor sandy road-side verges.

To find out whether or not the species concerned occur at poor sandy, open road verges, in the first phase of this study 10 poor sandy, open road verges in the Netherlands were sampled with the help of pitfall traps. Most of the species occurring in nearby heathy areas indeed were present at the road verges, and a multivariate analyses suggested a relationship between distance to a adjacent heathy area and the occurrence of certain species at the road verge (chapter 2).

The dispersal movements of three species, differing in their distribution at the road verge, were followed by mark- and recapture experiments. These three species were *Pterostichus lepidus*, occurring along the entire verge in about equal numbers, *Harpalus servus*, present in higher numbers closer to the adjacent heathy area, and *Cymindis macularis*, which was only caught in low numbers at the verge no further than 100m from the adjacent area (chapter 3). In all three species individuals were found moving from the heathy area towards the verge and the other way round. Dispersal along the road verge was established too, though most individuals did not displace more than 25-50m. from the release point per year. In general it can be concluded that distances bridged by beetles will be greater in broad verges and in a sizeable area of heathland. One species seems to be an exception to this rule. Individuals of *C. macularis* moved quickly at the verge and after a few weeks completely disappeared from it. The behaviour of this species suggests that it flew away from adverse conditions, which apparently were met at the verge. Therefore, the verge tested is not suitable as a habitat for this species in its present form.

Individuals of all three species were recaptured at a higher rate at the verge than in the open field situation. At a narrow verge this rate was highest. Apparently, the structure of the verge not only slowed down dispersal but also forced individuals to stay in it. To verify this idea, marked beetles were released in enclosures with a radius of 4m placed at the borders

of the verge with the surrounding areas. By every day checking the traps, which were placed in the enclosures with different kinds of vegetation inside, both the rate of movement and the chance of entering other kinds of habitat could be established (chapter 4). Beetles from poor sandy, open habitats appear to move slower in forest and in dense grass vegetations. Also, the borders of the open habitat with these other vegetations deflected the movements of the beetles. Only few individuals entered the other habitat, if so, in most cases they moved back to the poor sandy strip in the middle of the verge. The slowed down dispersal movements of beetles in the verge and the higher catching rate there is explained by the random movements of the individuals while being forced to stay in the corridor structure. Because beetles can not distinguish the longitudinal direction of the corridor they have an equal chance to walk further as to walk back. This will cause a slowing down of dispersal too.

To return to the original problem whether or not a road verge can be a dispersal corridor, the behaviour of individuals of certain carabid species in different landscape-structures as estimated in the field, was accumulated in a dispersal model. The dispersal programme presented draws numbers randomly from a frequency distribution of probabilities to enter and/or return from one type of habitat to another. It also draws numbers from a distribution of rates of movement in different kinds of vegetation as estimated in the enclosure experiments. After the proposed number of walking days and individuals have passed the simulation, the model gives the distribution of the released individuals in a landscape. Validation of the model with the mark- recapture experiment, mentioned above, showed that only ones in 50 simulations results occurred of a distribution significantly deviating from that at the road verge (chapter 5). The effectiveness of different kinds of corridors could be tested in this way. For a period of one year simulations were executed for 10,000 individuals per species. Dispersal distances did not exceed 200m. and were shorter in corridors than in open field situations. In narrow corridors the difference was most evident. The chance of an individual dispersing over a larger distance increased with a higher number of beetles walking in the simulation experiment. Therefore, a corridor connected to an area with a dense population will be more effective than one connected with an area with a sparse population. The mean dispersal distances increased at wider corridors as compared to narrower ones. At narrow sites in the corridors the beetles tend to accumulate. So those sites will decrease the chance of dispersal over large distances. The same applies to grassy patches in a corridor. Individuals living longer than one year, like those of *P. lepidus*, in the second year are moving over only a fraction of the distance of the year before.

Finally, also the net-reproduction values, derived from long-term field experiments at Kralo heath, were used in the simulations. This made it possible to execute simulations over several years (chapter 6). Simulations, done for 1000 individuals over 10 years, showed that on the long term losses to surrounding unsuitable areas become more and more important. When beetles encounter the borders more often, the chance of losing these individuals to the surroundings increases. This will happen more frequently at narrow corridors than at broader ones. The accumulation of individuals at narrow sites also increases the chance of losing some of them. By introducing borders with a higher barrier-effect, losses to areas adjacent to the corridor can be diminished. A corridor with a high habitat quality will be most favourable. Then a high reproduction rate will compensate the losses occurring from the corridor. In such cases a corridor might indeed connect habitat fragments over more than a few hundred metres. For a species like *P. lepidus* the existing road verges could already be suitable in that manner.

The final conclusion of this study is that poor sandy corridors, like some road verges, potentially may be dispersal corridors for carabid beetles of poor sandy, open habitats. When narrow, these corridors can only connect fragments close to each other. Every interruption of the corridor, like narrow or grassy sites, will lead to losses of individuals to unsuitable surroundings or to a slowing down of the rate of movement. Bad dispersal corridors (too long, too narrow, too many interruptions and/or too weak borders) can increase the probability of extinction of the population in a fragment, because the possibility of leaving the fragment is facilitated by the presence of the connected corridor, whereas the corridor does not lead to another suitable habitat. Such corrridors are sinks for dispersing individuals. Corridors, in which at least temporally a subpopulation can be build up, seem to be best. Such corridors can be regarded as part of the metapopulation and probably can even be refugia. However, the importance of a corridor differs from species to species. It is advisable to create a corridor for the most sensitive and vulnerable species, by which it may be hoped that also less critical species will profit. For planning adequate corridors the simulation programme developed might be a useful instrument. Probably it can be used for other kinds of organisms than carabids, and might appear appropriate for testing the support of network structures to the survival of (meta)populations.

Chapter 1

GENERAL INTRODUCTION

History of the dutch landscape

In the Netherlands, after the appearance of the first humans, the landscape gradually changed from ancient deciduous forest, moorlands and peat bogs into villages and agricultural fields. The rich clay soils in the river delta were most productive. Economic success in this area caused population growth and even lakes were transformed into arable land. On the other hand, the higher sandy parts in the North-East were less fertile. After the cutting of forest, which started already in prehistoric times, open landscapes on poor sandy soils were left, mainly usable for extensive cattle grazing. In the East of the Netherlands a large continuous area of heathland, occupying about 30% of the whole country in 1800, extended from Groningen in the North till the Belgium border and even further South, only interrupted by peat bogs, the big rivers and some small brooklets (Schuring et al, 1992). With the cutting of the last piece of primeval forest, the Beekbergerwoud near Arnhem in 1871 (van Zanden & Verstegen, 1993), hardly any forest was left. The only forest-like areas present, were small woodlots near villages, used as coppice, and the hunting area for the royal family near Apeldoorn. These areas were manipulated and partly planted at the end of last century and covered not more than 4% of the Dutch territory. Due to a shortage of wood for heating and cooking, peat was widely used as a fuel, and most peat bogs were drained and dug off (Schuring et al, 1992). After the introduction of artificial fertilizers at the end of last century man was able to turn the heathlands into more or less productive agricultural fields. At the same time areas of drift sand, created by overgrazing of the heathlands, were reafforested, but this time by pine trees.

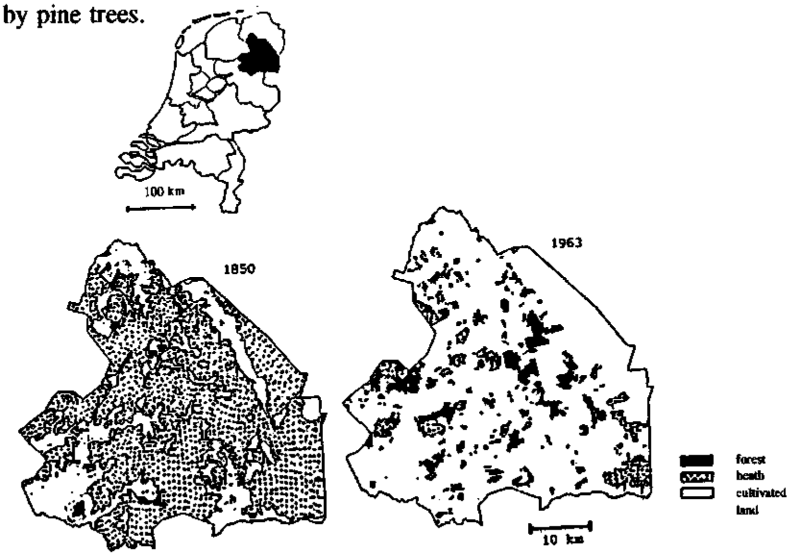


Figure 1.1. An example of the fragmentation of heathlands and dry grasslands in the Dutch province of Drenthe since 1850. The same kind of process took place in the whole North-East part of the Netherlands.

Finally, the semi-natural habitat of heathland, stable for thousands of years, was regarded as wasteland and turned into agricultural land on a large scale. The remaining fragments were scattered in isolated patches through the entire area. Fig. 1.1 illustrates this process for the province of Drenthe, in the North of the Netherlands. Although, already from the beginning of this century, the Dutch nature conservation organization the Vereniging tot Behoud van Natuurmonumenten in Nederland protested against the destruction of these wastelands, reclamations continued till the sixties.

The loss of species

Of course, by changing the dominant vegetation also the fauna was changed. As the last small remnants of primeval forest were already cut down in the middle of the 19th century, most characteristic forest species disappeared. The woodlots of coppice left were small, fragmented and highly affected by human activities. Probably, only the less critical species of forest could survive there. On the other hand, for the species of heathland the surface area of habitat increased enormously. They could settle down throughout the whole area, because the heath area continued existence for several thousands of years. Recently, this habitat area became highly reduced and fragmented.

For most larger animals of forest, like mammals and birds, usually it is known which species occurred in the past. For smaller animals, however, like invertebrates, it is hardly possible to reconstruct the species composition of these ancient forests. As reduction and fragmentation of heathlands occurred relatively recently, many of these heathland invertebrates probably still occur in the Netherlands. However, even on the small territory of the Netherlands, the group of invertebrates consists of several ten thousands of species. Therefore, it will be rather difficult to find out how many of these species are threatened to extinction. When carabid beetles are taken as indicators for the invertebrates of heathlands, we may conclude that most of invertebrates are highly endangered now (Desender & Turin, 1986, 1989, Turin, 1989).

Of course, one of the major reasons for this faunal impoverishment has to be the large scaled destruction of the heathland habitat. As far as the Netherlands are concerned, in 1833 heathlands still occupied 600,000 hectares from which only 40,000 are left at present. This loss of inhabitable area simply must have caused a decline of stenotopic animals restricted to heathy habitats. But at least in invertebrates the decline probably is larger than what can be expected from destruction of habitat alone (Hopkins & Webb, 1984; Webb & Hopkins, 1984; de Vries, 1994). For, the reclamation of the so-called wastelands took place part by part, leaving a few larger and many smaller pieces of heathland scattered over the Eastern part of the Netherlands. The originally large and continuous heathland areas were split up in hundreds of small or very small pieces, separated from each other by agricultural land and planted forests (Anon., 1990). These heathlands were rather stable habitats for a long period. At least among carabid beetles such stable conditions lead to a decrease of dispersal power, especially of flight capacity (den Boer, 1971; Aukema, 1986).

For stenotopic invertebrates of heathy habitats such fragments can be regarded as islands in a sea of unsuitable habitat, as only occasionally they can be found outside their heath habitat and in a very few exceptional cases at distances larger than hundred metres (Gardner, 1991). For oceanic islands, MacArthur & Wilson (1967) showed that survival times and extinction rates of populations are largely determined by the size of the islands. This means that smaller islands will lose their species more rapidly than bigger ones. They also showed that the distance to other islands or mainlands significantly decreases the chance of (re)foundation of populations on islands. The number of species on such islands fluctuate around a kind of balance between extinctions and refoundings. When changing the size of an island or the distance to another island this balance will shift to another level. Fragmentation of heathland can be considered splitting up a few large islands in hundreds of smaller ones. According to Diamond (1975) such fragments in a cultivated countryside will lose species by natural extinctions until a new (lower) balance level in the number of species is reached. This would imply that just after the reclamations in Dutch heathland remnants a number of species was present related to the original size of the area, but in the course of time species disappear untill a new balance, fitting to the size of the remnant, will be reached. In the latter situation species that can easily bridge distances between those remnants have a good chance to be observed everywhere, because they have the opportunity to refound populations in areas where they can survive. As stenotopic species with low powers of dispersal will not have this opportunity, these are probably not only endangered by reduction of their habitat, but also threatened by regional extinction, first disappearing from the small habitat fragments.

These concepts are thoroughly applied to carabid beetles living in heathland remnants in Drenthe by den Boer (1977). From his long-term observations on the distribution and numbers of 64 carabid species, den Boer (1979, 1990a) could show that extinctions of local populations or so-called interaction groups occur frequently. Hence, extinctions are not restricted to species from instable or temporal habitats, but occur also in species occupying stable or permanent habitats. As on small habitat islands only one or a few local populations of a species can live, the chance of extinction of the entire population will be higher than on larger islands. The estimated survival time for local populations usually is a few decades only (den Boer, 1985, 1986).

Circumstantial evidence for the correctness of den Boers calculations was later provided by de Vries & den Boer (1990) and de Vries (1994). A decline in number of species for stenotopic carabid beetles with low powers of dispersal was shown to occur for habitat sizes smaller than about 70 ha. As most of the habitat fragmentation of heathland took place about 50-100 years ago, it might be concluded that heathy habitat fragments should be larger than 70 ha to let most populations survive for longer than 50-100 years. However, from the same studies it appeared that only a few habitat fragments are larger than 70 ha, and if larger, the survival of certain species is not sure. At the 1200 ha heathland of the Dwingelderveld van Essen (1993) reported the disappearance of at least two and may be three stenotopic species of heathland occurring there 20-30 years ago.

It was also found that well dispersing carabid beetles, which can fly at least occasionally, declined in heathlands of 8 - 25 ha. In this respect the ability to fly can be important, because it enables to pass hostile surroundings and to recolonize empty patches. On the other hand, since the direction of dispersal through the air is mainly depending on the direction of the wind (van Huizen, 1990), individuals will recolonize patches only by chance. The high losses of dispersing individuals will make the remaining populations more vulnerable for extinction. Therefore, it might be expected that most small patches with populations of good dispersing species will be situated not far from a large habitat area with a large source population. Though even good dispersing species probably still need large habitat areas for regional survival, they will be less exclusively restricted to such areas as compared to beetles only dispersing by walking. Populations of the latter species do not suffer from losses by individuals flying away, but will have a very small probability to replace populations lost from heathy habitat remnants, even when nearby (> 100m). Carabid beetles walk only short distances and in rather random directions (cf. Baars, 1979; van der Ent & van Dijk, 1991; Klazenga & de Vries, 1994). As the chances of survival in areas between habitat fragments are very low, to (re)found populations of stenotopic beetles in separate fragments stepping stones or bridge habitats are needed(den Boer, 1977).

Nature management for saving species

In the "Natuurbeleidsplan" (Plan of Nature Management) the Dutch government proposes to connect remnants of (semi)natural areas (Anon., 1990). In a network structure of dispersal corridors between small and larger habitat fragments local populations are expected to support each other. When a local population becomes extinct dispersal through such a corridor must facilitate recolonization from areas where the species is still present. The entire network thus has to form a metapopulation in which the survival of species is improved (cf. Levins, 1970; Opdam, 1987, 1990; Gilpin & Hanski, 1991). Although dispersal corridors are already incorporated in some local plans of nature management, sofar there is only little and fragmented evidence on the suitability of different kinds and sizes of corridors, concerning their assumed function and the species supposed to be favoured (Getz *et al.*, 1978; Burel, 1989; Zerbe, 1989; Opdam & Hengeveld, 1990; Saunders & Hobbs, 1991; Vermeulen & Veenbaas, 1991; Hobbs, 1992; Petit, 1994). As stated above, stenotopic carabid beetles with low powers of dispersal are among the organisms which might profit from such dispersal corridors. The Ministry of Transport, Public Works and Water Management, which takes care of the verges of highways in the Netherlands, suggested a corridor function for road verges (Anon., 1988). Though a road verge, when running through a natural area, can be a barrier which is difficult to cross (Mader 1979, 1984, 1987; Mader *et al.*, 1990), as a ribbon-like structure through forest or arable land it might be suitable to connect natural areas adjacent to the road verge. Due to a management of low intensity road verges in the Eastern part of the Netherlands often are heathy. These features suggest a potential corridor function between fragmented heathlands.

The aim of this study

The overall aim of this study was to find out whether or not and under what conditions heathy road-side verges could be dispersal corridors for stenotopic carabid beetles of heathy habitats with low powers of dispersal. The choice for carabid beetles as a group to study was not only because of the lots of information available, but also they might be useful bioindicators (cf. Butovsky, 1994).

Short sections of a corridor at least must provide a suitable habitat for beetles to survive. For distances longer than the walking range of beetles, sufficient reproduction sites must be present in a corridor to enable beetles of next generations to continue dispersal through the corridor.

By sampling ten heathy road verges, differing in isolation and width, it was investigated which carabid species, restricted to poor sandy, open habitats could be present (chapter 2). Secondly, I analyzed the similarity between the species lists in road verges and that of adjacent heathland areas. A high similarity could be interpreted as an indication for the exchange of individuals. This exchange was studied by mark- recapture techniques (chapter 3). During two years movements of individuals of three carabid species were studied in one area. Individuals have to stay in the presumed corridor, otherwise leakage to the surrounding unsuitable areas will mean a loss of individuals. When the threshold of leaving a habitat area is lowered by a corridor connected to it, leakage from the corridor may have a negative effect on the survival of the population living in that habitat area. In chapter 4 the chance of leaving and re-entering the supposed corridor was tested as well as the rates of movement in the different vegetation strips constituting the verge.

To explore how the dimensions and vegetations of the verge interact with the distances covered by dispersal, a dispersal simulation programme was developed. This programme, which is presented in chapter 5, is based on the individual behaviour of carabid beetles, as analyzed in chapter 4 and connected with the results presented in chapter 3.

Finally, in chapter 6, several kinds of imaginary road verges were tested on their suitability to dispersal corridors on the long term. Also, expected bottlenecks and suggested improvements are examined.

Chapter 2

THE COMPOSITION OF THE CARABID FAUNA ON POOR SANDY ROAD-SIDE VERGES IN RELATION TO COMPARABLE OPEN AREAS.

SUMMARY

In the Netherlands, the majority of heathlands and dry, unproductive grasslands were brought into cultivation or afforested since the end of the 19th century. As a result the original landscape became highly fragmented. Nowadays the heath habitat occurs in more or less isolated patches only. Many of these fragments show a small spatial variation in conditions. Ground-dwelling arthropods, with a low dispersal power and a specific preference for poor sandy, open habitats, could disappear from such small fragments under the influence of temporally unfavourable conditions. As recolonization from other fragments often is very difficult because of hostile surrounding areas, isolated small fragments that lost their populations will remain unoccupied. The absence of some carabid species in such small, isolated fragments is thought to be the result of this situation. By introducing heathy corridors between such fragments animals might be enabled to pass a hostile environment. This study shows that heathy road-side verges possibly can function as such a corridor. On the studied road-side verges, carabid species of poor sandy, open habitats were present, including the more rare species. Some species even found a better habitat at road-side verges than in studied poor sandy open areas adjacent to such road-side verges. For other species the road-side verge seemed to be a more marginal habitat in which they only occur because of the presence of a suitable adjacent area. The distance to such an area as well as the width of the poor sandy, open strip on the road-side verge seem to be important conditions for the occurrence of the latter species. To increase the chance of survival in such a corridor, it is suggested to create some wider strips or patches at the road-side verges, suitable for reproduction. In this way road-side verges might contribute to a metapopulation structure by which species are better protected against regional extinction.

INTRODUCTION

More than 4000-5000 years ago the Netherlands mainly must have been covered with broad-leaved forests (Faber, 1942, van der Vlerk & Florschütz, 1949). The destruction and fragmentation of these original forests by man started not much later. The last remnants of the older coppice forests became fragmented more than 200 years ago. The landscape was gradually changed into small agricultural areas surrounded by coppice woodlots and large poor heathlands, used for cattle and sheep grazing. These poor open areas were stable and highly connected for a long period. In 1833 the total surface covered by these areas still amounted to 600.000 hectares (van der Kam, 1984). At the end of the 19th and the first half of the 20th century, the majority of these poor, unproductive areas were brought into cultivation or afforested. In 1963, the time that these reclamations came to an end, only 40.000 hectares were left in scattered patches. Consequently, also this semi-natural landscape became highly fragmented. Only more or less isolated heathy remnants were left.

For ground-dwelling arthropods, bounded to this kind of habitat, like some carabid species, this reduction and fragmentation of habitat resulted in local and eventually total extinction. Under the present conditions, especially species with low powers of dispersal will have a small chance to found new local populations (den Boer, 1977 & 1990a).

According to Turin (1989) the carabid species, restricted to the above mentioned habitat, significantly decreased since the last century. This decline was probably caused by reduction, fragmentation and isolation of their habitat, because the species that disappeared were known to be stenotopic and poorly dispersing (Turin & den Boer, 1988).

In the concept of metapopulation (Levins, 1970) as used by Opdam (1987) each species needs a certain minimum amount of habitat to maintain a stable population, which consists of a number of local populations, interconnected by dispersal. However, many fragments of habitat are too small and too isolated to support viable local populations, so that species, restricted to such fragments, sooner or later will disappear from that region under the influence of temporally disturbing factors. Den Boer (1985, 1986) showed that, when isolated, local populations of carabid beetles will only survive some decades. As an example, *Agonum ericeti*, a brachypterous carabid species restricted to peat moor habitats, at present only occurs in large peat moor remnants or in smaller remnants which became isolated recently (de Vries & den Boer, 1990). By constructing connections, or dispersal corridors, recolonization might take place and could contribute to stabilization of a network of local populations in a metapopulation structure (Gilpin & Hanski, 1991). Mader (1987) suggested that road-side verges of highways might play a role as dispersal corridors for carabid beetles, as it was found to occur for mice (Getz et al., 1978).

As in the Netherlands road-side verges have an extensive management they are often poor and heathy (van der Sluijs & Vissers, 1991). Their ribbon-like character suggests a possible function as dispersal corridors for ground-dwelling arthropods of poor heathy habitats.

The present research aims to find out which carabid species, restricted to poor sandy, open habitats, are present at poor sandy road-side verges. From the perspective of nature conservation, road-side verges with stenotopic carabid beetles, which are also geographically restricted, may be of great value. Furthermore, to establish whether or not these road-side verges are potential dispersal corridors between poor sandy, open habitat fragments, it has to be studied what kind of relationship exists between stenotopic carabid species present in poor sandy, open areas and at the road-side verges connected with these areas. Species that are only present at road-side verges connected with such areas may use the road-side verge as a dispersal corridor. To find out under what circumstances and over which distances a corridor function of the road-side verge might be expected, one location is studied more in detail.

METHODS

Study areas and sampling methods

Figure 2.1. The distribution of heathy fragments in the Netherlands and the location of the studied areas.

In 1989 at five locations in the North-East part of the Netherlands, fragments of heath and dry grassland connected to highway road-side verges as well as the road-side verges themselves were sampled for the presence of carabid species (Fig. 2.1.). The selected road-side verges showed about the same characteristics as the heathy fragments. Two of these road-side verges had a width of about 6 meters or less, and therefore, the heathy vegetation was hardly developed. All other road-side verges sampled were at least 10 meters wide. Disparate kinds of habitat, bordering these road-side verges, such as agricultural fields and forest, were presumed to be unsuitable for species restricted to heathy habitats. To test this assumption, such areas next to the road-side verges were sampled as well.

The sampling was done by a series of pitfall traps placed from the centre of the poor sandy, open area towards the road-side verge and continued for several hundreds of meters along the road-side verge. The results of these samplings will be compared both to those from road-side verges which had only contact with poor sandy, open areas at the time of road construction, about 20 years ago (2 locations), and to isolated road-side verges which became heathy only recently (3 locations). The last 3 locations were sampled in 1991.

The pitfall traps used were plastic cups with a diameter of 10 cm., about half filled with a 4% formalin solution. From the beginning of April to the end of October the study areas were sampled continuously and beetles were collected every 2-3 weeks. In total 149 pitfall traps were placed in the different areas: 15 at isolated road-side verges, 15 at road-side verges with a connection in the past, 42 at narrow road-side verges and in adjacent poor sandy areas, and 77 at wide road-side verges and the adjacent poor sandy areas.

All carabid beetles caught in pitfall traps were identified to species level using standard keys (Everts, 1898; Lindroth, 1974; Boeken, 1987), according to the nomenclature of Turin (1990).

Ecological characterization of species

To select the carabid species, which in the Netherlands are restricted to poor sandy, open areas, the ecological characterization of carabid species of Turin et al. (1991) is used. Species, which are mentioned in this paper as characteristic for peaty soils, oligotrophic sandy soils, Corynephoretum-vegetations and poor grasslands, are considered to be stenotopic species of poor sandy, open areas. Note, that the collected data are obtained independently of this characterization!

To find out whether or not the heath species caught at road-side verges are more commonly occurring in the Netherlands than species present at the poor sandy, open areas the data base of the Dutch Carabidological Association is used. In this data base all known catches of carabids in the Netherlands are recorded. From this database it is possible to establish in how many cells of 10 by 10 km in the Netherlands each species is occurring. The data used here for comparison to our, independently collected, data, are all catches obtained since 1975 (336 species), in 391 out of the 448 cells 10 by 10 km of the Netherlands. Since 15-20 years earlier reclamation of the heathlands came to an end, the first extinctions of local populations in small and isolated heathy fragments might have occurred in that period (den Boer, 1990), so that species, which recently became rare due to habitat fragmentation, are included.

Relationship between species of open poor, sandy areas and of road-side verges

In 1990 a single location, the Caitwickerzand and the road-side verges of the highway A1 bordered by forest, was selected for some carabid species to study the relationship between a poor, sandy, open area and the road-side verges more in detail. The purpose of this part of the experiment was to find out under what circumstances and over which distances a corridor function of the road-side verge might be expected. The abundances of some stenotopic species of this area were established at different distances from it at the road-side verge. Size and width of the poor sandy strip at the road-side verge and the type of vegetation was taken into account.

The Caitwickerzand is a former drift sand area, which now is mainly covered by lichens and some short grasses. At some places *Calluna vulgaris* is spreading. This area was selected, because it has an almost open connection with the road-side verge. The barrier effect of some pine trees, which in all studied areas were present in the transition-zones, was expected to be low here. The results, obtained in the first year, indeed did suggest so.

A series of pitfall traps was introduced from this former drift sand area towards the road-side verge and continued for 400 meters along this road-side verge. In order to increase the chance to catch beetles, widened pitfall traps were used. A widened pitfall trap consists of two plastic cups with an iron fence of one meter in between. In this experiment the beetles were caught alive in dry traps. At fixed distances three of these widened pitfall traps were placed, which were operating from the beginning of April till the end of September.

During the study period the numbers of carabid beetles caught, which belonged to species stenotopic for poor sandy, open habitats, were recorded, except *Harpalus neglectus*, which is difficult to distinguish by bare eye from other species. To compare the stenotopic species to the more eurytopic ones, all specimens caught of the genus *Calathus*, which can easily be recognized, were also recorded.

Data analysis

For the elaboration of the collected data, some tests from the standard statistical packages SPSS/PC+ V2.0 (Norusis, 1988) and Genstat 5. (1987) were used. To check how far distance and the two independently varying structural features of the road-side verges at the Caitwickerzand, width and vegetation, were related to each other, a correlation-matrix, based on the Pearson product-moment correlation (Sokal & Rohlf, 1981) was constructed. A one-tailed t-test was used to check the statistical significance of these correlations. The results are presented in Table 2.1. On the entire road-side verge a strip was present that had similar soil and vegetation characteristics as the Caitwickerzand itself. Therefore width of this strip was taken into account to represent size of the potential habitat patch. Similar correlation-matrices were used both to find out whether or not the species present showed relationships among each other, and to establish which species were somehow related with the independent variables. To specify the correlations found, Multiple regression analyses were used both for each of the 3 independent variables separately (marginal factors), and for the 3 independent variables together (conditional factors). As the numbers of beetles caught were varying highly, in this analysis these numbers were expressed as logarithms. Significance was given as F-probabilities.

Table 2.1. Correlation-matrix of three independent variables of the road-side verge at the Caitwickerzand: distance in meters from the former drift sand area, width of the poor sandy strip on the road-side verge, and the vegetation, which is split in 4 dominant plant species, *Festuca ovina*, *Corynephorus canescens*, young *Pinus sylvestris* and *Calluna vulgaris*. Only presence or absence of these plant species at the sampling sites is recorded.

distance	1.0					
width	-*	1.0				
vegetation						
Festuca			1.0			
Coryn.			-**	1.0		
Pinus					1.0	
Calluna	+*			-*		1.0
	distance	width	Festuca	Coryn.	Pinus	Calluna

* P<0.05; ** P<0.01; -negative relation; +positive relation

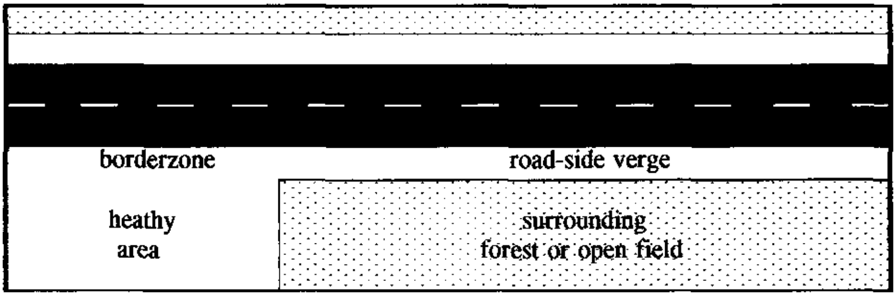
RESULTS

The presence of stenotopic species from poor sandy, open habitats

For the Netherlands as a whole, 45 species are considered as characteristic for poor sandy, open habitats. At the 10 sample locations 29 carabid species of them were caught. These catches are expressed in Table 2.2. 27 species were found near the road (Table 2.2, borderzone and road-side verge, in which the road-side verge is defined to be at a distance of at least 100 m from this borderzone). Although not caught at the road-side verge in 1989, in the experiment of 1990, *Cicindela hybrida* was also found at the road-side verge. This leaves only one species which may be regarded to avoid roads and road-side verges. On the road-side verge itself, at a distance of 100 meter or more from the borderzone, still 23 species were found. Some of these species were not caught at an open sandy site. Most of the latter species were caught at the 5 road-side verges that were not adjacent to a poor sandy, open area. Some species, although they are known to be stenotopic for poor sandy, open habitats, were also caught in the forest or at the field edge, close to the road-side verge. It is not known whether or not these beetles originate from the road-side verge or from the poor sandy, open area. When the numbers caught at these disparate sites are very low (< 10%) as compared to the numbers occurring at the road-side verge and in the poor sandy, open area, they are considered to be strayers from the nearby heathy habitat. Sometimes strayers can be caught at a distance of 100 meters from their habitat (Bauer, 1989), but most of the pitfall traps in which these catches occurred were only 10 meters or less from the poor sandy, open habitat.

In Table 2.2, the species are also classified according to the wing form and flight capacity as well as to their dispersal group (van Huizen, 1980; van Huizen & Aukema, 1992; den Boer, 1977). It is striking that all species, which were caught at the road-side verges only, were macropterous and had a high or unknown/uncertain dispersal power. In Table 3 the species caught as belonging to the different dispersal groups are compared with the habitat restrictions at the different kinds of road-side verges. In the toprows, the beetles are arranged

Table 2.2. Distribution of stenotopic carabid species of heathlands in the research areas. The figure above illustrates the general picture of an open poor sandy area (heathy area) connected (borderzone) to the road-side verge. Between borderzone and heathy area in most cases some trees are present.



carabid species of heathlands and/or drift sands	caught in :					wing form and f.cap.	disp. group
				surroundings			
name of the species	Heathy area	border zone	road - side verge	forest	open field		
Cicindela hybrida	*					M +	C
Cicindela sylvatica	*					M +	U
Amara infima	*	*				D	C
Bembidion nigricorne	*	*				B	A
Calathus ambiguus	*	*				D	C
Cymindis macularis	*	*				B	A
Amara equestris	*	*	*			M	A
Cicindela campestris	*	*	*			M +	B
Harpalus servus	*	*	*			M +	U
Harpalus neglectus	*	*	*			D	U
Masoreus wetterhalli	*	*	*			D	A
Trichocellus cognatus	*	*	*			M +	B
Acupalpus dubius			*			M	C
Amara curta			*			M	U
Amara lucida			*			M	U
Harpalus solitaris			*			M	C
Notiophilus aesthuans			*			M	U
Notiophilus substriatus			*			M +	B
Bradycellus ruficollis	*	*	*	±		M +	B
Miscodera arctica	*	*	*	±		M	U
Notiophilus germinyi	*	*	*	±		D	C
Pterostichus lepidus	*	*	*	±		B	A
Olistophus rotundatus	*	*	*	*		D	C
Carabus arvensis		*	*	*		B	A
Pterostichus minor	*	*	*	*		D +	B
Agonum sexpunctatum	*	*	*		*	M +	B
Harpalus latus	*	*	*	*	*	M +	B
Pterostichus diligens	*	*	*	*	*	D +	B
Cymindis humeralis			*	*		B	U

* kind of habitat where specimens were caught
± caught in the surroundings, but 10% or less than the mean catches in the other pitfall traps in the same area.
Wing form : M = macropterous, B = brachypterous, D = dimorphic.
f.cap : flight capacity, + = caught in window traps or observed in flight

Disp. group: dispersal group according to den Boer (1977) & pers.comm.
A = low dispersal power
B = high dispersal power
C = dispersal power uncertain
U = dispersal power not mentioned by den Boer

in the dispersal groups according to den Boer (1977). At the bottom of Table 2.3 the species are mentioned which sofar are unknown to fly. By excluding the macropterous species in this row too, the chance that the beetles are able to fly, but sofar are not caught or seen during flight, is reduced. However, for some wing-dimorphic species, it is known that some specimens are able to fly (for example *Pterostichus minor* in Table 2.2). In the last row of this table dimorphic species, which sofar have not been caught during flight, are included. Species that were caught outside the poor sandy, open habitat in more than 10% of the total catches, during this study are regarded as being less dependent on this habitat type. Therefore they are also excluded from the last category. This only leaves the species which are highly dependent on the poor sandy, open habitat for survival and dispersal at the bottomrow.

Table 2.3. Distribution of numbers of carabid beetle species, restricted to poor sandy open areas over dispersal groups, as distinguished by den Boer (1977), over the investigated road-side (r-s) verges and heathy areas.

Dispersal Power (den Boer 1977 & pers. comm.)	numbers of species present				
	isolated r-s verges	in the past connected r-s verges	connected r-s verges narrow	connected r-s verges broad	poor sandy open areas & borderzone
low (A)	1	2		4	6
high (B)	1	2	6	6	6
uncertain (C)	2	1	1	4	3
not mentioned (U)	3	4		7	7
total heath species caught	7	9	7	21	22
not macropterous, not caught in window traps and less than 10% in the surroundings	1	1	1	5	7

isolated or connected refers to the presence or absence of a poor sandy, open area to which the road-side verge is or is not connected. narrow road-side verge are 6 meters or less wide, broad road-side verge are 10 meters or more wide. If not mentioned, the r-s verges were broad. Species which are not macropterous, and from which no specimens have been caught in window traps (wing-dimorphic species with a high percentage of flying specimens), neither have been caught during this experiment more than 10% outside the poor sandy and open habitat, are listed in the last row. The poorest dispersers are found in the poor sandy, open areas and at borderzones as well as at the wide road-side verges connected to such areas. The same holds for the total number of stenotopic species. The single species in the bottom row of Table 2.3, present at both the isolated and the narrow road-side verges, was ***Notiophilus germinyi***, a species which is wing-dimorphic and shows some tolerance for forest borders (see Table 2.2). The last equally holds for *Pterostichus lepidus*, which was also caught at road-side verges connected to poor sandy, open areas in the past. Furthermore, species that are known to be good dispersers were caught in the same number of species in the poor sandy, open areas, in the borderzones, and at both the broad and the narrow connected road-side verges.

Tables 2.2 and 2.3 showed that, when the suitable site is large and sufficiently connected to poor sandy, open areas, carabid species of this habitat type can be present at road-side verges. In the following, it is questioned whether on not only the most common species are usually found at the road-side verges. Therefore, the stenotopic species caught in the study areas were ranked according to the number of 10 by 10 km cells in which each species was caught in the Netherlands since 1975. Species ranked in this way were divided in 9 classes. In the first class are the species occurring in 20 or less cells, in the second class those occurring in 21 to 40 cells, and so on. Figure 2.2 presents the results of this classification for the species caught in the poor sandy, open areas (heathlands), at the borderzones between the road and these areas, and at the road-side verges at a distance of at least 100 meters from these borderzones, respectively. The distribution of numbers of species over these classes does not differ significantly in the 3 kinds of habitat (chi-square tested, in all cases $P > 0.95$). In fact, the distributions are remarkably similar. So, in general, species with a restricted distribution, rare species, do not avoid road-side verges. Figure 2.2 also shows that most species of poor sandy, open areas caught, belong to the species with a restricted distribution. Apart from the carabid species stenotopic for poor sandy, open habitats, other carabid species with a limited geographical distribution in the Netherlands were caught at the road-side verges too. These other species caught at the road-side verges and occurring in less than 40 10 x 10 km cells in the Netherlands are: *Laemostenus terricola*, *Leistus spinibarbis*, *Harpalus anxius*, *Harpalus distinguendus*, *Harpalus smaragdinus*, *Amara preatermissa*, *Amara tibialis* and *Bembidion doris*. Most of these species prefer an open sandy habitat or ruderal sites, and were not found in the surroundings of the road-side verges.

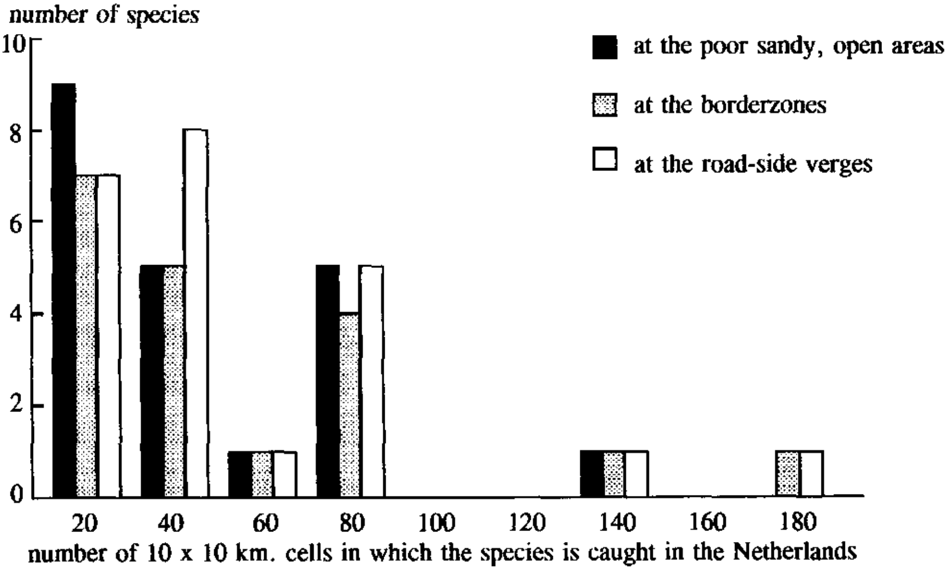
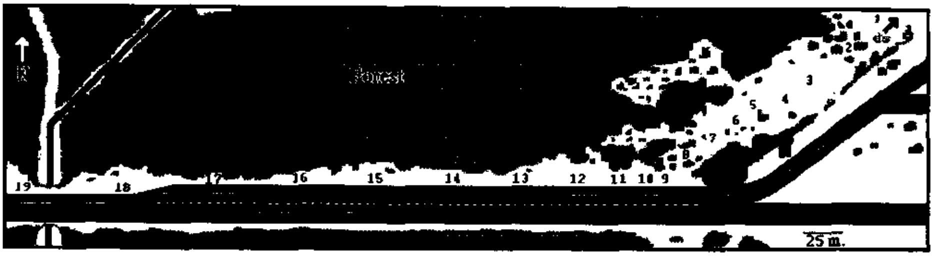


Figure 2.2. The frequency of the caught carabid species of poor sandy, open areas, arranged according to their geographic restriction (the number of 10 x 10 km cells in The Netherlands, out of the 391 cells examined, in which a species was found.).

The relationship between the poor sandy, open areas and the adjacent road-side verge for some carabid species.

At the location Caitwickerzand, the area studied more in detail, the presence of 13 species was recorded, 9 species of poor sandy, open habitats and 4 more eurytopic species belonging to the genus *Calathus*. All these species were present in the former drift sand area, although in differing densities. In Figure 2.3 a map of the study area with the places of the pitfall traps is given. For the 13 species, the table in Figure 2.3 shows the mean catches per corresponding set of pitfalls at different distances from the drift sand area. The eurytopic species *Calathus fuscipes* and *Calathus micropterus* were only present at the edge of the area,



Distance to the former drift sand in meters	600 pt19	550 pt18	500 pt17	450 pt16	400 pt15	350 pt14	300 pt13	250 pt12	225 pt11	212½ pt10	200 pt9	187½ pt8	175 pt7	162½ pt6	137½ pt5	125 pt4	100 pt3	50 pt2	0 pt1
stenotopic species																			
Calathus ambiguus							.3	.3	.3	.3	.3	.7	.3	2.3	2.8	3	11	.7	9.7
Cymindis macularis										.3		1	1.7	2.3	3.3	3.3	6.7	1.7	3.3
Miscodera arctica					.7					.3	.3	.7	1	1.3	1		.7	1	.7
Harpalus servus	3	.3		1	1		2	8.7	7	2.8	.3	5	55	71.7	34.8	27.7	.7	20.7	23.7
Cicindela hybrida	.3													1.3	2.3	.7	.7	.3	
Olistophus rotundatus	.3							.7		.2		.3	.3			.3	.7	1	.3
Masoreus wetterhalli	7	4.7	1	4	4.3		.3	4.7	8	2.7	.7	2.3	6	1	2.3	5.3	1	2	7
Pterostichus lepidus	9	11.3	2.3	3	13	10	4.7	12	6	9.3	1.3	3	6.3	3.7	3	1	1	.3	.7
Amara equestris	2.7	17	14	4	27.3	3	7.3	10.7	9.7	2.8	.3	1.3	2.7	5.3	2.5	.7	.3		
eurytopic species																			
Calathus erratus	8	4.7	.3	1	2		2.7	8.7	21.3	4.8	6.3	20.7	42	56.7	35.3	30.7	35.3	35	48.3
Calathus fuscipes	.7	.3	.7		1			.3		.5	.7		.7	2.3			.3	.7	1
Calathus micropterus										.8	.3	1.7		.7	.5				
Calathus melanocephalus	5.7	9	12.3	1	5	3	6.7	13	8.7	9	4	1.7	2.7	2.3	2.5	.7	2	5.7	9.3

pt. refers to the sampling site shown on the map above. The upper species are stenotopic species for poor sandy open areas, the species below are more eurytopic (according to Turin et al. 1991)

Figure 2.3. The research area at the road-side verge of the A1 connected with the former drift sand area Caitwickerzand (ds). The numbers indicate the places where sets of 3 pitfall traps were placed. The table shows the mean numbers of catches per pitfall trap.

some meters from the surrounding oak/pine forest and in the forest itself. *Calathus erratus* was one of the most numerous species in the centre of the former drift sand area. The 10 most abundant species, stenotopic or eurytopic, at the centre of the Caitwickerzand were *Harpalus anxius*, *H. servus*, *C. erratus*, *C. ambiguus*, *Cymindis macularis*, *H. neglectus*, *H. affinis*, *Broscus cephalotus*, *P. lepidus* and *Amara equestris*. The species are sequenced according to the highest numbers caught in pitfall traps. Although the species *Cincindela hybrida* was frequently observed and must have been very abundant in this area, it was hardly caught in pitfall traps, because it is a very good flyer. With the exception of *B. cephalotus* all these species were also caught near the adjacent highway, the A1. The species which are stenotopic for poor sandy, open areas according to Turin et al. (1991), and were only occasionally caught at the centre of the Caitwickerzand, *Masoreus wetterhalli*, *Miscodera arctica* and *Olistophus rotundatus*, are included in Figure 2.3. The distribution of the mean catches in Figure 2.3 is used in the analyses of Tables 2.4, 2.5 and 2.6.

Table 2.4 gives an impression of the correlation of the numbers of each species caught with each of the

Table 2.4. Correlation-matrix of the stenotopic carabid species and the species of the genus Calathus with the independant variables. For full names of the species see Figure 3.

	distance	width	Festuca	Coryn.	Pinus	Calluna
stenotopic						
C.ambi	-***	+***				
C.macu	-***	+**				
M.arct	-**					
H.serv	-**					
C.hybr				+*		
O.rotu	-*				+*	
M.wett						
P.lepi	+**	-*				+*
A.eque	+***	-**			-*	+**
eurytopic						
C.erra	-***	+*		+*		
C.fusc						
C.micr						
C.mela						

* P<0.05; ** P<0.01; *** P<0.001; + positive relation;
\- negative relation.

independent variables. This matrix suggests that most stenotopic species show a negative correlation with distance to the former drift sand area, and some of them also have a relation with width of the road-side verge. The more eurytopic species *C. erratus* shows similar relations. Remarkably, the species *P. lepidus* and *A. equestris* show a relationship opposite to that of the other stenotopic species.

When put together in a multiple regression analysis, each separate variable (Table 2.5, marginal factors) shows about the same relations as in Table 2.4. However, when all factors are given equal weight (Table 2.5, conditional factors), evidence for a distance/width relationship can only be shown for *C. ambiguus*. *Cymindis macularis* also approaches such a relationship. The species *C. erratus*, *M. arctica* and *H. servus* show an almost significant negative relationship with the distance to the Caitwickerzand. Accordingly, it is not appropriate to give the different factors equal weight, especially as vegetation structure seems to be less important than distance and width (Table 2.4).

Only *C. ambiguus* significantly reacts to distance and width, and it might be interesting to assess whether or not the occurrence of other species is related to that of its species and distribution. In this way it is possible to group species with the same kind of relation to the former drift sand area. These data are given in the correlation-matrix of Table 2.6. This matrix shows that stenotopic species can be divided into two groups: species which seem to react just as *C. ambiguus*, among them the most abundant species at the Caitwickerzand, and species which react oppositely. The first group can be distinguished by a positive correlation at the left side above of Table 2.6, the second group, consisting of *P. lepidus* and *A. equestris* only, by a negative correlation with the species on the left side. Only the stenotopic species *Masoreus wetterhalli* does not have a clear correlation with these two groups. With the exception of *C. erratus*, for the eurytopic species no distinct correlation with these 2 groups as well as to each other could be found.

Table 2.5. F-probabilities (F-pr) derived from Multiple regression analysis with the dependent variable ln(number of specimens per set of pitfall traps + 1) and independent variables distance, width & vegetation cover. Analysis with marginal factors is regression for each factor separately, analysis with conditional factors is regression with all three factors included.
- means a negative relation, + a positive one.

	marginal factors					conditional factors				
	distance		width		vegetation	distance		width		vegetation
	relation	F-pr	relation	F-pr	F-pr	relation	F-pr	relation	F-pr	F-pr
stenotopic										
C.ambiguus	-	<0.001	+	<0.001	0.578	-	0.040	+	<0.001	0.530
C.macularis	-	<0.001	+	0.004	0.455	-	0.057	+	0.076	0.901
M.arctica	-	0.005	+	0.318	0.496	-	0.055	+	0.950	0.840
H.servus	-	0.004	+	0.173	0.460	-	0.089	+	0.866	0.959
C.hybrida	-	0.155	+	0.472	0.173	-	0.576	+	0.775	0.307
O.rotundatus	-	0.049	+	0.167	0.075	+	0.889	+	0.105	0.096
M.wetterhalli	+	0.841	+	0.211	0.979	+	0.268	+	0.127	0.871
P.lepidus	+	0.005	-	0.056	0.196	+	0.257	-	0.249	0.439
A.equestris	+	0.002	-	0.027	0.035	+	0.321	-	0.065	0.080
eurytopic										
C.erratus	-	<0.001	+	0.035	0.129	-	0.066	+	0.132	0.250
C.fuscipes	-	0.744	+	0.387	0.988	+	0.972	+	0.544	0.997
C.micropterus	-	0.289	-	0.365	0.131	-	0.574	-	0.386	0.499
C.melanocephalus	+	0.344	+	0.946	0.765	+	0.522	+	0.630	0.935

Table 2.6. Correlation-matrix of the carabid species caught. For full names of the species see Figure 3.

	C.ambi	C.macu	M.arct	H.serv	C.hybr	O.rotu	M.wett	P.lepi	A.eque	C.erra	C.fusc	C.micr	C.mela
—stenotopic—													
C.ambi	1.0												
C.macu	+***	1.0											
M.arct	+*	+***	1.0										
H.serv	+*	+**	+**	1.0									
C.hybr	+**	+***	+*	+*	1.0								
O.rotu	+*	+*				1.0							
M.wett				+*			1.0						
P.lepi	-***	-**				-*		1.0					
A.eque	-**	-***	-*		-*	-**		+***	1.0				
--eurytopic--													
C.erra	+***	+***	+**	+**	+**	+*	+*	-*	-*	1.0			
C.fusc			+*								1.0		
C.micr			+*									1.0	
C.mela		-*			-*								1.0

* P<0.05; ** P<0.01 *** P<0.001; -negative relation; +postive relation

CONCLUSIONS & DISCUSSION

Roads are regarded as barriers for the dispersal of animals, including carabid beetles (Mader, 1979, 1984 & Mader et al., 1990). Many species seem to have difficulties in crossing them. When running through a natural area, a road will cut this in two separated, more or less from each other isolated, smaller pieces. From small isolated habitat patches a stenotopic species with low powers of dispersal can disappear more easily, as has been shown by de Vries & den Boer (1990) for the carabid species *A. ericeti*. By running through heathland fragments and cutting them in smaller pieces, roads could stimulate the extinction of species, which can only live in this type of habitat. As in the Netherlands many highways are intersecting these areas, an increasing number of extinctions can be expected, unless species are able to use the road-side verges as a corridor between intersected areas (Mader, 1987), as shown in Figure 2.4. In this way dispersal might help the fragmented populations to survive (Opdam, 1990). The results of this study show that carabid beetles, of which the occurrence is restricted to poor sandy, open habitats, do not avoid road-side verges with similar habitat characteristics. Almost all stenotopic species

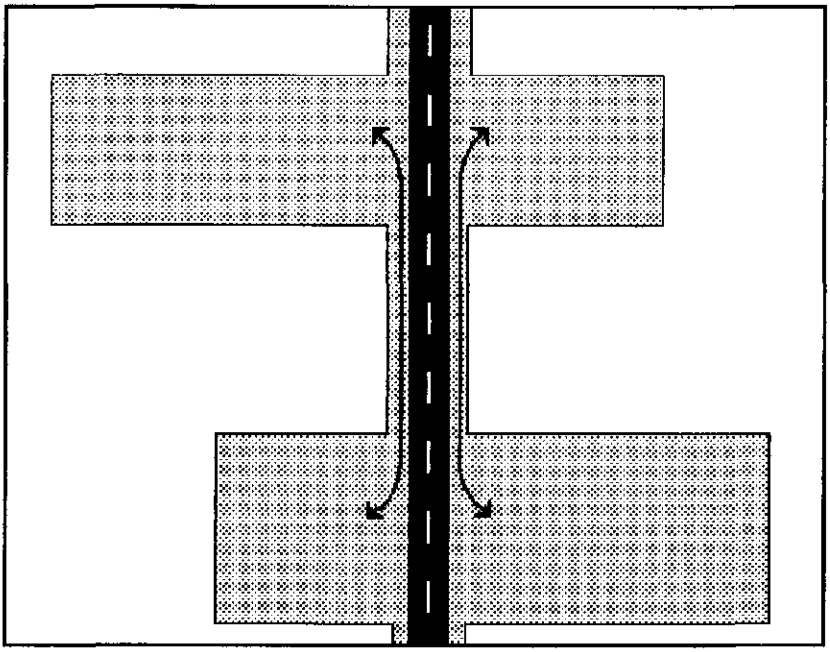


Figure 2.4. An example of a road intersecting two heathy fragments (dotted areas). Although the road is dividing the fragments in smaller pieces, a heathy road-side verge is forming a corridor along the road, connecting the pieces left after intersecting. Such road-side verges might be used by carabid beetles for exchange of individuals between fragments, through a hostile environment (white area).

caught at heathy fragments, adjacent to road-side verges, were also caught at the road-side verge itself (table 2.2). Most of them were even caught at the road-side verge at a distance of 100 meters and more from such an area, though the road-side verge was surrounded by an environment hostile for most of these animals. Among the species caught at the road-side verges were species commonly occurring in the Netherlands as well as the more rare ones (figure 2.3). Also more or less rare carabid species from other habitat types than the poor sandy, open habitat were caught at the road-side verges, by which these road-side verges become even more important from the point of view of nature conservation.

It remains to be studied whether or not these species had their origin in an adjacent poor sandy open area. The road-side verges in this study run from such an area through surroundings consisting of forest or agricultural field. Many species of poor sandy, open areas are regarded as bounded to these habitat types (Hopkins & Webb, 1984; Bauer, 1989; den Boer, 1990; Gardner, 1991; Turin et al., 1991), so it can be expected that they invade the road-side verge other adjacent habitats then the poor sandy, open habitat. The results of this study confirm that most of the species hardly occur in these other surroundings (table 2.2), although there are stenotopic species which are less restricted to the poor sandy, open habitat.

The importance of a connection between road-side verges and poor sandy, open areas for the occurrence of stenotopic species at the road-side verge is illustrated in table 2.3. On connected broad road-side verges not only the highest number of heath species were caught, but also the highest number of poorly dispersing species, as compared to all the other types of road-side verges. The latter species seem to need a continuous and wide poor sandy, open strip to be present at road-side verges over larger distances. They were lacking at connected narrow road-side verges, as well as at road-side verges with small heathy patches. As species with a high dispersal power were in equal numbers present both at narrow and at broad, connected road-side verges, dispersal capacity seems to limit the presence of species on narrow road-side verges. The necessity of connections is illustrated by the low numbers of stenotopic species of all dispersal categories, caught at broad but more or less isolated poor sandy, open road-side verges. Without such connections it seems impossible for many species to reach areas in which they usually occur.

In figure 2.3 it is shown that at certain distances from the poor sandy, open area along the road-side verge, some species are not caught any more, other species only incidentally, while others still increase in abundance. The correlation-matrix in table 2.4 suggests that, in most cases, distance to the poor sandy open area is the main factor for the stenotopic species, determining whether a species is present or absent on the road-side verge. The second factor seems to be width of the road-side verge. Remarkably, the species *P. lepidus* and *A. equestris* do show a reversed relation with these two factors: abundance increases at larger distances and at narrow sites of the road-side verge. A possible explanation is that although both carabid species do occur at the former drift sand area, they thrive better at sites where *Calluna vulgaris* is present. These sites are mainly found at larger distances from the former drift sand area (table 2.1 gives a positive correlation of *C. vulgaris* with distance).

Comparison of the tables 2.4 and 2.5 shows distance and/or width alone can not explain the occurrence of stenotopic species on the road-side verges. Still, they are the most important factors, which is supported when comparing to the more eurytopic species which, apart from *Calathus erratus*, do not show any relationship with these variables. *C. erratus* is mainly eurytopic because it occurs also at open arable fields (Turin et al., 1991), a type of habitat which was not included in the present study. Its distribution in the study area is dependent on the poor sandy, open habitat, and probably therefore it reacts like a stenotopic species.

By grouping stenotopic species on the road-side verge, two groups can be distinguished with different relations to the former drift sand area (table 2.6). The 6 species in the first group are more abundant at the former drift sand area than at the road-side verge. They may have their optimal habitat at the former drift sand area, and the road-side verge could be a more marginal habitat, especially at narrow places. It even could function as a kind of sink habitat (Pulliam, 1988), in which a species can only occur by a continued immigration from the former drift sand area. If we take into account that carabid beetles can move only a few hundred metres per year (Baars, 1979), the distribution of some species at the road-side verge indeed suggests such a situation (compare figure 2.3 the first two species). For the second group of 2 species the situation is quite different: they occur in higher numbers on the road-side verge than on the former drift sand area. Probably, before the road construction they lived at the former drift sand area. However, the road-side verge offered a type of habitat in which they can be more abundant. In this respect the former drift sand area was a more marginal habitat as compared to the road-side verge.

For both groups above-mentioned a road-side verge, as it is now, can function as a dispersal corridor from one to another poor sandy, open habitat fragment. However, for the first group the distance to cover over the road-side verge between such fragments can not be very long (probably only a few hundred metres). If we want them to colonize fragments along the road-side verge at greater distances, we have to create suitable reproduction sites at certain distances along the road-side verge. For hedgerow networks Burel (1989) mentioned the intersection of lanes, places in which the lanes are more wider, as places were forest species are more abundant and from which they can colonize connected hedgerows. For stenotopic species of poor sandy, open areas of the first mentioned group, this means widening of parts of the road-side verge, which is also suggested by the results of this study concerning the factor width of the road-side verge. If the road-side is only a strip which forces some species to disperse in a certain direction, without a connection to another suitable habitat, it can function as a kind of sink in which specimens disappear. In this respect Mader et al.(1990) can be right with their hypothesis that a network of linear infrastructure may adversely affect the rate of survival in metapopulations, by not only forming barriers between surrounding habitat patches, but also by guiding dispersal to wrong places. However, by using poor sandy, open strips along roads, which are already barriers, like heathy road-side verges, both as connections between poor sandy, open habitat fragments, and as reproduction habitats, such strips might contribute to the survival of poorly dispersing species in a metapopulation as mentioned by den Boer (1990). In this way road-side verges can help to maintain the enormous species diversity of arthropods, characteristic for poor sandy, open areas (Usher, 1992), also in small heathy fragments, where otherwise species will become extinct as a result of fragmentation (den Boer, 1990a).

According to Nève de Mévergnies and Baguette (1990) the more vulnerable species can be characterised as stenotopic, occurring at low density and having a small dispersal power. Such carabid beetles restricted to forest habitats probably became extinct already (see also Mabelis & van Velden, 1992) in most parts of the Netherlands. The fragmentation of the poor sandy, open areas occurred more recently so that it can be expected that in many fragments stenotopic species with low powers of dispersal will still be present. However, these species are highly endangered at the moment (Desender & Turin, 1989), and therefore this study was concentrated on stenotopic carabid species of poor sandy, open soils. Possibly, it is not yet too late to create suitable metapopulation structures for these species, which will enable them to survive in our cultivated landscape.

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Chapter 3

CORRIDOR FUNCTION OF A ROAD VERGE FOR DISPERSAL OF STENOTOPIC HEATHLAND GROUND BEETLES (CARABIDAE)

SUMMARY

To reduce the effects of habitat isolation dispersal corridors between habitat fragments are often proposed. In this study the corridor function of a poor sandy road side verge, adjacent to an open area of drift sand was investigated for ground-dwelling arthropods. Three species of carabid beetles characteristic of this habitat, Pterostichus lepidus, Harpalus servus *and* Cymindis macularis, *were marked and released at four different sites. Exchange of individuals of these species was recorded between the road verge and the open sandy area, and dispersal along the road verge was established. The rate of movement along the road verge was low compared to that in the open area. Sites with trees and narrow sites at the road verge had a barrier effect. Reproduction was recorded for two species at broad areas in the road verge. Under certain conditions (re)colonization of habitat areas by dispersal along a long, ribbon-like habitat might occur. For each species the specific features of such a corridor is discussed.*

INTRODUCTION

In the Netherlands, fragmentation of habitats is regarded as a threat to many species (Turin & den Boer, 1988, den Boer, 1990a, b, de Vries & den Boer, 1990, Opdam, 1990, Verboom & Van Apeldoorn, 1990, Mabelis & Van Velden, 1992, Van Apeldoorn, et al 1992). The Netherlands government has therefore developed a management programme for nature conservation (Anon., 1990) which proposes the establishment of a network structure between small and larger habitat fragments. Some local authorities already try to incorporate these ideas in their planning activities. One programme involves removing the top layer of soil and ceasing to use fertilizer in a farmland area so that it becomes more similar to adjacent heathland fragments. In two other plans, habitat corridors are proposed between patches of heathland or forest in a predominantly agricultural area. However, so far there is only weak and fragmented evidence on different kinds and sizes of corridors, their assumed function and the species supposed to benefit (Getz et al., 1978, Burel, 1989, Zerbe, 1989, Saunders & Hobbs, 1991, Hobbs, 1992, Petit, 1994, Vermeulen, 1994, Vermeulen & Opsteeg, 1994 and chapter 2). Stenotopic carabid beetles with low powers of dispersal that occur in heathlands and poor grasslands are among the organisms which might benefit from such connections between habitat patches (den Boer, 1977, 1990b, Turin & den Boer, 1988, de Vries & den Boer, 1990).

Road verges in the eastern part of the Netherlands are often heathy, and their ribbon-like character suggests that they might function as dispersal corridors. The aim of this study was to find out how effectively carabid beetles disperse along such a narrow sandy corridor bordered by unfavourable habitats, and to compare their movements there with those in a more open area. The exchange of individuals between these two areas was also studied, and the effects of different kinds of vegetation in the corridor.

METHODS

Study area and species

In 1989 the composition of the carabid fauna was examined in several heathy road verges in the north-eastern part of the Netherlands (chapter 2), and one, along the highway A1, and an adjoining area, Caitwickerzand, were selected for further study. They were mainly covered by a sparse Corynephoretum vegetation and connected by a belt of similar habitat with a few *Pinus* trees (fig. 3.1). Three carabid species, *Pterostichus lepidus*, *Harpalus servus* and *Cymindis macularis*, occurring in quite high numbers in the Caitwickerzand area, are regarded as characteristic of poor sandy and open areas (Turin *et al.*, 1991) and were selected for study. All three species are also caught at the road verge, at least where the road verge was connected to the Caitwickerzand. Previous studies (Vermeulen & Veenbaas, 1991 and chapter 2) had shown that these three species were not present in the surrounding forest habitat, and avoid moving into this habitat (Vermeulen, 1994). *P. lepidus* and *C. macularis* are monomorphic brachypterous species (den Boer, 1977) and therefore unable to fly. *H. servus* was only seen making short flights (< 1 m) during this study so that dispersal of this species probably also takes place mainly by walking.

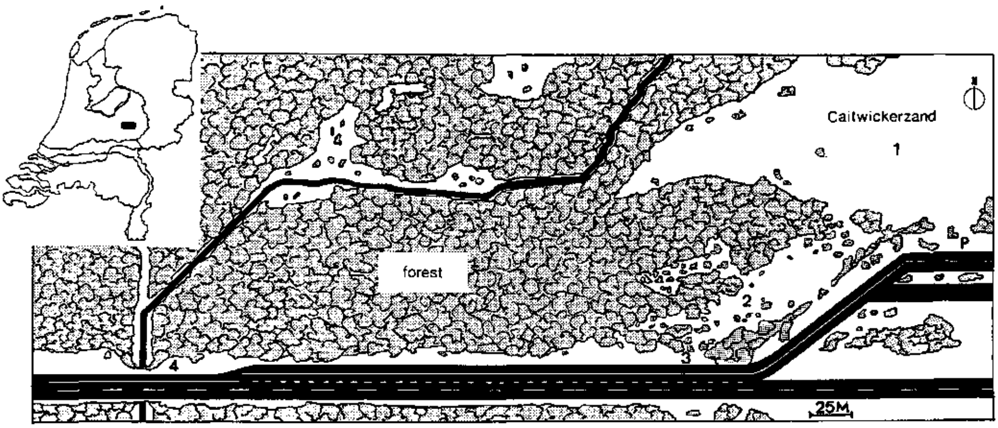

Figure 3.1. Location of the study area Caitwickerzand in the Netherlands showing the four release points at this former drift sand area and the adjacent roadside verge of the A1 highway. 'P' is the parking place; the cycle underpass is situated near point 4.

Marking and recapture of beetles

In 1990, from April until the end of September, the three species were recorded from pitfall traps (sunken plastic cups) at the Caitwickerzand and the road verge. Sites where reproduction had occurred were recognized by the presence of recently emerged (teneral) adults. All *H. servus* and *C. macularis* except the teneral individuals were marked to recognize groups from the same release date and point (Schøtz-Christensen, 1965); *P. lepidus* were marked with an individual code (van Huizen, 1980). They were released in small groups at four different points (fig. 3.1), in a small hole with some litter to prevent them from walking away immediately.

Release point 1: At the centre of the open Caitwickerzand area, situated at about 250 m from the road, near a parking place, and more than 50 m from the surrounding forest. Dispersal from this release point was supposed not to be affected by structures directing their movements and therefore represents the control for dispersal along the road verge.

Release point 2: About 55 m from the road (fig. 3.1), where the Corynephoretum strip was about 15 - 20 m wide. The composition of the carabid fauna here was approximately the same as in the middle of the Caitwickerzand, with the addition of some species from the surrounding forest.

Release point 3: 5 m from the road, where the verge was connected to the drift sand area and where the Corynephoretum strip was about 8 m wide.

Release point 4: On the road verge at a distance of 350 m from point 3 and 5 m from the road, where the Corynephoretum strip was only 3 m wide. Ten metres further west there was a cycle underpass where the verge narrowed to 2 m and was covered only by dense grass.

To increase the number of recaptures, most pitfall traps were placed in groups of four at the two ends of a metal barrier 1 m long around all these release points. Recaptured beetles were recorded and released again 2 m from these "barrier traps", which were checked every two days.

Barrier traps were placed at each release point in the following arrangement:

Release point 1: four, eight, 12 and 16 barrier traps at distances of 12.5, 25, 37.5 and 50 m respectively (see fig. 3.3), and a further six and eight barrier traps at distances of 75 and 100 m respectively in the direction of the highway.

Release point 2: seven barrier traps at 12.5 m and a further three traps were placed at intervals of 12.5 m in the direction of the road verge (see fig. 3.4), two on the edges of the Corynephoretum strip and one in the middle.

Release point 3: sets of three barrier traps were placed at distances of 12.5 m, 25 m, 50 m, 100 m, 200 m, 300 m and 325 m along the road verge. Those at 325 m were 25 m from release point 4. Single barrier traps were placed at 150 and 250 m. Single pitfall traps were also placed at the same intervals close beside the edge of the asphalt, to see if this directed beetle movements.

Release point 4: one barrier trap and two single pitfall traps at the road verge at a distance of 12.5 m, in the middle of the cycle underpass. Three barrier traps were also placed 12.5 m beyond the cycle track to catch any marked beetles that might pass this obstacle.

Because of low catches, *C. macularis* were only released at release point 3, where it was possible for the beetles to move in two directions, towards the open Caitwickerzand and along the road verge. The other species were released at all four release points.

To catch beetles that crossed the 20 m wide asphalt road, a barrier trap spanning 4 m, was placed on the other verge opposite release point 3.

All pitfall traps were removed in October 1990 and replaced in the same positions in mid April 1991, but only along the road verge with addition of a trap at a narrow site at 120 m and five in the adjacent forest. To assess the possible role of trees as barriers in the corridor between the verge and the open area a 15 m barrier was installed at the most wooded site in 1991, between release points 2 and 3 (see fig. 3.1). Pitfall traps were placed on both sides of the barrier in open sites and in sites under the tree canopy.

RESULTS

Distribution of the species

The distribution of the three species in the traps in the more or less homogeneous Caitwickerzand area did not indicate a significant preference for a particular area. Teneral individuals of *C. macularis* and *H. servus* were caught in almost every pitfall trap, with over 20 individuals of *H. servus* per trap in one year. Relatively few teneral individuals of these two species were caught in the road verge (fig. 3.2) so the former can be regarded as a better reproduction site. By contrast, the highest numbers of adult and teneral individuals of *P. lepidus* were caught in the broader parts of the road verge, especially at a distance of about 3-4 m from the road, and no teneral individuals were recorded near the Caitwickerzand. The homogeneous distribution of individuals in this open area suggests that immigration from other areas is unlikely. It is therefore probably a permanent, though marginal, habitat for this species too.

Table 3.1. The number of unmarked beetles caught inside enclosures of 50 m² in 1991 at the Caitwickerzand and at 400 m from the Caitwickerzand on the road verge. The third column gives the number of 10 x 10 km cells (from the 391 cells sampled) in which the species is recorded in the Netherlands since 1975 (data from the Dutch Carabidological Association).

	Caitwickerzand	road verge	number of 10 x 10 km cells in The Netherlands
Harpalus servus	148	8	26
Cymindis macularis	32	0	11
Pterostichus lepidus	1	19	61

The absolute densities of the three species in 50 m² enclosures in 1991 (table 3.1), at the Caitwickerzand and at the road verge at a distance of about 400 m from this area, confirm the pattern described for 1990.

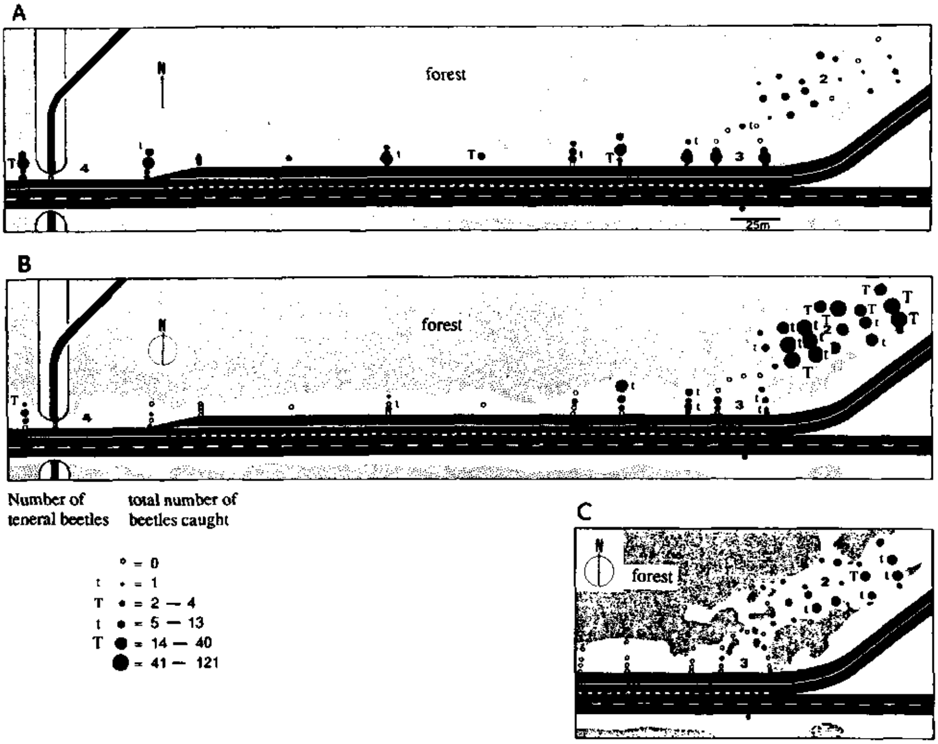

Figure 3.2. The distribution of the unmarked catches of (A) *Pterostichus lepidus*, (B) *Harpalus servus* and (C) *Cymindis macularis* on the road verge. Total numbers of beetles and of teneral individuals are shown in the key. 2, 3 and 4, release points for marked beetles.

Movement of marked beetles

Figures 3.3, 3.4, and 3.5 show the recaptures of the three carabid species, released at the first three points. The percentage figures show where the highest recaptures occurred; further calculations are based on the numbers of individuals recaptured.

Recaptures of *H. servus* and *P. lepidus* around site 1 (fig. 3.3) in the Caitwickerzand were divided among four quadrants (north, east, south, west), each containing equal numbers of traps at each distance. A chi-squared test on the figures (Batschelet, 1981) showed that the distribution of beetles did not differ from random ($p > 0.1$) in the middle of this open area. This was supported by the equal distribution of unmarked beetles over 40 traps in this area.

Few individuals of *H. servus* and *P. lepidus* were capable of reaching the road verge from release point 2, even though there were few trees and bushes in between (fig. 3.4). However, individuals of all three species moved from the road verge to beyond point 2 (fig. 3.5). Thus, some exchange of individuals between the Caitwickerzand and the road verge was possible. None of the 1552 individuals of the three species released at point 3 was caught by the large barrier trap on the other side of the road, 25 m away. By comparison, 17 recaptures were recorded at the same distance along the road verge, within 3 m of barrier traps. This demonstrates that a road can provide a barrier to dispersal, as found by Mader (1984).

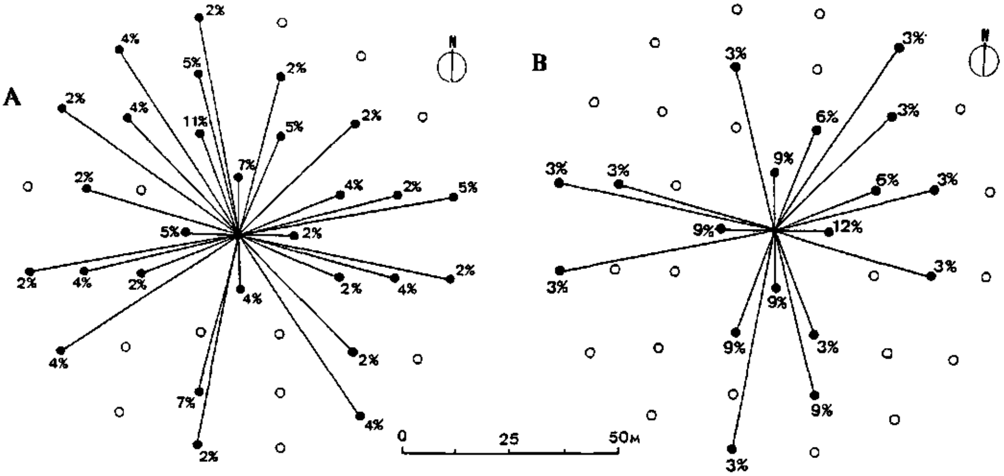

Figure 3.3. The distribution of the recaptures (A) *P. lepidus* and (B) *H. servus* in 1990 at the Caitwickerzand around release point 1, expressed as percentage of the total number recaptured. Sixty-one of the 237 marked individuals of *P. lepidus* and 37 of the 690 marked individuals of *H. servus* were recaptured. The open circles represent traps in which no specimens were recaptured.

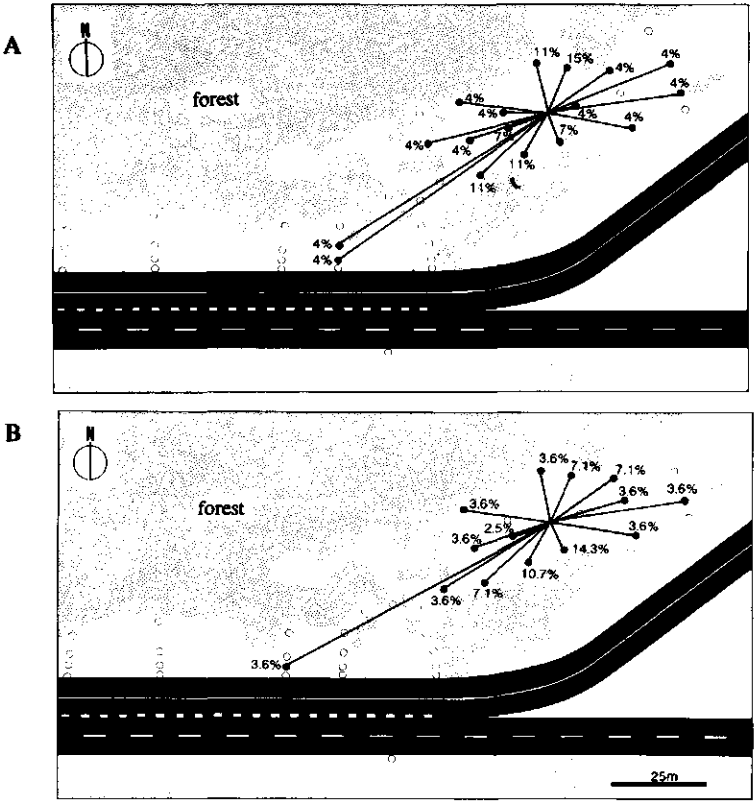

Figure 3.4. The distribution of the recaptures of (A) *P. lepidus* and (B) *H. servus* in 1990 around release point 2, in the heathy area connecting the Caitwickerzand with the road verge, expressed as percentages of the total numbers recaptured. Twenty-seven of the 60 marked individuals of *P. lepidus* and 28 of the 500 marked individuals of *H. servus* were recaptured. The open circles represent traps in which no specimens were recaptured.

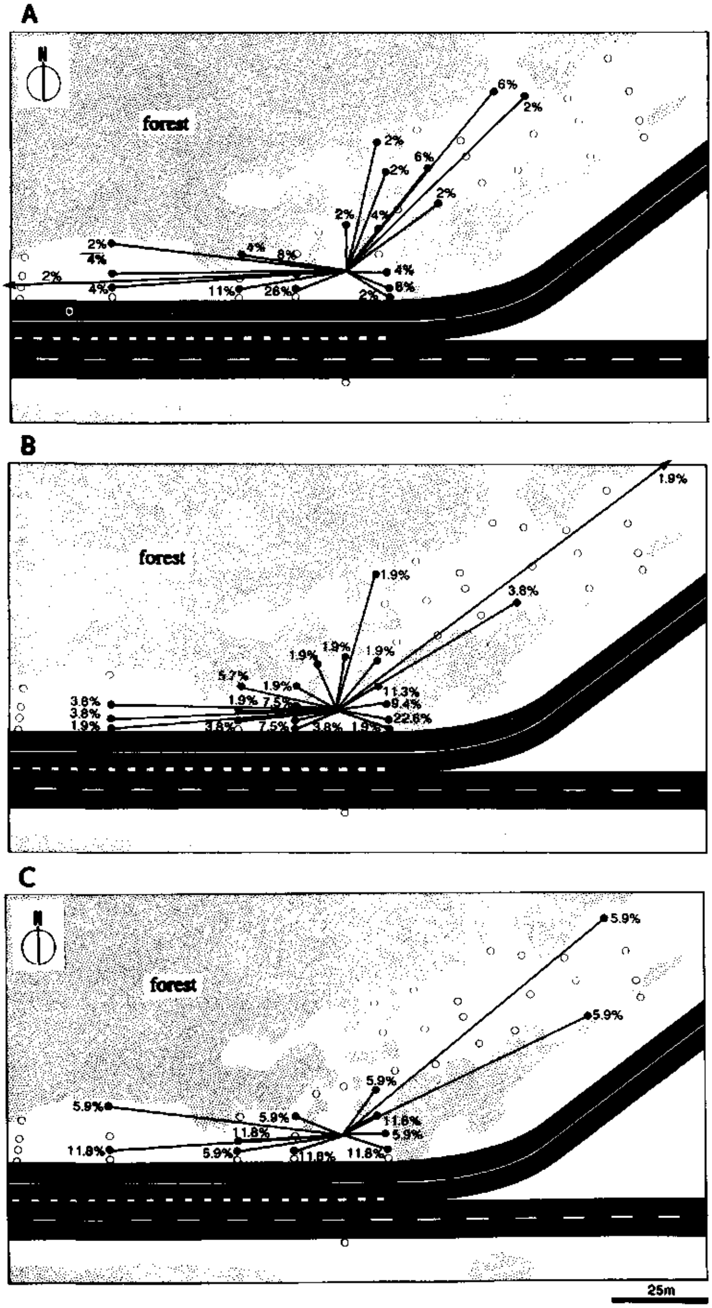

Figure 3.5. The distribution of the recaptures of (A) *P. lepidus*, (B) *H. servus* and (C) *C. macularis* in 1990 around release point 3 at the road verge, expressed as percentages of the total numbers recaptured. Fifty-three of the 200 marked individuals of *P. lepidus*, 53 of the 1000 marked individuals of *H. servus* and 17 of 275 marked individuals of *C. macularis* were recaptured at this site. The open circles represent traps in which no specimens were recaptured.

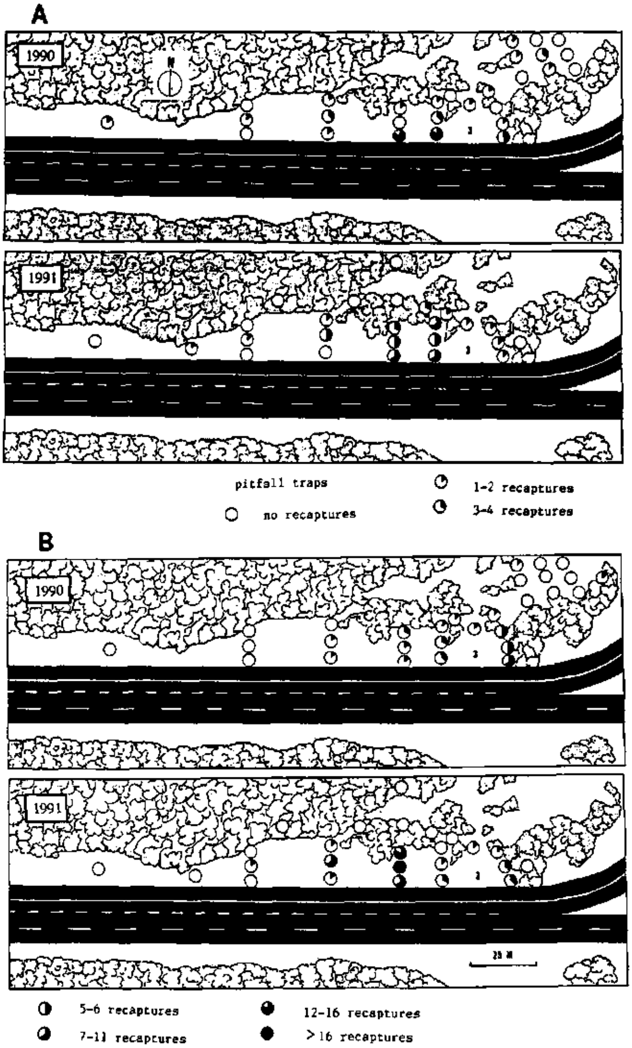

Figure 3.6. The distribution of the recaptures of (A) *P. lepidus* and (B) *H. servus* in 1990 and in 1991 along the road verge and the connection with the Caitwickerzand. The circles show the positions of the barrier traps and the numbers of recaptures. 3 = release point for marked beetles in 1990.

Some marked individuals of *P. lepidus*, released in 1990 at point 3, were recaptured in both 1990 and 1991. The mean recapture distance in a westerly direction along the verge was 26.5 m in 1990 and 27.2 m in 1991, though in both years one individual was caught at more than 100 m away (fig. 3.6).

A similar figure for *H. servus* (fig. 3.6) shows that most recaptures in 1990 were located 12.5 m from the release point. One year later, most recaptures were at 25 and 50 m and one marked individual was caught at a distance of 100 m. It is striking that more recaptures were made in 1991 than in 1990; in one barrier trap 52 recaptures were recorded (solid black circle in fig. 3.6). The mean recapture distance in a westerly direction was 24.4 m in 1990 and 28.4 m in 1991.

No recaptures of *C. macularis* released in 1990 were made in 1991. This species completely disappeared from the road verge. Only two unmarked individuals were caught, close to the Caitwickerzand.

Movements along the road verge

Most individuals did not disperse along the road verge more than 50 m in one season (fig. 3.5). In the case of *P. lepidus*, the largest of the three species, two individuals were recaptured at a distance of 150 m from release points 3 (fig. 3.5) and 4 (fig. 3.9) respectively. As *P. lepidus* can survive for two years, some direct exchange between release points 3 and 4 may take place, as well as indirect exchange by reproduction in this zone (fig. 3.2a).

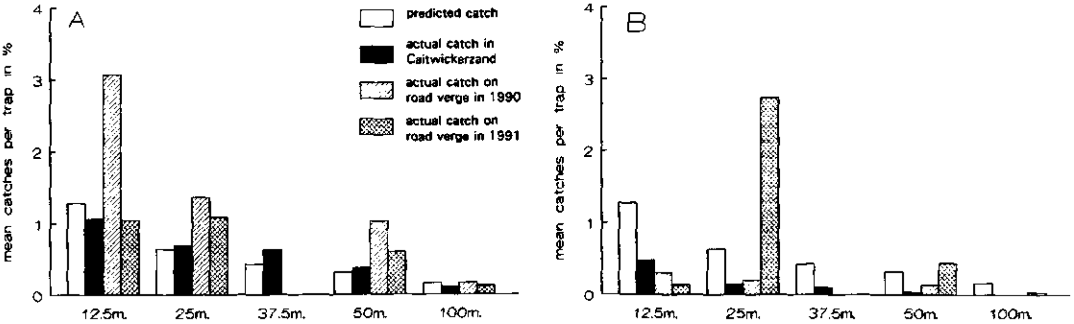

Figure 3.7. The numbers of recaptures per barrier trap at different distances from the release points and for different areas for *P. lepidus* (A) and *H. servus* (B) respectively, expressed as a percentage of the numbers released. The "predicted catch" is that produced by a barrier of 1 m. if beetles move by random diffusion. The "actual catch in Caitwickerzand" is the recaptures in the Caitwickerzand from release point 1, the "actual catch on road verge in 1990/1991" those on the road verge of the A1 in the west direction from release point 3 in 1990 and 1991 respectively.

In the open Caitwickerzand area, recaptures of both *P. lepidus* and *H. servus* declined with distance from the release point, as would be expected by random diffusion (fig. 3.7, black columns); the actual numbers of *P. lepidus* closely matched predicted values up to 100 m. However, recaptures of *H. servus* were significantly lower than predicted at all distances from 12.5 to 100 m ($p < 0.05$, paired comparison t-test, Sokal & Rohlf, 1981). This indicates that many beetles avoided the traps or moved less than 12.5 m.

In the road verge corridor *P. lepidus* was recaptured more frequently in 1990 than at the Caitwickerzand at all distances up to 50 m ($p < 0.05$, paired comparison t-test), though the distribution did not differ significantly. At 100 m *P. lepidus* was caught in about the numbers expected with random diffusion. In 1991, there were fewer recaptures of *P. lepidus* and the distribution was also more homogeneous.

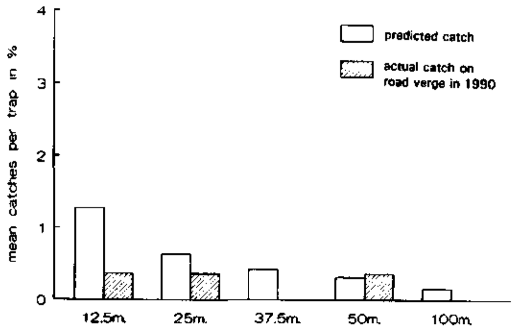

Figure 3.8. The numbers of recaptures of *C. macularis* (actual catch on road verge 1990) per trap at different distances from release point 3 in 1990 at the road-side verge of the A1 in the west direction, expressed as a percentage of the numbers released. The "predicted catch" is that produced by a barrier of 1 m. if beetles move by random diffusion.

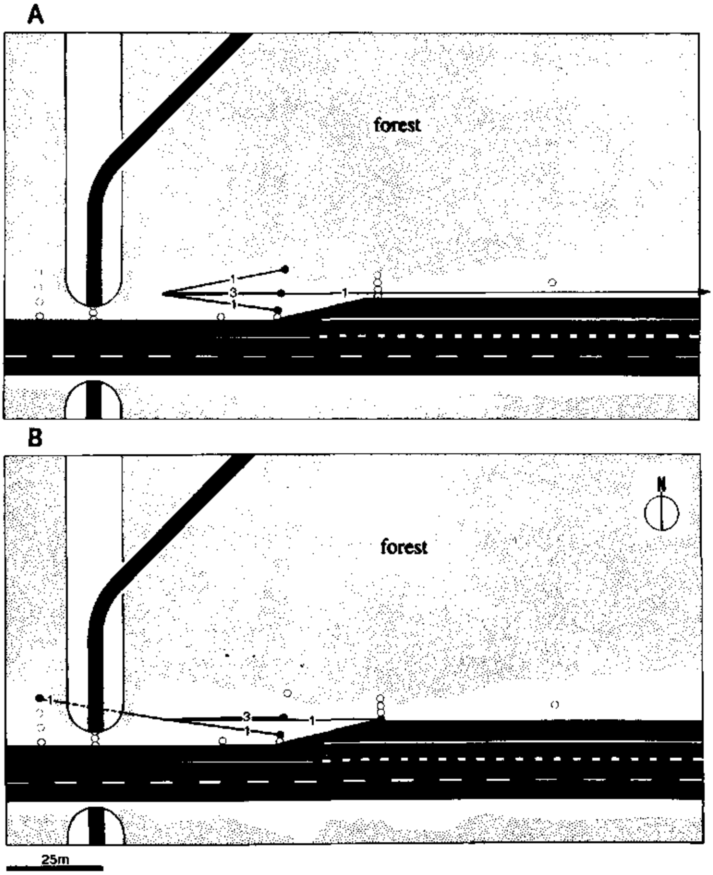

Figure 3.9. The distribution of the recaptures of (A) *P. lepidus* and (B) *H. servus* in 1990 at road verge of A1 near the Caitwickerzand (release point 4). On the west side of the release point a cycle track passes under the highway, and the road verge is only 2 m wide. Seventy-seven marked individuals of *P. lepidus* and 500 marked individuals of *H. servus* were released at this point. The open circles represent traps in which no specimens were recaptured.

The total numbers of *H. servus* recaptured at the road verge in 1990 and at the Caitwickerzand did not differ significantly, but the numbers gradually decreased with distance in the open area, and hardly declined in the corridor up to 50 m ($p < 0.05$, Fig. 3.7b).

In 1991, recaptures of *H. servus* on the road verge showed a significant spread of individuals ($p < 0.01$) notable at 25 m, and a first recapture at 100 m (Fig. 3.7).

Figure 3.8 shows similar results obtained for *C. macularis*. Because this species was only released at the road verge, comparison with an open area is not possible. Neither the numbers recaptured nor the distribution differed significantly from the predicted catch. All recaptures were made within a few days after release, so the beetles moved relatively fast compared to the other two species.

Rate of movement

Rates of linear movement from release points could be estimated for individually marked *P. lepidus*. The highest rate of 3.08 m/day ($n=58$) was in the open drift sand area (from release point 1). Near and at the road verge it moved faster in the broad open sites (release point 2: 2.57 m/day, $n=21$, and release point 3: 2.85 m/day, $n=33$) than in narrower, more grassy sites (release point 4: 2.05 m/day, $n=6$). The difference between rates at points 1 and 4 was significant ($p < 0.05$, t-test, Nijdam & van Buren, 1983). The slowest rate of linear movement was recorded between points 2 and 3 (1.21 m/day, $n=7$), which may be attributable to the presence of scattered trees.

Barriers in a corridor

In 1990 not a single individual of *P. lepidus* released at point 4 was caught in the dense grass section of the verge near the cycle underpass or beyond this point (fig. 3.9). At the east side of release point 4 such narrow sites were absent, and 5 marked individuals were caught at 25 m. Recaptures at this distance were almost twice as high as those at release point 3, situated at the road verge where beetles can move in two directions (fig. 3.10). This suggests that most beetles moved in one direction only. In 1991 one marked individual was caught at the other side of the underpass, at a distance of about 100 m from release point 4. An interruption of the poor sandy strip thus seems to cause dispersal problems for *P. lepidus*.

H. servus also showed reduced westward movement from point 4 (fig. 3.9b). The avoidance by this species of dense grass vegetation, such as that of the verge above the underpass, was noted earlier by Vermeulen (1994). As some specimens have been seen in flight, this individual might have flown over the underpass.

Table 3.2 shows the numbers of four heathland ground beetles caught in 1991 between release points 2 and 3. These species clearly favour open areas and avoid the shade of trees, even at this small scale. Three stenotopic species, *C. macularis*, *Calathus ambiguus* and *Harpalus neglectus*, which were found in quite high numbers between points 2 and 1, in the connecting strip to the drift sand area, were not caught in this site at all. Catches of *Pterostichus oblongopunctatus*, a forest species of about the same size show the reverse pattern (table 3.2, below). These results suggest that trees can be obstacles to dispersal of open-area species along a corridor, and if this site was completely covered by trees the exchange of individuals of open area species between the road verge and the drift sand area would be greatly reduced.

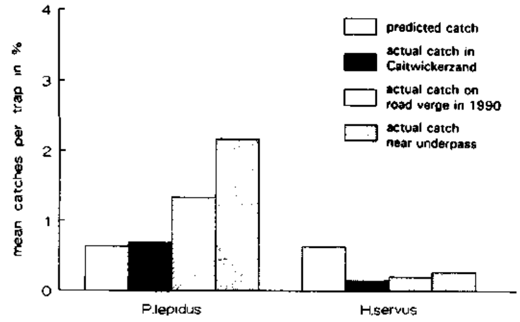

Figure 3.10. The numbers of recaptures of *P. lepidus* and *H. servus* per trap at a distance of 25 meters from a release point expressed for different areas as a percentage of the numbers released. The "predicted catch" is that produced by a barrier of 1 m. if beetles move by random diffusion. The "actual catch in Caitwickerzand" are the recaptures in the Caitwickerzand from release point 1, the "actual catch on road verge in 1990" those on the road verge of the A1 to the west of release point 3 in 1990, and "actual catch near underpass" those from release point 4 in easterly direction.

Table 3.2. The numbers of unmarked individuals of all heathland species caught at the barrier between release points 2 and 3, close to release point 3 (see fig. 3.1). Catches of a forest species of the same size are given for comparison.

species	open sites	under trees
heathland		
Harpalus anxius	15	2
Amara equestris	6	2
Pterostichus lepidus	9	4
Harpalus servus	11	7
forest		
Pterostichus oblongopunctatus	25	45

DISCUSSION

Dispersal along a corridor

Beetles walking in a corridor are forced to move mainly in two directions. One therefore expects that recaptures in the corridor will be higher and more constant at different distances within their walking range, as compared to a situation in which they can walk in any direction. Conversely, recaptures over different distances in a corridor, compared to those in an open area, may indicate whether or not a certain species will disperse along the corridor.

Results of this study indicate that the species studied tend to stay in the presumed road verge corridor. However, the distances covered at the road verge were not as long as that found by Baars (1979) in his study of an equal-sized carabid beetle with a comparable activity period in a heathland (mean distance covered per season for *Pterostichus versicolor* 160 m). The beetles probably move in any direction, and as soon as they reach a less preferable habitat they change direction randomly, resulting in a decrease of movements along the corridor. This will happen more often at a narrow passage and therefore the reduction in linear distance covered will be even greater. These expectations were confirmed by simulation experiments in which such random walking patterns were introduced (Vermeulen & Opsteeg, 1994). If the corridor is shaded by trees the suitability of the habitat is reduced. Grüm (1971 a, b) concluded that mobility of the beetles increased at the edge of the habitat. In this study, however, the rate of movement decreased at such places. This may be caused by the Raumwiderstand (the resistance of the environment, Heydemann, 1957). For small species of non-forest areas, litter in the soil could also be an obstacle.

Corridor function of the road verge

Corridors are thought to connect habitat areas in such a way that individuals can move from one habitat area to another, allowing recolonization of areas where local populations became extinct, forming a metapopulation structure (Opdam, 1990). However, the results presented in this study show that heathland carabid beetles only move short distances (50 - 150 m) a year in a corridor. It therefore seems necessary that habitat areas connected by road verges should not be separated by more than 100 m, unless the road verge itself can function as a kind of breeding area.

For *P. lepidus* the verge did indeed allow breeding in the broader areas, and it was present along the entire verge (fig. 3.2a). Movements of individuals along the verge are sufficient (figs 3.5 and 3.9) to allow exchange between the broader sites. In this species larger habitat areas could be connected over at least 400 m by such a corridor system. A similar picture was seen in the case of *Abax ater* (Burel, 1989, Petit, 1994) using hedgerows with broad nodes.

Individuals of *H. servus* were shown to cover distances of over 100 m in two years, but the numbers collected along the road verge gradually decreased with the distance from the drift sand area. The subpopulations on the road verge can probably only survive because of continuous immigration of individuals from the Caitwickerzand. For this species the road verge therefore acts as a sink habitat (Pulliam, 1988), and at larger distances than studied here (± 400 m) it can be expected that the species would disappear from the road verge. If larger habitat nodes were created at intervals of about 0.5 km, the verge might function as a corridor system between habitat areas.

The road verge was evidently quite unsuitable as a habitat for *C. macularis*. This species was only found in small numbers on the road verge close to the Caitwickerzand, indicating modest incursions towards the road verge. Some individuals released on the road verge were able to cover a distance of 50 m in a short time, but the species disappeared with larger distances. Baars (1979) observed quickly moving beetles in what he presumed to be unfavourable habitats. Thirty-two individuals of this species were released in 1991 in an enclosure of 16 m^2, placed at a broad Corynephoretum site at the road verge. In 1992 no recaptures were made, of either marked or unmarked new beetles. It may be concluded that the road verge functions as a sink for this species too, and Mader *et al.* (1990) are right in thinking that corridors can increase chances of the extinction of local populations. If such a road verge is to function as a dispersal corridor for *C. macularis*, sufficiently large habitat areas would have to be created at close intervals.

Establishing corridors

If connected to several heathy areas, corridors such as the road verge studied could diminish the risk of complete extinction of a species in a region (den Boer, 1968). At the moment such conditions do not exist in the Netherlands, but there are proposals to create them. This study shows that not all animals of poor sandy open habitats share the same needs in such a corridor. Simply establishing a heathy strip between heathy areas would probably only benefit a few less demanding and less rare species.

From this study it appears that *P. lepidus* is already favoured by the road verge. With the addition of broader areas mentioned above *H. servus* could also benefit. According to the data base of the Dutch Carabidological Association none of the three species is now really common in the Netherlands, but *P. lepidus* is the most widespread (table 3.1) and *C. macularis* the rarest. From the point of view of nature conservation, it would be advisable to establish a corridor from which *C. macularis* could also benefit, which would probably also be suitable for the two other species. Nature conservation organizations should therefore consider which species they want to favour by a corridor and find out which other species would also benefit.

Though this study makes the existence of a corridor function more plausible, a long-term study is needed to find out the real effect of such a structure.

Acknowledgements

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Chapter 4

DISPERSAL MOVEMENTS OF CARABID BEETLES IN AND AROUND A CORRIDOR

SUMMARY

Both walking direction and rate of movement in a corridor structure were studied for 8 species of carabid beetles (Coleoptera: Carabidae) with different habitat preferences. The corridor, a poor sandy road-side verge, was bordered by several linear strips of a different vegetation. The central strip was mainly comprised of a Corynephoretum *vegetation. Beetle movements were monitored by pitfall traps within enclosures, placed in the centre and edges of the road verge and in the centre of an adjoining area of drift sand consisting of a similar vegetation to the central strip of the road verge. Within the enclosures, stenotopic carabids of poor, sandy and open habitats, walked out of and away from forest habitats. They also avoided dense grass vegetation. These beetles preferred the* Corynephoretum*-strip at the road verge. The walking directions exhibited by the forest carabids were the reverse of these, i.e. towards the forest. The time necessary to walk 4 m., the radius of the enclosures used, was highly variable within and between species. All carabids tested walked most slowly in dense grass vegetations. Beetles, stenotopic for poor, sandy and open habitats, usually also walked more slowly in forests. It is discussed that road verges as a corridor structure can enhance survival of stenotopic carabid species of poor, sandy and open habitats in heathland/forest mosaics.*

INTRODUCTION

In the Netherlands, in the first part of this century, cultivation and afforestation of drift sands, heathlands and poor grasslands led to an enormous reduction and fragmentation of these areas, from 600,000 hectares in 1833 to 40,000 hectares in 1963. Most of the fragments left are considered to be too small to support populations of ground-dwelling arthropods on the long term (den Boer 1977, 1985, 1990a, 1990b, 1990c, Hopkins & Webb 1984). The disappearance of populations of the carabid beetle *Agonum ericeti* Panzer from small fragments of peat moor (De Vries & den Boer 1991) is an example of this phenomenon. As one of the possibilities to stop and even reverse this process, the Dutch government, advised by nature management organizations (Anonymous, 1990), decided to establish a network of suitable habitat patches, in which local populations can survive in a metapopulation structure. (Levins, 1970, den Boer 1990c, Opdam 1991). In such a network exchange of individuals between these suitable habitat patches is essential. However, small stenotopic species are hardly found outside their habitat (den Boer 1977; Rijnsdorp 1980; van Dijk, 1986, Bauer, 1989, Turin *et al.*, 1991), and if ever, they are probably unable to survive in and disperse through these areas. Therefore, a habitat bridge or dispersal corridor between isolated habitat fragments is required, especially for species that disperse only by walking. Many local nature management plans in the Netherlands already incorporate dispersal corridors, despite the debate over the effectiveness of such structures as dispersal routes for wildlife (Saunders & Hobbs, 1991, Hobbs, 1992). For instance, Mader (1984) and Mader *et al.*, (1990) suggested that such corridors will function as a sink in which individuals enter and disappear. Of course, suitable corridors which end in unsuitable habitats may increase the extinction rate of species. Therefore, a corridor should lead from one suitable habitat patch to another. An open question is whether or not an animal will follow the corridor. Research in Germany on the behaviour of the eurytopic carabid beetles *Pterostichus versicolor* Sturm and *Pterostichus cupreus* Linnaeus (Zerbe, 1989) showed that movements of the beetles were not restricted to a grass strip corridor but extended into the surroundings. This study also showed that activity and density of the beetles were less within the corridor than in the habitat patches connected by it. Stenotopic species have a rather narrowly defined habitat range. When they are not able to survive outside that habitat, dispersal into the surroundings of a corridor would mean a loss of individuals for such species.

Stenotopic carabid beetles of heathlands with a low dispersal power are regarded as one of the most vulnerable groups to heathland fragmentation (De Vries, 1994). These arthropods appear to be present in sandy verges along highways in the Netherlands (chapter 2). Therefore, when situated between heathland fragments, those road verges may function as dispersal corridors for such species.

Poor sandy road verges consist of several longitudinal strips, in which the central strip is poor and sandy. From this strip towards the borders the vegetation is gradually affected by the adjacent area, so there is no clear hard border. Although it is known that certain forest carabids from some distance orientate towards a forest border and some field-inhabiting species react oppositely (Neumann, 1971, Rijnsdorp, 1980, Wallin, 1986), little is known about the reactions of stenotopic carabids from poor, sandy and open habitats when reaching the edge of a habitat patch. When they continue their random pattern of movement (Baars, 1979) at soft borders of their habitat they have a high chance of entering the wrong kind of habitat. Furthermore, it is not known whether or not these carabids can find their way back when having entered an inadequate habitat. As ribbon-like structures, road verges have a very long border with adjacent areas. If carabid beetles were not to be deflected by this border, the road verge would act as a sink instead of a dispersal corridor.

In this chapter I will try to examine whether or not densities of certain carabid species are affected by the corridor structure of the road verge and how this can be explained in terms of losses to adjacent areas or habitat quality. Furthermore I will investigate the influence of adjacent habitats of another kind on the dispersal in such a structure. How quickly can they move in the different road verge strips compared to their rate of movement in a habitat area? By extrapolation of these results we might get a better idea about the functioning of corridors and their essential properties for small ground-dwelling arthropods.

METHODS

Study area and vegetation

The study was carried out in 1991 at Caitwickerzand and the adjoining road verges of the highway A1, in the central eastern part of The Netherlands (Fig. 4.1.). Caitwickerzand is a former drift sand area, and now is mainly covered by a vegetation dominated by tussocks of the grass *Corynephorus canescens* L., dry mosses and lichens (*Corynephoretum*). At the northern road verge, which is connected to this area, a continuous *Corynephoretum* strip, varying in width, is present.

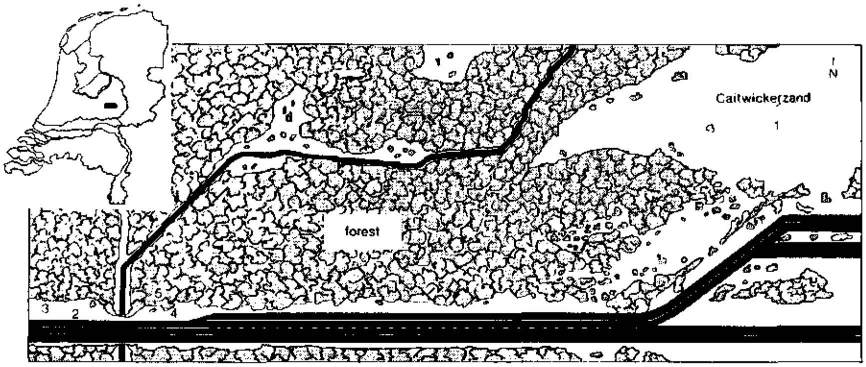

Figure 4.1. Location of the enclosures (1 - 5) at Caitwickerzand and the adjoining road-side verges of the highway A1. The black rectangle on the map of The Netherlands shows the location of the study area.

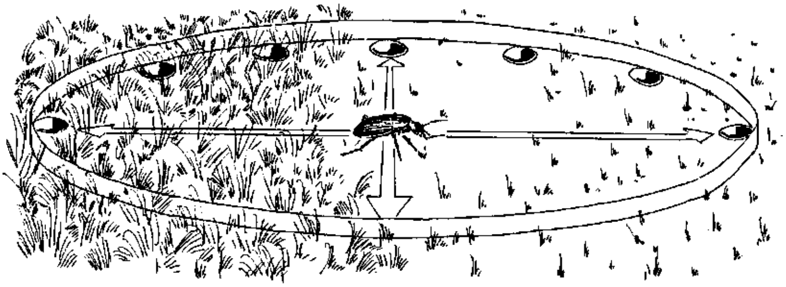

Figure 4.2. Schematic drawing of an enclosure with a radius of 4 m. Marked beetles were released in the centre and could walk in any direction. Twelve pitfall traps, equally distributed along the inside of the fence, were used to determine preferred direction and rate of movement.

Five circles of polyester plate were dug 20 cm into the soil, forming a closed fence of 20 cm high above the soil (Fig. 4.2.). The enclosures had a diameter of 8 m. At the inside of each fence 12 pitfall traps were placed at equal distances and closely fitting the fence.

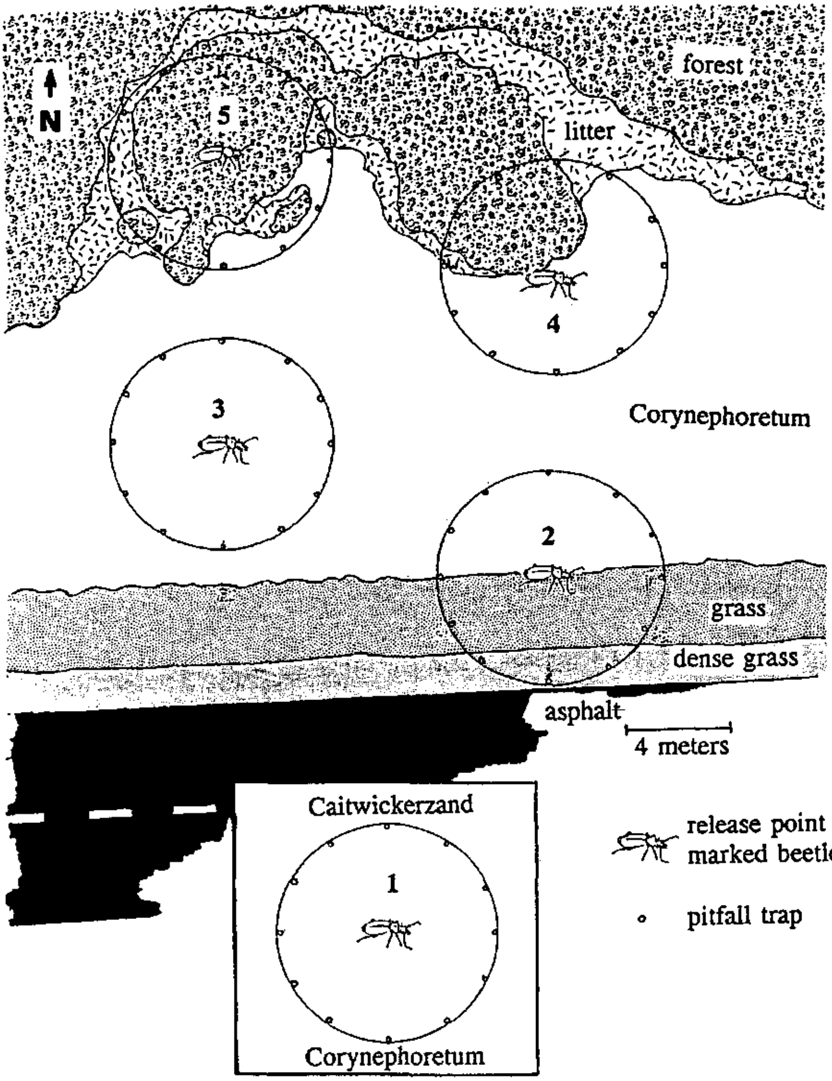

Figure 4.3. Schematic picture of the vegetations in which the enclosures were placed. Though put together in this picture, the enclosures 2 and 3 were placed 50 meters east from the enclosures 4 and 5 at the road-side verge (see fig. 4.1.). The enclosure at Caitwickerzand (1, below) was placed at about 400 m. from the others.

The enclosures, except number 1, were placed nearby or at the borders of different vegetations, according to the following scheme (Fig. 4.1 and Fig. 4.3.):

1. At the centre of Caitwickerzand. Inside this enclosure a homogenous *Corynephoretum* vegetation was present. Very few grass species other than *C. canescens* were found here. The distance to the forest was at least 50 m.. This enclosure represented the control for the others.
2. Near the asphalt strip of the highway. The centre was at the edge of a dense grass vegetation. The grass nearest to the asphalt consisted of a dense vegetation of *Festuca rubra* L., bordered by a less dense vegetation of *Festuca ovina* L., which again merges into an open *Corynephoretum* vegetation. This enclosure was the most grassy one.
3. At the *Corynephoretum* strip, 4 m. from forest. This enclosure was most comparable to enclosure 1, although some *F. ovina* was present, mainly at the side of the road.
4. At the *Corynephoretum* strip, with part of the forest edge included. The centre of the enclosure was just in the *Corynephoretum*. The *Corynephoretum*-part hardly contained any grasses other than *C. canescens*.
5. At the forest edge with a small piece of *Corynephoretum* enclosed. The centre of the enclosure was in the forest.

The enclosures 2 to 5 were located at the road verge at about 400 m. from the former drift sand area. Here the *Corynephoretum* strip at the road verge is broader than at other places. Fig. 4.3. shows the experimental set-up of all enclosures.

Species studied and experimental design

Beetles for the experiments were collected from the end of May till the end of August at Caitwickerzand, the road verge, and the surrounding forest. Eight species were used in the experiments. They belonged to 3 groups, according to the ecological characterization of Turin *et al.* (1991): 1. stenotopic species from poor, sandy and open habitats, *Amara equestris* Duftschmid, *Calathus ambiguus* Paykull, *Cymindis macularis* Fischer von Waldheim, *Harpalus servus* Duftschmid and *Pterostichus lepidus* Leske, 2. an eurytopic species from open and another from shaded habitats, *Calathus erratus* Sahlberg and *Calathus micropterus* Duftschmid, respectively, and 3. a stenotopic species of forest habitats, *Pterostichus oblongopunctatus* Fabricius. Among the above mentioned species only *Calathus ambiguus* and *Cymindis macularis* were not found at the road verge at a distance of 400 m. from the drift sand area (chapter 2).

Individuals of these species were brand-marked according to the method described by Schφtz-Christensen (1965). The beetles were released in small groups of the same species (up to 20 individuals at the same time) in the centre of each enclosure. By mixing the beetles with some soil and releasing them in a small hole, it was possible to prevent them from running away immediately. Recaptured beetles were removed from the experiment. Unmarked carabid beetles of all species caught in the enclosures were identified and counted per pitfall trap and removed from the enclosures.

Furthermore, only few specimens of the two forest species, *C. micropterus* (coniferous plantations) and *P. oblongopunctatus*, were available for the experiments. Therefore they were only released at the road verge or, in case of *C. micropterus*, only in the two forest enclosures (enclosures 4 and 5).

Pitfall traps were emptied daily. The numbers of beetles recaptured in the pitfall traps in the different directions from the centre not only gave an estimate of the preferred directions of movement but also of the vegetations preferred by the different species. The recaptures within each enclosure were transformed to a mean vector on the unit circle. The preferred walking direction, represented by this mean vector, is Rayleigh tested for directedness of the movements (Batschelet, 1981). The rate of movement was expressed as the number of days in which each individual covered the 4 m. distance from the centre of the enclosure in a straight line to the pitfall trap. These experiments ran from the beginning of June till the end of September 1991.

RESULTS

Distributions of species over vegetation types

The numbers of unmarked beetles caught inside the enclosures gave an estimate of densities of species in various parts of the corridor (Table 4.1.). The highest number of species was caught in the enclosure near the asphalt (Fig. 4.3., enclosure 2). Many of these species were caught in low numbers only, and are both eurytopic and good dispersers (den Boer 1977, 1990a). Three species of the *Corynephoretum*, *Cymindis macularis*, *Harpalus neglectus* Serville and *Calathus ambiguus*, were only caught at the former drift sand area. Another species of the *Corynephoretum*, *H. servus* was also captured at 400 m. from the former drift sand area at the road verge, among which a single teneral specimen. Most species of *Corynephoretum* and oligotrophic sandy soils, present at the road verge, were found in the highest densities at the *Corynephoretum* strip close to the grass strip (Fig. 4.3., the part of enclosure 2 in the *Corynephoretum*). Inside enclosure 2 only *P. lepidus* was also captured in the grass and dense grass part. At the road verge several teneral individuals of *P. lepidus* and *A. equestris* were caught. Species stenotopic for poor open, sandy habitats (habitat preferences c and o in Table 4.1.), were absent from the enclosures at the forest edge (enclosures 4 and 5), except for single specimens of *A. equestris* and *Masoreus wetterhalli* Gyllenhal, which were caught in the *Corynephoretum* parts of these enclosures. Although *M. wetterhalli* was classified by Turin *et al.* (1991) as a species of *Corynephoretum*, it was not captured in the enclosure at the former drift sand area (enclosure 1). Nevertheless, catches outside this enclosure showed that it is present in this area.

None of the identified species caught in the drift sand area (enclosure 1) and in the middle of the road verge (enclosure 3) could be considered forest species. However, some of the big-sized forest species, *Carabus violaceus* Linnaeus, *Carabus problematicus* Herbst and *Cychrus caraboides* Linnaeus were caught in the enclosure near the asphalt (enclosure 2), in the grassy strip. The other forest species were only caught close to and in the forest (enclosures 4 and 5).

Table 4.1. The numbers of unmarked beetles, per species, caught in the five fenced circles at the Caitwickerzand and the road-side verge of the A1, connected to this area. The circles had a surface of 50 m² each. The numbers caught are given as total numbers caught per circle. The species are ranked according to the habitat preferences in The Netherlands (Turin et al. 1991). c = *Corynephoretum*, dune habitats and poor grassland; o = oligotrophic sandy soils; s/p = sandy arable land and coniferous plantations; e = eurytopic; f = forests; ? = group with more species and diverse preferences.

	circle 1. drift sand area	circle 2. r. verge near the asphalt	circle 3. r. verge in the middle	circle 4. r. verge near the forest	circle 5. forest near the r. verge	habitat prefer-ences
Harpalus servus	146	6	5			c
Cymindis macularis	32					c
Harpalus neglectus	8					c
Calathus ambiguus	3					c
Masoreus wetterhalli		8	1	1	1	c
Pterostichus lepidus	2	21	7			o
Amara equestris	1	15	2	1	1	o
Harpalus latus		1				o
Pterostichus diligens		1				o
Harpalus solitaris			3			o
Harpalus anxius	177	172	67	3	1	s/p
Harpalus rufipalpis	5	26	20	12	9	s/p
Harpalus smaragdinus	1	3	1			s/p
Calathus micropterus				1	9	s/p
Calathus erratus	10	76	8	2	32	e
Harpalus affinis	7	4	3	1	1	e
Calathus melanocephalus	2	148	4		4	e
Harpalus tardus	1	1	1	1		e
Syntomus spp.	1	17	3	1		e
Amara aenea		3	1			e
Bembidion lampros		2				e
Harpalus rufipes		2	1			e
Agonum fuliginosum		1				e
Agonum muelleri		1				e
Amara apricaria		1				e
Trechus spp.		1				e
Calathus fuscipes		1		1	2	e
Loricera pilicornis				1		e
Bradycellus harpalinus				1	2	e
Leistus ferrugineus					4	e
Calathus rotundicollis					1	e
Carabus nemoralis					1	e
Carabus violaceus		13			7	f
Carabus problematicus		7			12	f
Cychrus caraboides		1			1	f
Pterostichus oblongopunctatus				1	4	f
Abax parallelepipedus					1	f
Leistus rufomarginatus					1	f
Notiophilus spp.	8	71	10	33	69	?
Amara spp.		10	7	1	4	?
Asaphidion spp.		1				?

The numbers of beetles recaptured in the forest enclosure (Fig. 4.3., enclosure 5) were usually lower than those in the other enclosures (Table 4.2.). Two species, *C. ambiguus* and *Cymindis macularis*, showed the highest recaptures in enclosures consisting mainly of *Corynephoretum* (enclosures 1 and 3). Lower numbers were recaptured in the enclosure with a grass strip (enclosure 2). As mentioned previously, these two species were absent from the road verge at a distance of 400 m. from the former drift sand area.

Tabel 4.2. The number of marked and released beetles and the number of recaptured beetles per fenced circle with the ratio between the number of recaptured beetles and those released. rel. = number of beetles released; rec. = number of beetles recaptured; rr. = the recapture rate, recaptured beetles divided by the numbers released.

	1. former drift sand area			2. road verge near the road			3. road verge in the middle			4. road verge with forest			5. forest with road verge		
	rel.	rec.	rr.	rel.	rec.	rr.	rel.	rec.	rr.	rel.	rec.	rr.	rel.	rec.	rr.
Pterostichus oblongopunctatus	-	-	-	6	6	1.00	6	5	0.83	11	7	0.63	13	6	0.46
Calathus micropterus	-	-	-	-	-	-	-	-	-	12	9	0.75	8	7	0.88
Calathus erratus	79	56	0.71	84	70	0.83	101	92	0.91	116	82	0.70	108	75	0.69
Calathus ambiguus	24	24	1.00	40	33	0.83	104	101	0.97	40	40	1.00	29	22	0.76
Pterostichus lepidus	130	117	0.90	134	106	0.79	113	93	0.82	102	74	0.72	83	50	0.60
Harpalus servus	196	144	0.73	203	145	0.71	138	103	0.74	128	76	0.59	110	69	0.62
Amara equestris	90	85	0.94	98	90	0.92	100	94	0.94	98	96	0.98	96	70	0.73
Cymindis macularis	18	18	1.00	36	21	0.58	47	44	0.93	30	29	0.97	25	8	0.32

The mean vector for directedness of movement is drawn in the circles depicted by Fig. 4.4. The more beetles are recaptured in the same direction, the longer the vector. If all beetles were caught in the same trap, the vector on the unit circle would have value one, i.e. twice the radius of the circles drawn in Fig. 4.4.

Both forest species, *P. oblongopunctatus* and *Calathus micropterus*, mainly walked towards the forest, but only the first significantly so (enclosure 4 and 5). *P. oblongopunctatus* also tended to prefer the grass zone above the *Corynephoretum* zone, though not significantly so (enclosure 2). Because of the low numbers tested it was difficult to show significant directedness for the two forest species, but the length of the vectors suggests that the preference to walk towards the forest and the grassy strip might be rather strong, at least in *P. oblongopunctatus*.

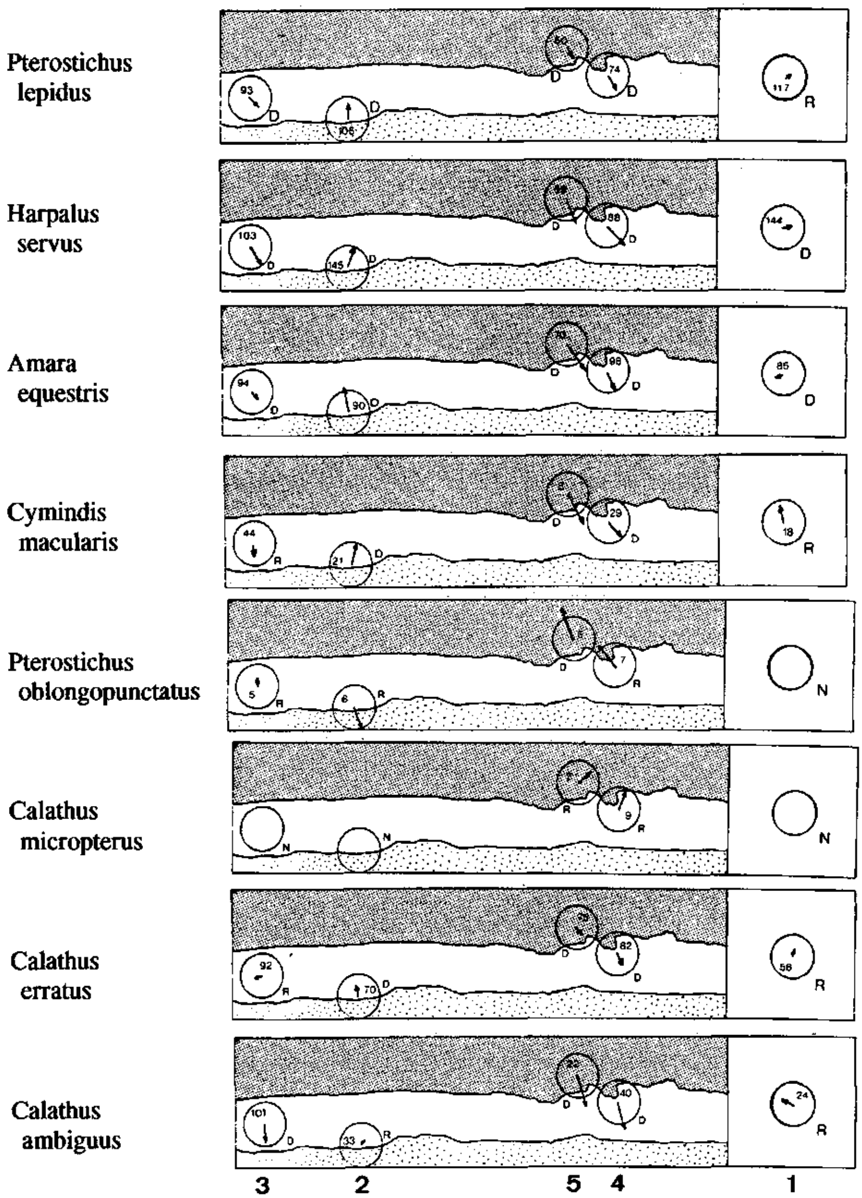

Figure 4.4. The preferred walking directions in the enclosures, expressed as the mean vector on a unit circle. For each species the positions of the circles at the road-side verge are given. On the right: the circle at the former drift sand area (1). A length of the mean vector of 0.5 corresponds with the radius of the circle. Rayleigh tested: D = significantly directed movement, R = random movement, i.e. no significant direction could be established, and N = not tested. Numbers in the circles are the numbers of individuals recaptured. Numbers below the figures are the numbers of the circles corresponding to the text and fig. 4.3.

Densely dotted area = forest; white area = Corynephoretum; dotted area = grass

All non-forest species, significantly preferred directions out of and away from the forest. Even the eurytopic species *C. erratus* directedly walked away from the forest. However, compared to the other 5 species, it showed the weakest reactions in all vegetations. *C. ambiguus* most strongly walked away from the forest. All species, stenotopic for open and poor sandy habitats, significantly preferred a direction away from the forest, even at a distance of 4 m. from it (enclosure 3, with the exception of *Cymindis macularis)*. Among these species only *Calathus ambiguus* did not show any reaction to the strip with a dense vegetation, though the closely related eurytopic species *C. erratus* did. The strongest reactions away from forest were found in *C. ambiguus*, *H. servus*, *Cymindis macularis* and *A. equestris*, in that order. With respect to the dense grass vegetation this order is *A. equestris*, *C. macularis* and *H. servus*. Although for *H. servus* and *A. equestris* directedness of movement was also found at the drift sand area, the directions found do not relate to those at the road verge.

Rate of movement

Table 4.3. The rate of movement of 6 carabid species in the circles in different kinds of vegetation. Rate of movement is expressed as the mean minimum distance covered by the beetles per day. Coryn. = Corynephoretum; mean dist. = mean distance walked by the beetles per day; numbers = number of individuals; st.dev = standard deviation.

		1. drift sand area	2. dense grass to Coryn.	3. Coryn. near forest	4. Coryn. with forest	5. forest with Coryn.
Calathus erratus	mean dist.	3.71m.	1.32m.	2.29m.	2.48m.	1.85m.
	numbers	35	60	60	53	55
	st.dev.	0.85	1.43	1.53	1.62	1.64
Calathus ambiguus	mean dist.	3.32m.	1.73m.	2.75m.	2.54m.	1.54m.
	numbers	19	30	15	34	18
	st.dev.	1.19	1.28	1.43	1.46	1.22
Pterostichus lepidus	mean dist.	2.47m.	1.17m.	2.18m.	2.03m.	1.78m.
	numbers	103	103	86	70	46
	st.dev.	1.48	1.23	1.50	1.36	1.36
Amara equestris	mean dist.	2.43m.	1.28m.	1.46m.	2.29m.	1.58m.
	numbers	52	56	54	60	37
	st.dev.	1.57	1.26	1.17	1.49	1.27
Cymindis macularis	mean dist.	1.29m.	1.45m.	2.15m.	1.43m.	0.81m.
	numbers	14	20	6	26	3
	st.dev.	0.97	1.57	1.38	1.35	0.38
Harpalus servus	mean dist.	1.12m.	0.68m.	0.67m.	1.26m.	1.00m.
	numbers	96	99	71	48	46
	st.dev.	1.38	1.10	1.01	1.49	1.41

The quickest movements were reached by the biggest beetles, *C. erratus*, *C. ambiguus*, and *P. lepidus* (Table 4.3.). All beetles showed a tendency to move more slowly in the grass vegetations, with the exception of *Cymindis macularis*, as well as in the forest, with the exception of *H. servus*. Highest velocities were reached at the drift sand area and at the more open *Corynephoretum* strip at the road verge. Only adults of *C. macularis* move relatively slowly at the drift sand area and those of *H. servus* at the *Corynephoretum* strip of the road verge.

Because individual movement velocities differed highly, it is hardly possible to show this more distinctly. The forest species were not included in Table 4.3. because of the low numbers of individuals.

DISCUSSION

Not all species regarded as characteristic for poor, sandy and open habitats were present in the highest numbers in the former drift sand area, Caitwickerzand, as compared to the adjoining road verges of the highway. Two of the species tested in enclosures, *P. lepidus* and *A. equestris*, occurred at the road verge in higher densities than at the former drift sand area. As the abundance of carabid beetles in an area can be considered an indication of habitat suitability, as is assumed by Grüm (1971a), it may be concluded that these two species found a better habitat at the road verges. According to Turin *et al.* (1991) these two species usually show higher abundances in dry *Calluna*-heathland than in *Corynephoretum* vegetation. The present road verge is more grassy than the drift sand area and has other kinds of vegetation at its borders. These conditions suggest that the road verge as a habitat may be more suitable for these two species, because the conditions are less uniform and provide more possibilities to switch between different vegetation structures in response to changing environmental conditions.

For the most stenotopic species (*H. neglectus*, *H. servus*, *C. macularis*, and *Calathus ambiguus*) the former drift sand area, with its *Corynephoretum*, is the most suitable habitat. Three of these species from the *Corynephoretum*, *Cymindis macularis*, *H. neglectus* and *Calathus ambiguus*, were only caught there.

All the non-forest carabids showed a tendency to move out of and away from the forest (enclosures 4 and 5). The forest species showed an opposite tendency, and therefore it is likely that the distribution of catches for non-forest species is caused by habitat preference rather than a higher rate of trapping of traps outside the forest.

Observations on the forest species confirm that these beetles orientated towards forest, as described by Neumann (1971) and Rijnsdorp (1984). According to these authors, forest carabids recognize the forest silhouette from a certain distance. At a distance of 4 m. from the forest (enclosure 3) adults of most of the stenotopic species of poor, sandy and open areas significantly moved away from it. Therefore, it is likely that they also recognize the forest silhouette from a distance.

In this study the eurytopic species *Calathus erratus* showed the same kind of orientation as stenotopic species from the poor, sandy and open habitats (Turin *et al.* 1991), but less strongly so. Nevertheless, it is a species of open habitats and, at the border of the forest habitat, it reacts in the same way as the species which are stenotopic for *Corynephoretum* and oligotrophic sandy habitats.

In the forest the species of open habitats moved relatively slowly. Therefore a piece of forest between two open habitat fragments will form a dispersal barrier because of both the low chance of entering the forest habitat and the low rate of movement there. An open and broad corridor structure between suitable habitat areas through the forest will lower both effects and therefore enhance dispersal between the two areas. However, the dispersal through such corridors will be hampered at sites which are narrowed or occupied by trees. A previous study showed that *C. ambiguus*, *H. neglectus* and *Cymindis macularis* only occur at the road verge at less than 100 m. from the drift sand area (chapter 2, Vermeulen & Veenbaas, 1992). No further catches were made at the road verge beyond the first site where the *Corynephoretum* strip was interrupted by trees. The other species of the *Corynephoretum*, *H. servus*, was still present at 400 m. from the drift sand area in a section where the *Corynephoretum*-strip had widened up to 8 m. Since a teneral specimen, thus just emerged, was caught there, this section appears to be suitable for the species to complete its development.

During this study *H. servus* was observed in flight. So far no flight observations of *C. macularis*, *H. neglectus* and *Calathus ambiguus* have been recorded in the Netherlands (Van Huizen, 1980, Van Huizen & Aukema, 1992). Its capacity to fly might explain the presence of *H. servus* at the road verge at 400 m. from the drift sand area.

Most species of *Corynephoretum* and oligotrophic sandy soils, present at the road verge, occurred in highest numbers in enclosure 2. They were mainly caught in the *Corynephoretum* part of this enclosure. The mark-recapture experiments showed that most individuals of these species move out of the grassy area. Therefore, one of the explanations for the relatively high abundance of individuals near the grass strip might be that they do not like to enter the dense grass strip and prefer to stay away from the forest as far as possible. This dense grass strip appears to be important in preventing adults of these species from entering the asphalt strip. With a traffic of about 30,000 cars per day, the chances of survival will be very low when crossing the highway.

Locomotory activities are not only low when food conditions for the beetles are good, (Mols, 1986), but also when the physical resistance of the vegetation is high, for instance because of a dense vegetation (Heydemann, 1957). Although the dense grass strip harbours enormous amounts of small prey animals, like springtails, mites and sow-bugs, the slow rate of movement of carabid beetles will mainly be caused by physical resistance of the vegetation. Therefore most beetles prefer to walk away from this dense grass strip, being the edge of their *Corynephoretum* habitat. This is quite opposite to the experiences of Grüm (1971b), who found that the mobility of individual carabids was highest at the edge of their habitats.

For the species *P. lepidus* and *A. equestris* the road verge apparently is an extension of the habitat area, the Caitwickerzand, (chapter 2). This is suggested by the higher numbers of beetles of these species caught at the road verge. Therefore, the risk of extinction will be spread (den Boer, 1968) over a larger and more heterogeneous area. On the other hand, for species like *H. servus*, *Cymindis macularis* and *Calathus ambiguus* the road verge will be a kind of sink habitat (Pulliam, 1988). Their numbers are low at the road verge, reproduction is marginal and they are negatively influenced by other vegetations at and adjacent to the road verge. Individuals of these species entering this road verge probably will have a low chance to survive and reproduce under the present conditions. If this is correct, Mader (1984) and Mader *et al.* (1990) could be correct in that linear structures in the landscape can increase the chance of extinction of local populations by leading individuals to marginal habitats. A linear structure which is a marginal habitat can only connect two suitable habitat areas over short distances, for carabid beetles this is only a few hundred metres (Vermeulen *et al.*, 1994). However, when barriers such as narrow sites are removed, and the width is extended so that it can become part of their habitat, such a structure can have a positive effect on survival, even for the three last mentioned species, because not only their habitat area is enlarged, but they can establish a kind of metapopulation structure over greater distances (Levins, 1970, Opdam, 1990).

This study showed that stenotopic carabid beetles from poor, sandy and open habitats tend to stay in a *Corynephoretum* corridor and move quickest in this type of vegetation. When such corridors are broad enough and reproduction sites are sufficiently present, exchange of beetles between larger habitat areas via such a corridor must be regarded as possible.

Reactions of beetles on certain small vegetation elements in an area might enable us to predict their dispersal flow in that landscape. An example of this can be found in the diffusion model for tenebrionid beetles, which reacts to the presence of tussocks of grass (Wiens & Milne, 1989, Johnson *et al.*, 1992). By extrapolation of the reactions of individuals on border zones and their rate of movement in different kinds of vegetation, together with reproduction and survival chances in these vegetations it might be possible to give an estimate of the effectiveness of planned corridors for a certain species.

Acknowledgements

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Chapter 5

A SIMULATION MODEL FOR RANDOM DISPERSAL TESTED FOR HEATHY CORRIDORS

SUMMARY

At the request of the Road and Hydraulic Engineering Division of the Ministry of Transport, Public Works and Water Management in the Netherlands we developed a simulation programme to predict the distribution of carabid beetles in a landscape.

In the simulations a number of beetles are released at a certain point, from which they walk for a number of days. All parameters used in the programme are derived from field measurements. Rate of movement and preferred direction depend on the kind of habitat through which the beetle passes. Borders between different kinds of habitat may be barriers for these movements. The beetles can reproduce and may die during the walking period. The simulations generate distribution patterns similar to those seen in independent mark and recapture experiments at a heathy road-side verge and in an open, poor sandy area.

Both in the field and in the simulations several features of road verges, which are thought to act as dispersal corridors, resulted in different dispersal distances for three species of carabid beetles. In general, corridors connected to areas with a high density of individuals gave the greatest dispersal distances. Replacing the heath strip by an open grass strip does increase the chance of getting lost in adjacent areas and lowers dispersal distances. Increasing the width of the road verge does increase dispersal distances along this road verge. Narrow sites in the road verge have a barrier effect for dispersal, so more individuals move into adjacent areas. An absolute barrier between the corridor and adjacent areas increases dispersal flow but not mean dispersal distances. However, the chance of a few long dispersal movements increases.

The programme can be used to examine the effects landscape structures (particulary differently sized dispersal corridors) on the distribution of populations. These examinations can provide an economic function for proposed corridor networks.

INTRODUCTION

Poor sandy or heathy road verges may contribute to the survival of carabid beetles stenotopic for these habitats (chapter 2). Connecting small, heathy fragment areas with heathy corridors (see metapopulations: Levins 1970; Opdam 1990; Gilpin & Hanski 1991), such as road verges, may improve chances of survival for these stenotopic species. Habitat fragments which lost populations of some species (de Vries & den Boer 1990) migth be recolonized from other fragments in which the species are still present. Corridors are thought to enhance the ability of individuals to move through a hostile environment from one heathy fragment to another. Although in theory this seems rather plausible the critical properties of effective corridors are usually unknown (Saunders & Hobbs 1991; Soulé & Gilpin 1991; Hobbs 1992). Nevertheless, some local authorities in the Netherlands have already planned corridors between heathland fragments.

To help landscape managers design corridors and ecological networks, we present a simulation programme. With parameters and variables estimated from field data (chapter 4 and Vermeulen 1994), we will test whether the results obtained by the programme correspond to results obtained by an independent mark and recapture experiment (chapter 3). Furthermore, for three species of carabid beetles characteristic of the sandy, open habitat, we will test the influence of several features of a corridor on both dispersal distances and the amount of dispersal. These features are width of the corridor (see also Soulé & Gilpin 1991), narrow sites at the corridor, the type of vegetation inside the corridor and the barrier effect of the borderline with adjacent areas. We will also estimate the dispersal distances reached with different starting numbers of individuals and what distances are reached after one year and after two years.

METHODS

The operation procedure of the model

In this programme (Fig. 5.1.) the user draws a map of a landscape that defines the spatial arrangement of different kinds of habitat. The user has to decide how many days and beetles the simulation has to run. The simulation starts with the first beetle at either a starting point, defined by the user, or a random position in a starting habitat area. Every walking day the beetle chooses a direction, either at random or drawn from a probability distribution, defined for the given type of habitat. The distance it walks at a certain day is drawn from a distribution of distances (For maximal distances covered per day according this distribution see Table 5.1.). For every kind of habitat three different distributions of

Table 5.1. The maximal rate of movement per day and life time per species as used in the simulations. All species are restricted to poor sandy, open habitats (Turin et al., 1991). The species are ranked according size, the biggest at top.

	Maximal distance covered per day	life time in years
Pterostichus lepidus Leske	5.92 m.	2
Cymindis macularis Fischer von Waldheim	5.30 m.	1
Harpalus servus Duftschmid	4.13 m.	4

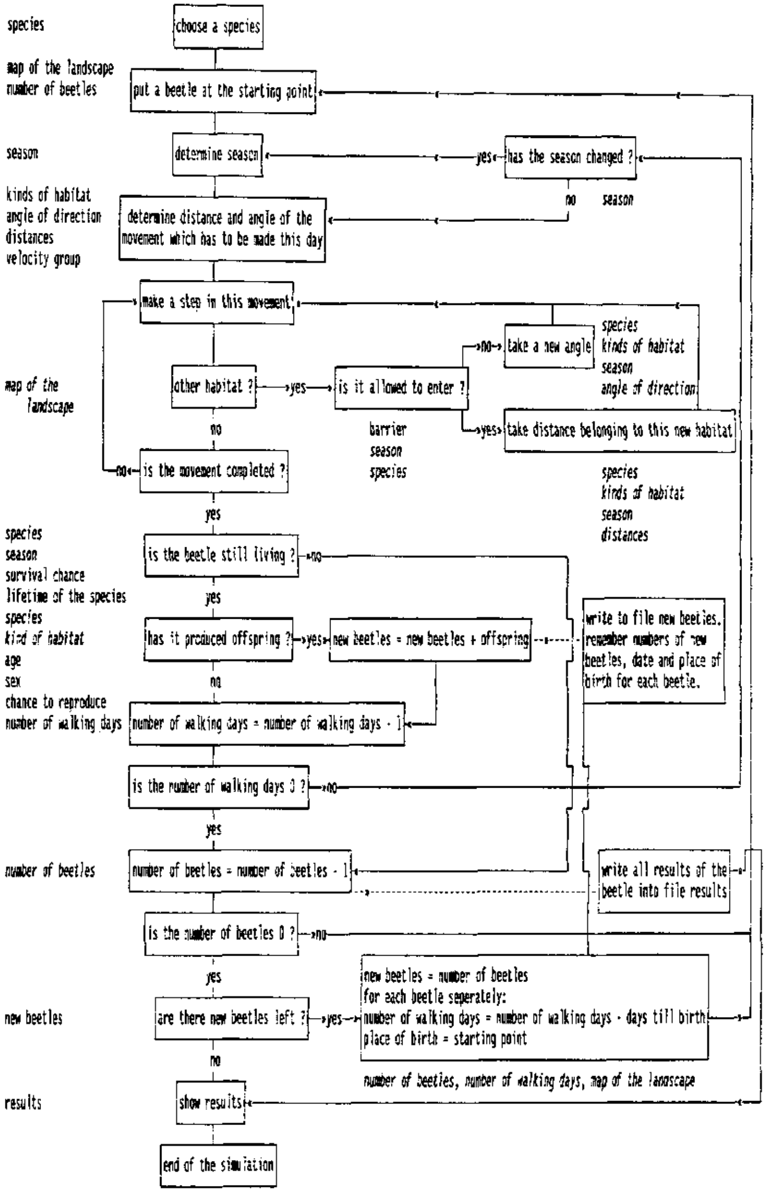

Figure 5.1. Flow chart of the simulation programme for the dispersal of carabid beetles in landscapes with different kinds of habitat. All input, from file or directly by the user, is placed outside the blocks. When necessary the programme will scan information for a second time. This input is then written in italics.

Table 5.2. The distribution of probabilities to enter one habitat from another as used in the simulations, expressed in percentages, for *Pterostichus lepidus*, *Cymindis macularis* and *Harpalus servus*. 100% indicates no barrier effect between two habitats, lower percentages express the chance that a beetle will enter the other habitat after reaching the border. The relative velocity in a habitat is shown between brackets in the row "from " for each of the species used. From "a" to "e" the rate of movement in a habitat decreases. 1 to 6: type of habitat, explained below.

A. *Pterostichus lepidus*

from to	1(e)	2(e)	3(a)	4(b)	5(c)	6(c)
1	100	53.8	12.5	21.4	96.9	100
2	100	100	23.3	39.7	100	100
3	100	100	100	100	100	100
4	100	100	52.5	100	100	100
5	100	92.3	15.6	29.8	100	100
6	91.9	81.1	4.4	8.4	28.2	100

B. *Cymindis macularis*

from to	1(b)	2(b)	3(c)	4(a)	5(e)	6(e)
1	100	0	0	0	0	100
2	100	100	16.7	29.9	100	100
3	100	100	100	100	100	100
4	100	100	66.7	100	100	100
5	100	97.3	13.9	20.8	100	100
6	91.9	0	0	0	0	100

C. *Harpalus servus*

from to	1(e)	2(e)	3(a)	4(b)	5(c)	6(c)
1	100	3	12.2	22.7	100	100
2	100	100	18.9	35.3	100	100
3	100	100	100	100	100	100
4	100	100	14.4	100	100	100
5	89.7	83	1.9	14.4	100	100
6	88.1	81.4	0.3	2	15	100

1 = dense grass vegetation
2 = open grass vegetation
3 = *Corynephoretum*
4 = *Corynephoretum* near forest
5 = forest edge
6 = forest

distances are defined. These different distributions are indicating directed walk (long distance) and random walk (short distance) as defined by Baars (1979) from following individually many radioactively marked carabid beetles of heath during the entire reproductive season and an intermediate type of behaviour. Every habitat defined in the programme has its own frequencies in which these kinds of behaviour are performed (for parameters and data used for every separate species see appendix). An example of the walking pattern of a beetle, obtained by the programme after four months of walking in a homogenous open area, is given in figure 5.2b. (compare Fig. 1 in Baars 1979).

When reaching another kind of habitat the programme determines whether or not it is possible to the beetle to enter this habitat (based on field experiments, chances to enter a habitat from another are given in table 5.2.). When it is not possible, the beetle has to choose a new direction and completes the distance it had to walk that day. When the beetle is allowed to enter the new habitat, it completes the distance for that day according to the rate of movement belonging to that new habitat. Also this kind of decisions is based on field experiments by Baars (1979) and Vermeulen (1994 and chapter 4).

At the end of the day the programme determines whether or not the beetle is still alive and whether or not it has reproduced (chances are drawn from a probability distribution based on data of the Biological Station Wijster).

For that beetle, the simulation continues till the last day of the simulation or the death of the beetle.

After the first beetle the programme continues with the second one from the same starting point in the landscape and so on, till the last beetle has finished. Then it is determined how much reproduction has taken place during the simulation. The newly born beetles start from the point where they originated i.e. the place of birth. Futher each individual goes through the same procedure as its parents. After the yime given for the simulations has passed, all end positions of the beetles in the landscape are given, together with the minimum, mean and maximum distances covered during this simulation. If relevant data are available, also seasonal effects on dispersal can be introduced into the programme. The results of the programme should be checked with newly collected field data, if possible.

The programme

We used Pascal as a programming language. The programme has basically four parts:

1. The properties of the organism.
   Input that can be given:
   - The maximum and expected mean lifetime of individuals of that species
   - The expected mean number of offspring produced by the species both per day and in total during its life time (input must be given by an average and a standard deviation).
   - The percentage of the population which can produce offspring (females), and the average age at which they start to reproduce.
   - The preferred walking directions in a certain kind of habitat.
   - Three frequency distributions with average day distances in each kind of habitat for different seasons.
   - The survival chance in each kind of habitat per day for different seasons.

- The chance to reproduce in each kind of habitat per day for different seasons.

Of course it is not necessary to enter all these data. You can put in the information you have. It is possible not to use reproduction, survival and seasons. The other information necessary might be supplied by the random generator for a first orientation. For short-term dispersal simulations only mean rates of movement and preferred directions, defined per kind of habitat, will suffice.

2. The variables necessary for each simulation.

Input that is available for the programme:

- Starting date of the simulation and the number of days the user wants the simulation to run.
- The number of beetle generations in this simulation.
- The *maximum number of pixels* the beetle can walk *in* the landscape on screen. Depending on the scale of the landscape a pixel represents a certain distance.
- The frequency distribution of the angles of direction per kind of habitat from which the beetle has to take its walking direction. It is possible to let it walk randomly.
- Whether or not the user wants to follow the simulation on screen during processing.

3. The drawing of the landscape.

The input has to be given by the arrow keyboard:

- On a graphic screen the user can create a landscape. Though the basic elements for drawing are rather simple (rectangles, triangles, quadrangles and lines) a quite complex environment can be drawn.
- In the landscape drawn, only the common start position or habitat of all individuals of the first generation has to be given.

4. Output.

Output which will be given automatically by the programme:

- The end position of all the individuals in relation to the starting point. The landscape drawn will appear on screen, in which the end positions are lighting up.
- A table in which minimum, maximum, mean and standard deviation is written down of: A. the distances covered in a straight line (effective way) from the starting point(s). B. the effective way along a Y-vector and along a X-vector. C. The summation of the daily distances walked by the individuals from the starting point(s) (total way). D. the angles taken by the individuals. D. the ages of the individuals.
- Graphs of the distribution of the results mentioned above. It is possible to get the results for every separate generation only.
- The distribution of the beetles over all kinds of habitat defined by the user.

A flowchart of the programme is presented in Figure 5.1. All results can be written to ASCII-files, so that they can be processed in other programmes. The ownership of the programme will be in the hands of the Ministry of Transport, Public Works and Water Management of The Netherlands and the Institute for Forestry and Nature Research, but for non-commercial use, the author can be asked for the text of the programme.

RESULTS

Basal data for and validation of the model

In 1990, from April till the end of September, three carabid species, *Pterostichus lepidus*, *Harpalus servus* and *Cymindis macularis*, were collected with pitfall traps at a former drift sand area with a *Corynephoretum* vegetation, which gave the basal data for the construction of the model (chapter 2 and 3). These three species are all stenotopic species of poor sandy, open habitats. The adult beetles were brand-marked (Schϕtz-Christensen 1965) and released in small groups at both the centre of the drift sand area and an adjacent road verge with a similar vegetation. At different distances from the release points pitfall traps were placed. For every separated trap the recaptured beetles were counted. Maps of the experimental framework are presented by figures 5.2a and 5.3a.

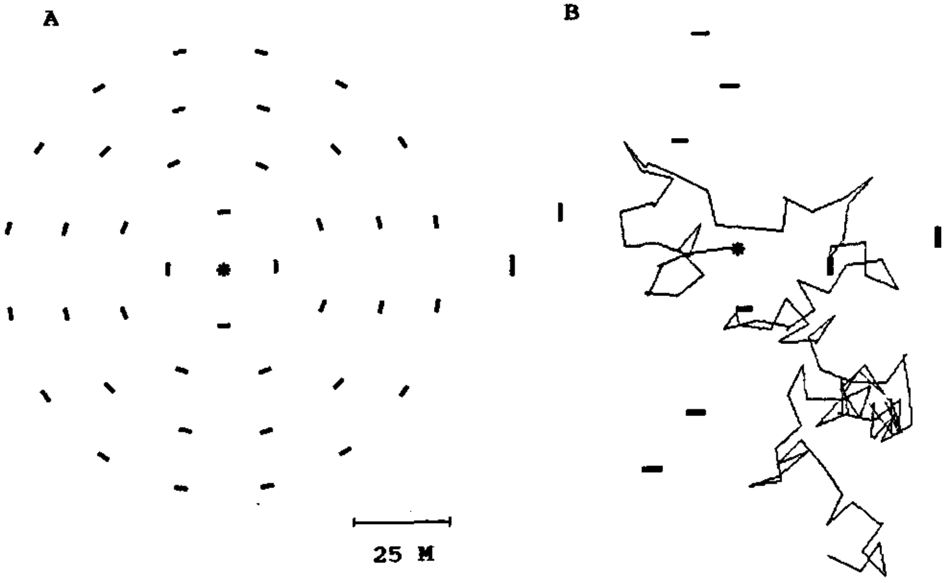

Figure 5.2. The arrangement of the pitfall traps in a homogeneous open *Corynephoretum* area (Caitwickerzand, the Netherlands) in the field experiment (A). Every trap had a catching possibility extending over one meter. At right (B) the pattern of the traps in the simulation. Every trap in the simulation had a catching possibility extending over four meters, so that the total catching capacity of the traps in both the field situation and the simulation is similar at the same distances. Beetles moved randomly from the release point (*). As an example the walking pattern of one beetle (*P. lepidus*) according to the programme is drawn in the figure.

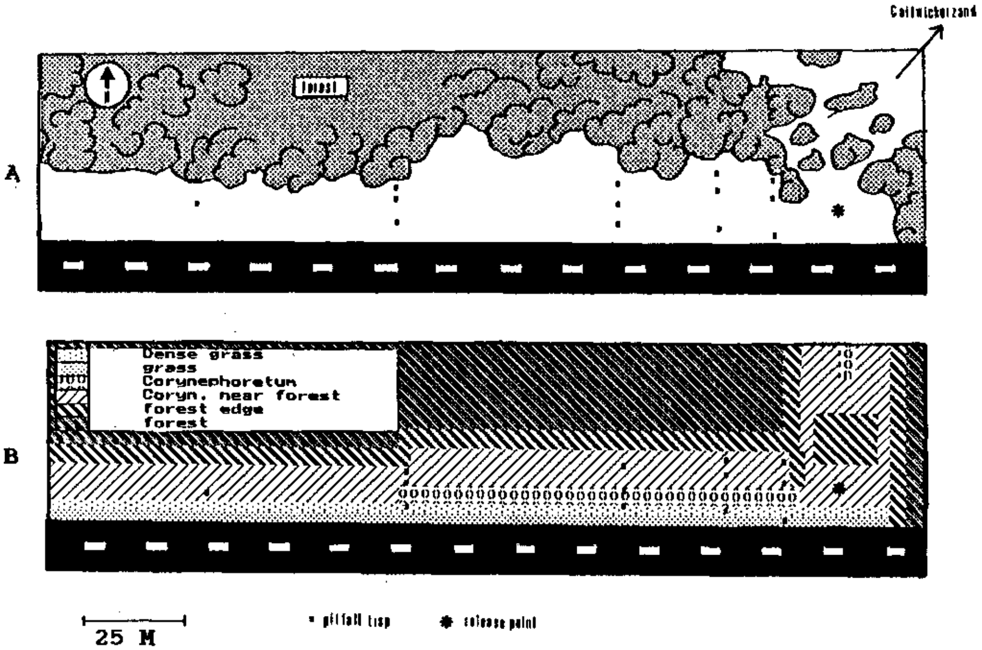

Figure 5.3. The places where pitfall traps occurred at a road verge with grasses, *Corynephoretum* and forest in the field experiment (A, along the highway A1, connected to the Caitwickerzand, the Netherlands). Every trap had a catching possibility extending over one meter. Below (B), the places where traps occurred in the simulated landscape. Every trap in the simulation also had a catching possibility extending over one meter. Each beetle moved randomly from the release point (*).

In our version of the programme comparable situations were drawn. Pitfall traps were placed at similar distances from the release points (fig. 5.2b. and 5.3b.). The catching capacity of the traps in the simulations at all distances were the same as in the mark and recapture experiments, which means that in fig. 5.2b, i.e. in the open, homogeous habitat, one trap of 4 m. has the same catching capacity as four traps of 1 m in fig. 5.2a. To save comparability we used the same arrangements of pitfall traps in the corridor (see chapter 3). Barrier effects and rate of movement in habitats used were calculated from results obtained in a study in 1991, at a site nearby but independent of that of the mark and recapture experiment (chapter 4 and Vermeulen 1994).

After having installed all parameters and variables, derived from this last study, the same release experiments as in the field were processed 10 times by the programme. The results of these simulations are presented in tables 5.3 and 5.4. The species *C. macularis* in the field experiment was only released at the road verge (table 5.4.), because catches of unmarked beetles were too low to release beetles of this species in sufficient numbers at more sites (chapter 3).

The distributions of the catches in the simulations were compared to that of the field experiments and chi-square tested on differences (Sokal and Rohlf 1981). In only one case of the fifty simulations a significantly different distribution (*H. servus*, table 5.3.) of the catches was found.

Table 5.3. Test scheme at a homogeneous open *Corynephoretum* area (Caitwickerzand, the Netherlands). Found = the numbers of beetles recaptured in the mark and recapture experiment in traps at different distances from the release point, 1 - 10 are the recaptures found in 10 simulations with the same numbers released as in the field experiment. Chance (P) is the chi-square tested chance that the distribution in the simulation is similar to that found in the field.

I. *Pterostichus lepidus*, 237 releases
25% of the encounters with a trap in the simulations result in a catch.

traps at	found	1	2	3	4	5	6	7	8	9	10
12½ m	10	15	11	14	10	14	18	15	10	11	17
25 m	13	19	16	16	18	23	14	10	13	17	24
37½ m	18	9	19	19	19	16	14	18	20	13	18
50 m	13	13	15	10	11	10	11	12	14	16	12
chance (P)		>0.11	>0.80	>0.57	>0.80	>0.26	>0.39	>0.57	>0.80	>0.57	>0.39

II. *Harpalus servus*, 690 releases
10% of the encounters with a trap in the simulations result in a catch.

traps at	found	1	2	3	4	5	6	7	8	9	10
12½ m	13	21	17	17	12	15	15	26	19	14	12
25 m	8	5	7	5	12	12	9	12	7	6	10
37½ m	8	5	5	2	3	2	5	4	3	4	2
50 m	4	4	3	2	0	2	2	0	1	0	4
chance (P)		>0.26	>0.56	>0.17	>0.07	>0.11	>0.56	**<0.03**	>0.11	>0.17	>0.26

Table 5.4. Test scheme at a road-side verge with grasses, *Corynephoretum* and forest (aside the A1, near Caitwickerzand, the Netherlands). Found = the numbers of beetles recaptured in the mark and recapture experiment in traps at different distances from the release point, 1 - 10 are the recaptures found in 10 simulations with the same numbers released as in the field experiment. Chance (P) is the chi-square tested chance that the distribution in the simulation is similar to that found in the field.

I. *Pterostichus lepidus*, 200 releases
25% of the encounters with a trap in the simulations result in a catch.

traps at	found	1	2	3	4	5	6	7	8	9	10
12½ m	18	20	19	12	15	17	14	15	13	18	15
25 m	8	10	12	7	9	9	9	11	8	12	7
50 m	5	6	6	9	5	4	7	7	7	10	7
100 m	0	2	1	0	1	0	1	0	1	1	0
150 m	1	0	0	0	0	0	0	0	0	0	0
chance (P)		>0.56	>0.56	>0.40	>0.56	>0.74	>0.56	>0.56	>0.80	>0.40	>0.74

II. *Harpalus servus*, 1000 releases
10% of the encounters with a trap in the simulations result in a catch.

traps at	found	1	2	3	4	5	6	7	8	9	10
12½ m	9	6	7	17	12	13	15	9	18	18	10
25 m	6	4	7	6	11	8	12	11	4	9	11
50 m	5	3	1	2	3	3	2	3	1	0	2
100 m	0	0	0	0	0	0	0	0	0	0	0
chance (P)		>0.80	>0.39	>0.26	>0.57	>0.57	>0.26	>0.57	>0.11	>0.05	>0.39

III. *Cymindis macularis*, 275 releases
5% of the encounters with a trap in the simulations result in a catch.

traps at	found	1	2	3	4	5	6	7	8	9	10
12½ m	3	4	1	8	3	2	3	3	5	3	4
25 m	3	2	2	2	8	1	2	1	3	2	4
50 m	3	4	1	0	0	5	2	0	0	1	0
100 m	0	0	0	0	0	0	0	0	0	0	0
chance (P)		>0.80	>0.80	>0.20	>0.20	>0.57	>0.80	>0.39	>0.26	>0.80	>0.26

As the data used were collected at a road verge, these are suitable to test the efficiency for dispersal of the corridors. Vegetations tested in the study by Vermeulen (chapter 4 and 1994) will be used in comparable road verges drawn in the simulations. The parameters and variables derived from these data and used for these simulations are given in tables 5.1, 5.2 and the appendix. The basic road verge used is a narrow one with a heathy vegetation, as can be found in the Eastern part of the Netherlands (Fig. 5.4a). Except for the broad one (Fig. 5.4b) and the open field situation all other simulations processed are a variation of this narrow verge. Simulations were run for the three species mentioned with 10.000 individuals starting individually from at the release point, for only one generation, except in cases where the influence of numbers released on dispersal distances was tested. For the dispersal distances at road verges only those beetles were taken into account which

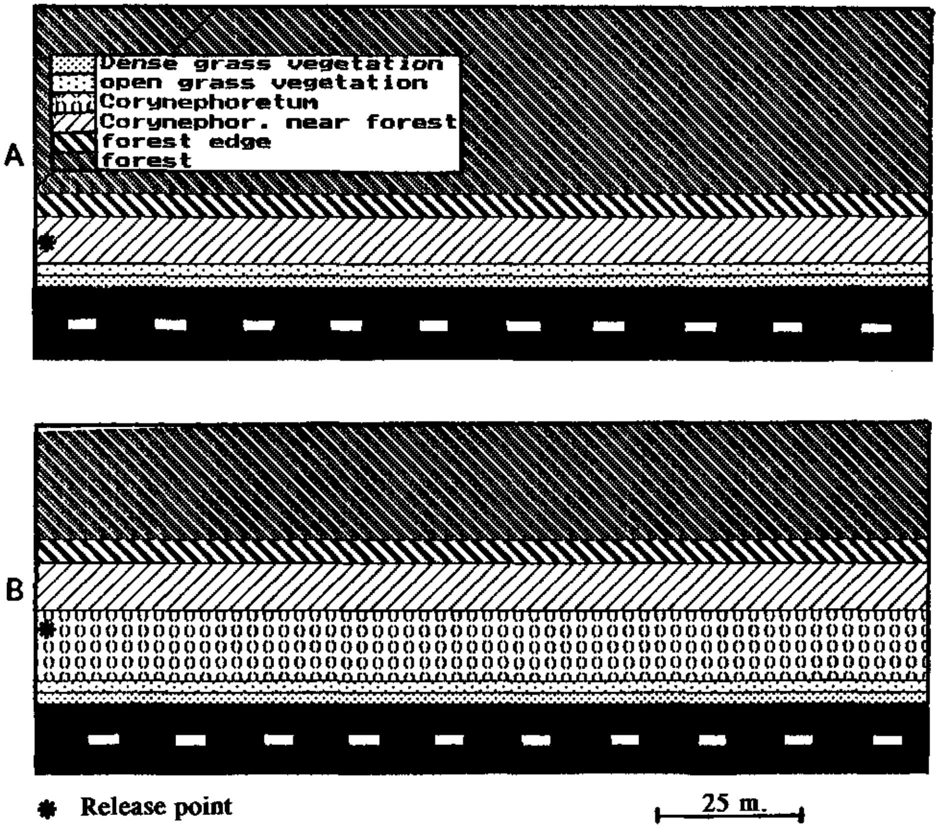

Figure 5.4. Two imaginary road verges similar to situations along the A1 near the Caitwickerzand, in the Netherlands. A: a narrow verge (width 12 m.) with uniform vegetation strips, parallel to the road, B: the same situation but now with an extra *Corynephoretum*-strip of 12 m. All simulations in road verges are variations of the narrow verge, except for the broad one. Beetles in the simulations started to walk from the release point.

at the end of the simulation are still present at the verge. All other beetles left this habitat and are regarded as lost for dispersal along the road verge. As during the field experiments not a single individual of the more than 3000 individuals of these three species released nearby the road pavement was caught at the other side of the road (chapter 3), in the simulations the road itself was regarded as an absolute barrier.

All simulations were ran several times. After simulating 10.000 individuals the mean distances covered differed only + or - 1 metre in similar simulations, though the standard deviation showed high variation.

Numbers of beetles dispersing and dispersal distances

In the simulations each beetle every day is choosing a walking direction randomly. This means that every day it has a similar chance to walk back as it has to move further. Therefore, one can expect that the higher the number of beetles performing their walks the higher the chance that some disperse over a great distance. This is illustrated for the three species tested in table 5.5.

With low numbers of beetles the mean distance covered can fluctuate more than with high numbers of beetles, though on average it will be the same. With high numbers the chance that an individual coincidentally walks away from the release point in a more or less straight line increases (maximum distances in table 5.5.).

In general we can say that the denser the source population, the further the maximum dispersal distance covered by at least some individuals.

Table 5.5. Mean and maximum distance (max.) in metres walked by the individuals of 3 species of ground beetles along the standard narrow road verge in the simulations. Starting numbers of individuals are increasing from the most left column to the right.

starting number	100 ind.		1000 ind.		10000 ind.	
	mean	max.	mean	max.	mean	max.
Harpalus servus	12.3	49.1	13.7	56.4	13.4	67.8
Cymindis macularis	36.3	119.3	33.0	161.6	33.6	158.8
Pterostichus lepidus	42.7	183.9	41.1	171.3	41.8	208.3

Dispersal in the open field, broad and narrow road verges

When comparing the distribution of the released numbers of the three species in an open heathland to those in a broad and a narrow road verge, it becomes clear that *H. servus* and *P. lepidus* cover the greatest distances in the open heathland (Fig. 5.5.). In both corridor situations most individuals stay closer to the release point, which is most obvious in the narrow one. Only *C. macularis* shows the highest dispersal distances in the narrow verge. In the field experiment this species was hardly found at the road verge and it showed a high rate of movement when placed at the verge.

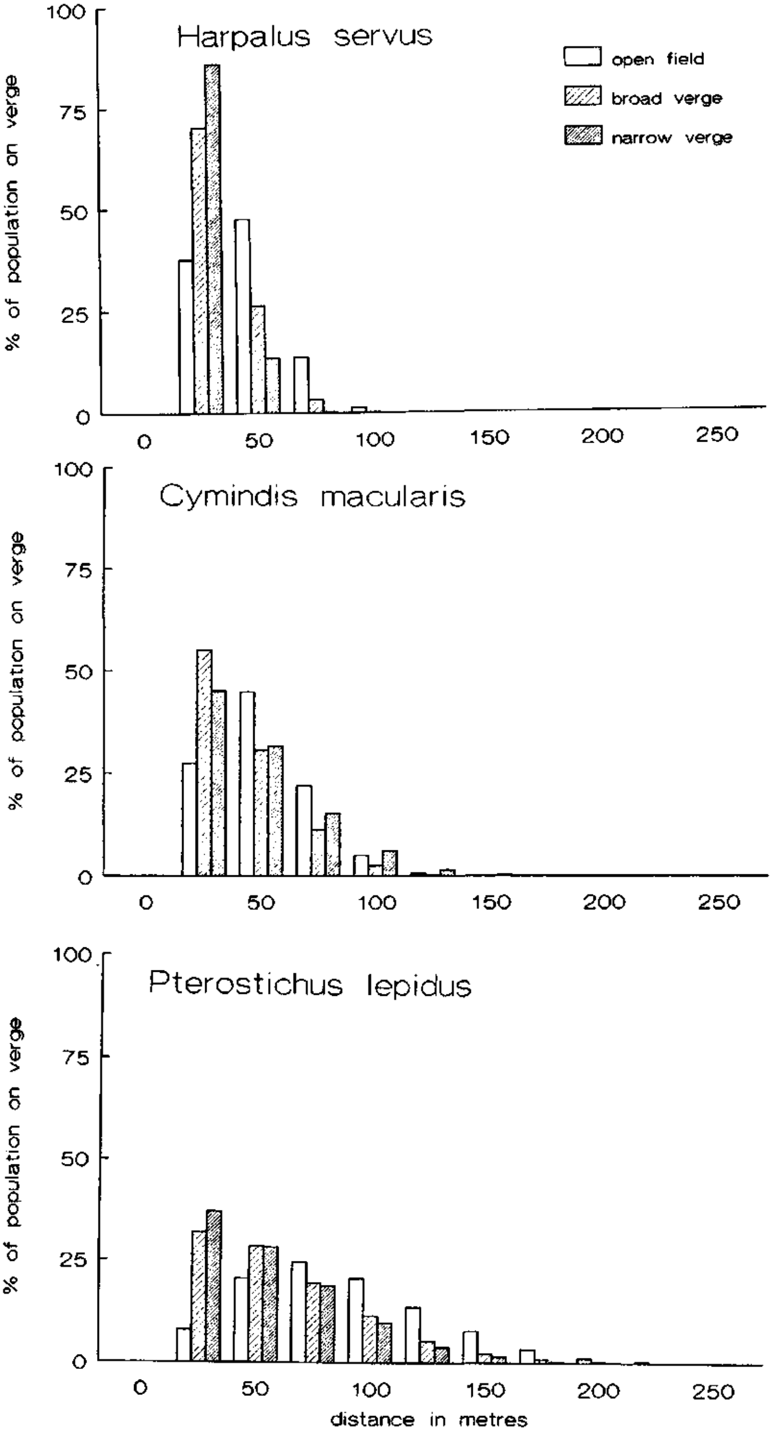

Figure 5.5. Distribution of the distances of the end positions from the release point of individuals of three carabid species in classes of 25 m., expressed as percentages of the population. Results are obtained from simulations in an open field situation, at a broad (24 m.) road verge and at a narrow one (12 m.) during one year.

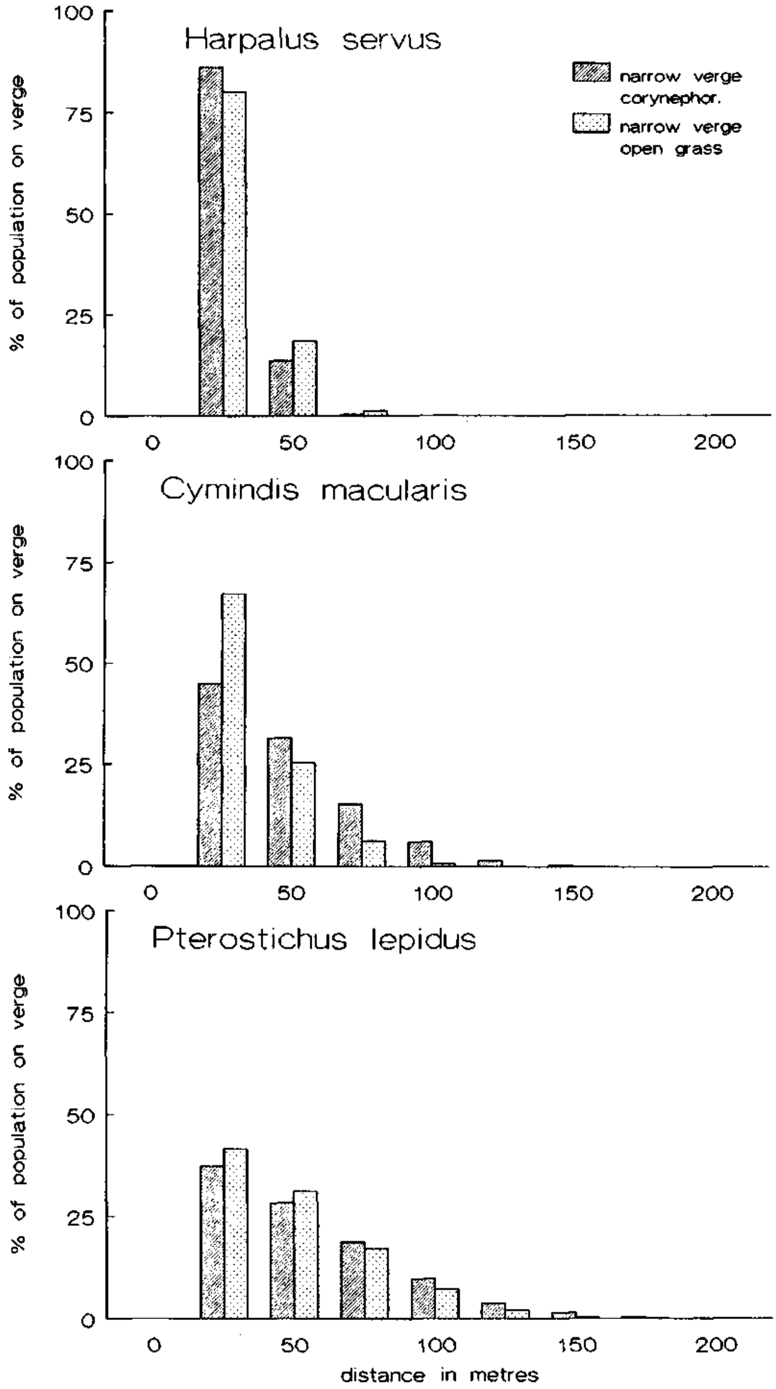

Figure 5.6. Distribution of the distances of the end positions from the release point of individuals of three carabid species in classes of 25 m., expressed as percentages of the population. Results are obtained from simulations during one year at a narrow road verge (12 m.) with a 8 m wide *Corynephoretum* strip and the same verge in which the *Corynephoretum* strip is replaced by an open grass strip.

Dispersal along a corridor with an open grass vegetation

Heathy road verges are often interrupted by a more grassy vegetation. By changing in the simulations the *Corynephoretum* strip into an open grass strip we can test the effect of such a feature. In figure 5.6 the results of these simulations are shown.

Especially in *C. macularis* a higher portion of the beetles stays closer to the release point when moving in an open grass strip than in a *Corynephoretum* strip. Apparently they are hindered in their dispersal by the grassy structure. For *H. servus* an opposite result is derived. In *P. lepidus* there is hardly any difference.

The effect of a narrow site in a corridor

At some sites in road verges the adjacent vegetation comes more close to the road. The effect of such a bottleneck in the road verge vegetation on the dispersal of beetles is shown in figure 5.7. Here, at a distance of 25 m. from the release point the forest (edge) is immediately adjacent to the open grass strip over a distance of 10 m., thus interrupting the *Corynephoretum* strip.

The beetles tend to accumulate before the narrow site in the road verge, especially in *C. macularis*.

Dispersal in a corridor over 2 years

So far we regarded dispersal only during one activity period (1 year). However, in many species, individuals live for more than one season, for instance *P. lepidus* and *H. servus*. Therefore, figure 5.8 presents the dispersal distances of these two species after one and two years respectively. From this figure it is obvious that in two years dispersal distances are slightly longer than in a single year and not twice as long.

Corridors with hard and soft boundaries

In a situation where beetles are moving in a verge bounded by a road at each side, losses from the corridor probably will be very low. As mentioned previously the road pavement act as almost an absolute barrier. As high numbers of dispersing beetles by chance result in more beetles covering relatively long distances, it is interesting to investigate the dispersal distances when beetles are not allowed to leave the corridor.

By defining an absolute barrier in the simulations between the vegetation strip *Corynephoretum*-near-forest and the forest edge such a corridor was simulated (Fig. 5.9.). In both *P. lepidus* and *C. macularis* more individuals are present in all distance classes. Because the distribution pattern of the classes is almost similar to the standard verge, the longer maximum distances covered by some individuals must be the result of a higher number of dispersing beetles present at the end of the simulation. The effect in *H. servus* is small, if any.

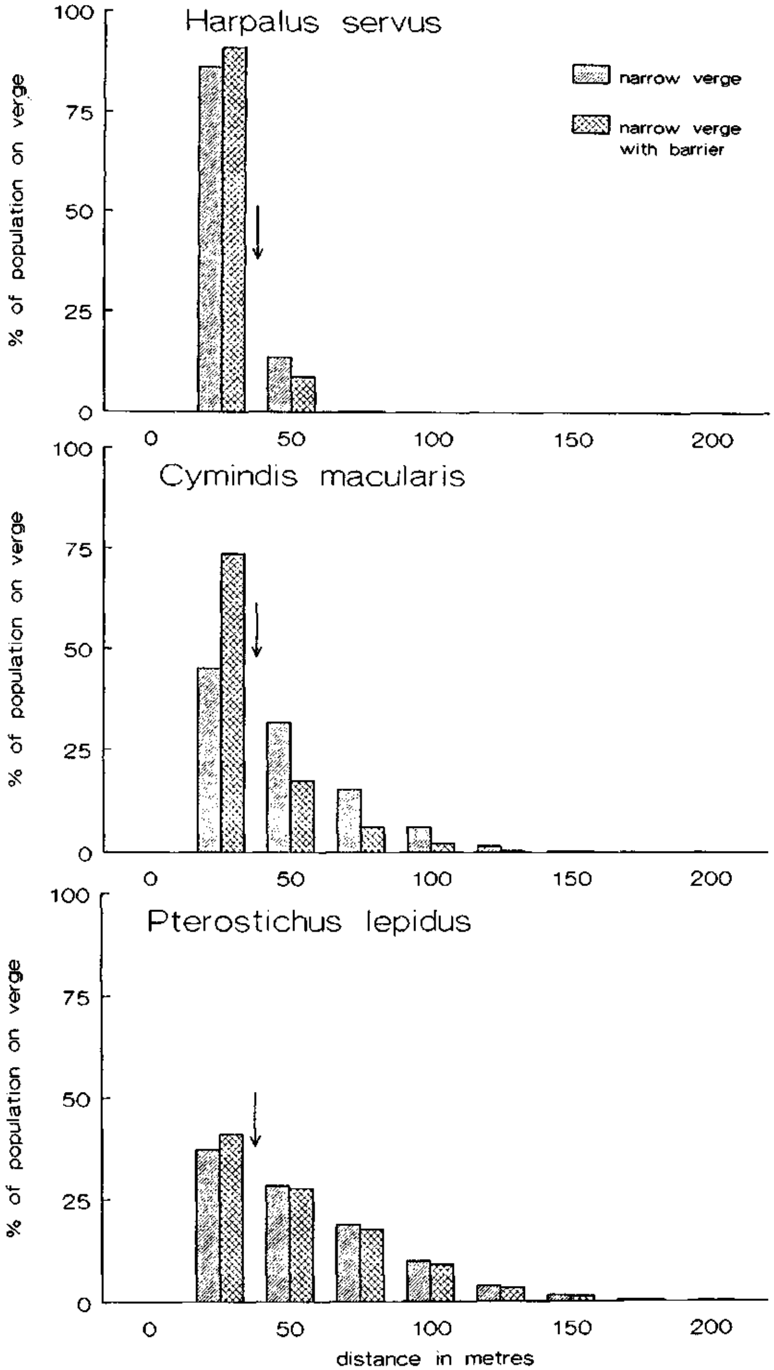

Figure 5.7. Distribution of the distances of the end positions from the release point of individuals of three carabid species in classes of 25 m., expressed as percentages of the population. Results are obtained from simulations during one year at a narrow road verge (12 m.) with a 8 m wide *Corynephoretum* strip and the same verge in which the *Corynephoretum* strip is, over a distance of 10 m., interrupted by trees at 25 m. from the release point. This site in the verge is marked by an arrow on the distance scale.

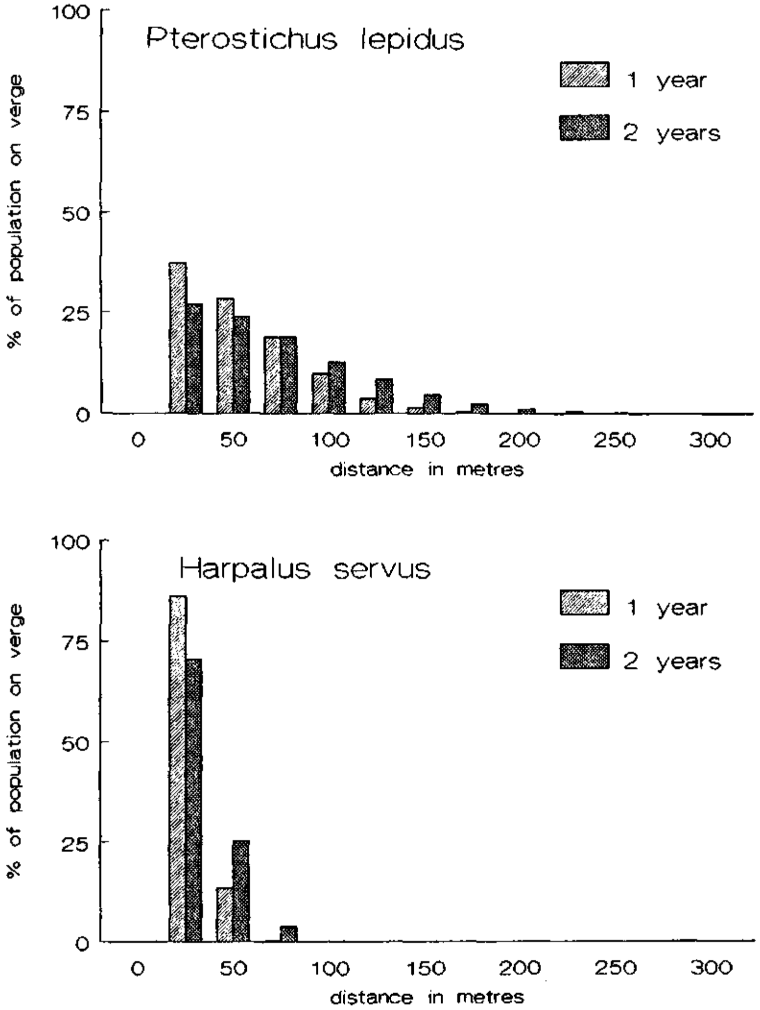

Figure 5.8. Distribution of the distances of the end positions from the release point of individuals of two carabid species in classes of 25 m., expressed as percentages of the population. Results are obtained from simulations during one and two years respectively at a narrow road verge (12 m.) with a 8 m wide *Corynephoretum* strip.

When losses to areas adjacent to corridors are low, the magnitude of the dispersal flow increases. On the long run this effect will result in a more effective dispersal (more about this in chapter 6). However, it might affect the mean dispersal distances on the short term as well. Therefore, table 5.6 presents both the mean dispersal distances and the losses to the adjacent areas for all simulations done. In general table 5.6 shows that the higher the losses to the adjacent areas the lower the mean distance walked along the road verge. The few exceptions to this rule are discussed below. Narrow sites and narrow verges show higher losses to the adjacent areas. Because the barrier effect of an open grass vegetation towards forest is lower than that of a *Corynephoretum* vegetation towards forest, losses are higher in the first case.

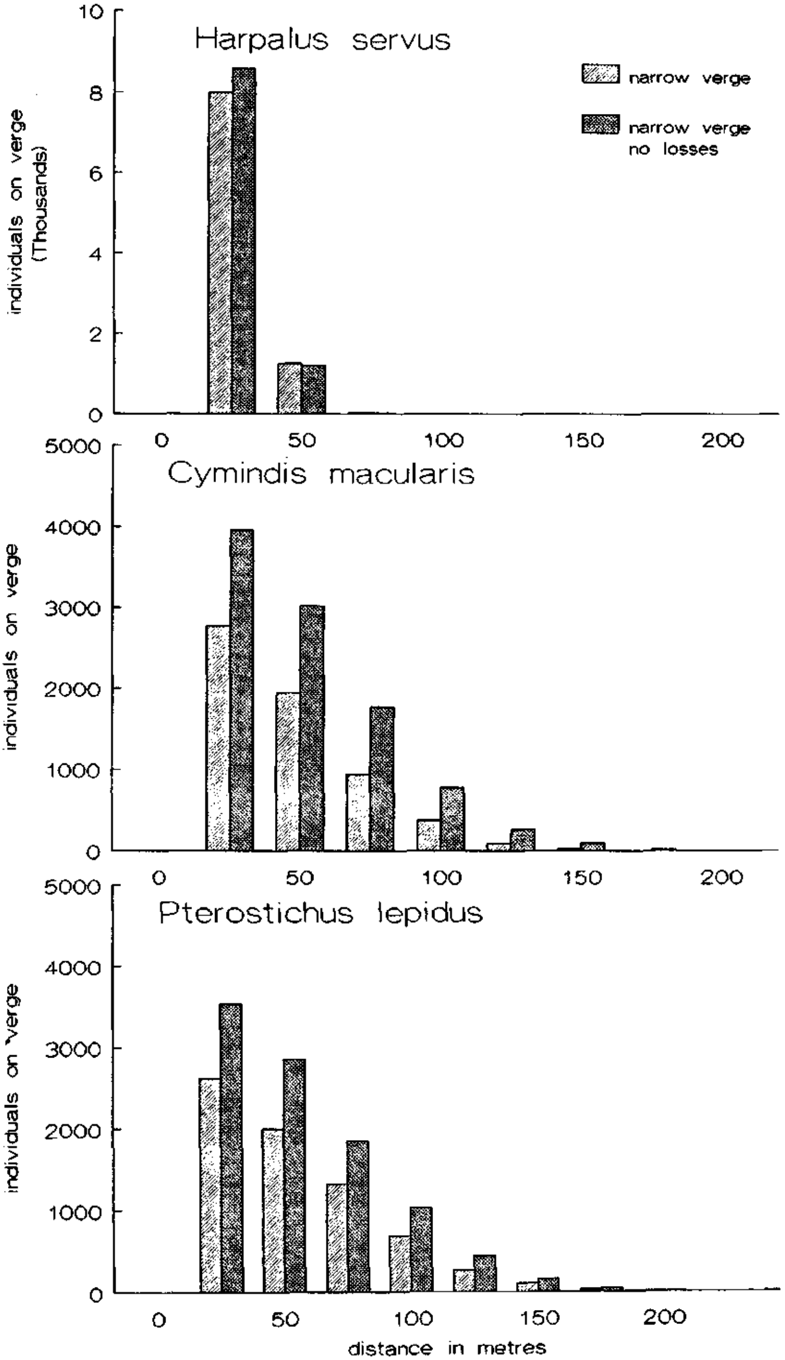

Figure 5.9. Distribution of the distances of the end positions from the release point of individuals of three carabid species in classes of 25 m. Results are obtained from simulations during one year at a narrow road verge (12 m.) with a 8 m wide *Corynephoretum* strip. and at the same verge with an absolute barrier between this strip and the forest edge to prevent beetles getting lost into this habitat (narrow verge no losses).

Table 5.6. Mean distances walked in the simulations, in metres, and losses of individuals to adjacent areas, expressed as percentages of the starting numbers, of 3 species of ground beetles in all situations tested. When not specified the starting number always was 10,000 individuals, the verge always consisted of a strip of *Corynephoretum*, except in the situation where it was replaced by an open grass strip.

	Harpalus servus		*Cymindis macularis*		*Pterostichus lepidus*	
	mean distance walked	losses to adjacent area	mean distance walked	losses to adjacent area	mean distance walked	losses to adjacent area
narrow verge	13.4 m.	5.5 %	33.6 m.	38.4 %	41.8 m.	29.4 %
narrow verge start 1000	13.7 m.	3.8 %	33.0 m.	38.1 %	41.1 m.	29.1 %
narrow verge start 100	12.3 m.	5.0 %	36.3 m.	37.4 %	42.7 m.	23.0 %
narrow verge after 2 years	19.1 m.	6.2 %	lives only 1 year		59.0 m.	35.0 %
open field	32.3 m.	no adj. areas	39.2 m.	no adj. areas	76.7 m.	no adj. areas
broad verge	19.1 m.	0.7 %	26.8 m.	10.9 %	47.3 m.	9.4 %
narrow verge with barrier	10.1 m.	7.4 %	18.6 m.	45.4 %	40.1 m.	31.6 %
narrow verge open grass strip	15.6 m.	22.2 %	21.1 m.	71.1 %	36.4 m.	46.8 %
narrow verge no losses	13.1 m.	no access to adj. areas	38.3 m.	no access to adj. areas	43.4 m.	no access to adj. areas

DISCUSSION

The results for the three species presented here show that we might expect longer dispersal distances in broad and suitable corridors. The only case in which the narrow road verge showed better results, *C. macularis*, it proved to be a species moving in a non-habitat area. So it probably tries to run away from adverse circumstances (compare Baars 1979). For such a species this kind of corridor probably is a refuge for a short time only, because it can be supposed that it is not able to reproduce there, so that a next generation can not continue dispersal (see chapter 6).

In narrow corridors dispersing animals are more often confronted with habitat borders. At those places there is a chance to leave the corridor (higher losses to the adjacent areas). On the other hand, when not moving to the other habitat the beetle has to choose a new direction, which will cause a delay in dispersal along the corridor. In a broad corridor and the open field situation beetles can make longer movements in one direction and therefore have a higher chance to cover great distances.

When by chance a beetle often is moving towards the border of a corridor, it will not move far away from the original release point. Such beetles will lower the mean distance walked by all beetles. When such beetles have a chance to leave the corridor, a number of these slow beetles will be removed from the dispersal corridor, by which the mean distance walked along the corridor will increase for the remaining beetles. This might explain the result obtained for the species *H. servus*. This species shows greater mean dispersal distances with increasing losses to the adjacent areas, but as compared to the other two species these losses are still low. Probably when the threshold to the adjacent areas will be lowered more, also a lot of individuals with only a few encounters with the border will enter the wrong type of habitat, so that especially persevering dispersers have a chance to get lost for the dispersal along the corridor, decreasing the mean distance walked.

When a heathy corridor becomes more grassy, in general dispersal distances become shorter. The species *H. servus* seems to be an exception, but at the standard narrow road verge it showed hardly any losses to the adjacent area (Table 5.6). As dispersal distances in this species are shorter in the situation with no losses to the adjacent area than at the narrow verge, it might be that when a certain portion of short dispersers can move to the adjacent area a relative large portion of long dispersers will stay in the verge. In the open grass situation the barrier to the adjacent area is smaller than in the *Corynephoretum* situation. The latter holds for the other two species too, where a very high portion of beetles leaves the verge. Probably, in the long run these losses are so high that we can hardly speak of a dispersal corridor.

Narrow sites in corridors lead to a decrease of persevering dispersers and do increase the chance of getting lost in a wrong habitat. If in such a habitat mortality would be higher and reproduction lower, such a situation can lead to a lowering of population numbers. Therefore, it is advisable to avoid such sites in a corridor, either narrow or broad.

From the results discussed it becomes clear that certain structures in road verges affect the movements of the beetles. Such results can be used to design road verges, that are more favourable for carabid beetles.

The data used sofar only concern carabid beetles in road verges. However, every kind of organism with random movements can be introduced into these simulations when the correct data input is given.

The programme presented here tries to help people in simulating the consequences of changes in the landscape for small ground-dwelling organisms, such as carabid beetles. It does not have the pretention to be perfect, for all factors involving dispersal and survival of populations are not yet known. On the other hand, it can accumulate suggestions how to get better information. The thus extended knowledge can be used to predict what may happen with populations of certain species, after changing the landscape. The programme may prevent the user, who has to structure landscapes, from making mistakes at the population level which might easily be avoided.

With this programme it will be possible to find out whether or not the kinds of corridor structures as mentioned by Mader (1984) and Mader et. al. (1990), which lead beetles to wrong kinds of habitat, will have a sink effect (Pulliam 1988). It is also possible to test where in a corridor a suitable site for reproduction and survival is necessary, like the cross-sections in a network of hedgerows, as mentioned by Burel (1989) and Petit (1994).

Decisions based on this programme not always need to be correct, but they are better than decisions made without such evidence.

Acknowledgements

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Chapter 6

EFFECTIVENESS OF ROAD-SIDE VERGES AS DISPERSAL CORRIDORS FOR SMALL GROUND-DWELLING ANIMALS: A SIMULATION STUDY

SUMMARY

Linear landscape elements are supposed to be suitable as dispersal corridors, and therefore are considered as possible solutions to mitigate the negative effects of fragmentation of more natural areas in agricultural landscapes. In the Netherlands certain road verges may offer good opportunities to connect heathland fragments. With the help of a simulation programme (with parameters estimated from field observations), we tested several concepts of road verge construction on their suitability as a dispersal corridor for carabid beetles with poor dispersal capacities.

In broad road verges long dispersal distances occur more frequently than in narrow ones. Losses of individuals to the adjacent areas are less in broad verges, leaving more individuals to continue dispersal. Only if these losses are fully compensated by reproduction, road verges may be dispersal corridors over more than a few hundreds of meters. Broader sites at the road verge, within reach of the next local population, can slightly increase the chance of long dispersal distances along the verge.

The three species studied differ in their capacities to use the road verge as a corridor, mainly depending on their rates of movement, their response to the verge borderline, and their ability to reproduce in the narrow strip.

INTRODUCTION

Habitat fragmentation is considered as one of the major problems to the conservation of the biodiversity of natural and semi-natural ecosystems of the Netherlands. In current land consolidation plans and in the National Nature Conservation Plan this notion often leads to the development of corridor strips, stepping stones, technical devices and other measures which are supposed to improve the connectivity between habitats which are regarded to be "too small or too isolated".

The ecological evidence to support such measures is, however, poor. A diagnosis of the fragmentation problem is often lacking, and an explicit choice for the best solution is usually not given. Designing a system of linear elements and stepping stones which is supposed to form a corridor is the usual option. There is practically no evidence about how such corridor systems have to be designed for particular animal or plant groups, and over which distances they can link habitat sites (Saunders & Hobbs, 1991, Vermeulen & Veenbaas, 1991, Hobbs, 1992).

This paper explores the spatial conditions under which strips of poor heathland may serve as dispersal corridors to a group of small ground-dwelling arthropods with poor dispersal capacities. To this purpose, we use a simulation model (Vermeulen & Opsteeg, 1994).

Heathland habitats were severely fragmented during the last two centuries. In 1963 only 5% of former heathlands were left, mainly scattered over the eastern and southern parts of the country. Many species which are characteristic for heathlands became rare, and often vanished from the remaining heathland areas. Evidence for the role of fragmentation in this process is accumulating (Opdam et al. 1993).

Recent studies show the effect of size and spatial configuration of remnants of heathland for the black grouse (Celada & Reijnen, unpubl.), for the carabid beetle *Agonum ericeti* (de Vries & den Boer, 1990), for heathland butterfly species (Verspui, unpubl.) and for grasshoppers (Mabelis, unpubl.). Ground-dwelling arthropods with a low dispersal power are likely to be susceptible to fragmentation. The case of carabid beetles has been documented extensively (den Boer, 1968, 1977). These arthropods frequently disappear locally under influence of temporarily adverse conditions. In a large and continuous area or in a slightly fragmented landscape, recolonization from nearby sites might occur. Such fragmented populations may persist in a network structure (metapopulation, Opdam et al. 1993). However, in a highly fragmented landscape recolonization is improbable, and presumably this is often the case for these heathland carabids. On the long term these species will disappear from all fragments and hence from the whole region (e.g. de Vries & den Boer, 1990). The decline of carabid species characteristic for poor sandy, open habitats in the Netherlands and neighbouring countries is thought to be the result of this process (Turin & Peters, 1986, Turin & den Boer, 1988, den Boer, 1990a). Some of these species are nowadays threatened by total extinction (Desender & Turin, 1989, Blab et al., 1984). For long term persistence, either the existing heathland remnants must be considerably enlarged or a network of fragments joined by corridors must be established (den Boer, 1990b, Opdam, 1987, 1990). In this paper, we try to investigate how corridors must be designed to be effectively incorporated into a network structure.

In our study, we used corridors which already existed for a considerable time: the road verges along highways in sandy moraine landscape. We took advantage of the fact that these roads originally cut heathland areas into smaller pieces. Hence, these verges were still covered by vegetation which closely resembled that of the heathlands, and some verges were still connected to heathland patches. Consequently, these road verges could be considered to be potential corridors to stenotopic carabids. These carabids may be regarded as representatives of the group of ground-dwelling arthropods with low dispersal power.

According to chapter 2 carabid beetles of poor sandy, open habitat are not avoiding roadsides. Chapter 5 and Vermeulen & Opsteeg (1994) showed that in narrow corridors the movement of some carabids is slowed down as compared to that in broader ones. Also, bottleneck passages in broad corridors reduce the probability that long dispersal distances occur. The fraction of long dispersal distances increases with the numbers of individuals in the source population, but even with an abundant source the distances covered by one generation of beetles do not exceed 100-150 m. Consequently, to be able to function over longer distances, corridors must allow reproduction.

The aim of this study is to find out over which distances road verges can be connecting corridors for carabid beetles in a landscape network, and also how corridor width, bottleneck passages, and the presence of reproduction sites in the corridor influences suitability. This suitability will be expressed in terms of the distribution of distances covered by a certain minimum number of individuals. The results can be used to design effective dispersal corridors for ground-dwelling arthropods with low dispersal capacities.

METHODS

The simulation programme

Movements of beetles in corridors of various shapes were simulated by a computer programme (chapter 5 and Vermeulen & Opsteeg, 1994). In this programme the user has to draw a model landscape encompassing different kinds of vegetation. To start a simulation, a number of beetles is released at a starting point, defined by the user. The user selects the number of days of one simulation, and the date at which the simulation starts. The programme starts with one beetle at the starting point. When the activity period of the beetle is reached, the animal starts walking. As long as the beetle keeps walking, each day it randomly chooses a walking direction. In the selected direction it starts to walk the mean distance that the kind of habitat allows adults of that species to cover in one day.

When reaching another kind of habitat the programme introduces values determining whether or not it is possible to enter this habitat. If not, then the beetle has to choose a new direction and completes the distance for that day. When the beetle is allowed to enter the new habitat, it completes the daily distance in the original direction according to the rate of movement related to that new habitat.

At the end of the day the programme determines whether or not the beetle is still alive and whether or not it has reproduced (chances are drawn from a distribution defined by the user).

For that beetle the simulation goes on till it has reached either the last day of the simulation or its maximum lifetime, if it did not die before that.

After the programme finished the first beetle, it simulates the movements for a second one in the same way, and so on, till the last beetle has walked. Then the programme determines whether or not reproduction took place. The newly born beetles start walking from the site of reproduction. They go through the same procedures as their parents. After the time given for the simulation has passed, all positions of the beetles in the landscape are fixed. The output shows these positions, together with the minimum, mean and maximum distances covered. These walking patterns are continued over the entire activity season of that species as long as the beetle is still alive. If the beetle survives diapause it might continue its walking, when the user wants to continue the simulation over more than one year. Previous simulations with this programme of dispersal during one season (year) were compared with results of mark- and recapture experiments in a field situation. Only 2 out of 50 simulations showed significant differences with the observed distances. For more information about the programme we refer to chapter 5 and Vermeulen & Opsteeg (1994).

Model parameters

Field observations of 3 different carabid species of poor sandy, open habitats, *Cymindis macularis*, *Harpalus servus* and *Pterostichus lepidus*, are used to estimate the chance to enter other kinds of habitat and the rate of movement in different vegetations (chapter 4 and Vermeulen, 1994). During the field study no records occurred of beetles passing the road. Therefore, in the simulations we assume that the road pavement itself is an absolute barrier which they do not enter.

The period of the year that the species is active was taken from the extensive data in Turin et al. (1977). This period includes the reproduction period (den Boer, unpubl.). The lifetime of individuals of a species is estimated on the basis of own observations and data from Schøtz-Christensen (1965).

Reproduction and mortality are estimated from the net reproduction values (lnR-values) obtained by den Boer for beetles on Kralo Heath (den Boer, 1981). The lnR-values, for a particular species, are derived from the numbers of adults caught each year in a number of sites during 30 years of pitfall-trapping. They represent the fluctuations of numbers in a local population and therefore include both reproduction and mortality. In the programme the values are converted to the mean net reproduction per female. The daily chance of reproduction is taken in such a way that a population of 1000 individuals is fluctuating around this number in a large homogenous habitat area. Sites which are not poor, sandy and open were considered to be marginal or non-habitat areas (forest and grass vegetations). Here, the net reproductive rate per female was arbitrarily lowered by the standard deviation. In this way we consider the most favourable kind of reaction in marginal habitats. Of course, in many of the adjacent habitats there will be no reproduction at all. In the simulations we take the percentage of females in the population to be 50%. For all species table 5.1 and the appendix give the parameter values used.

The chance of crossing borderlines between kinds of habitat and the relative rates of movement per kind of habitat are shown in Table 5.2.

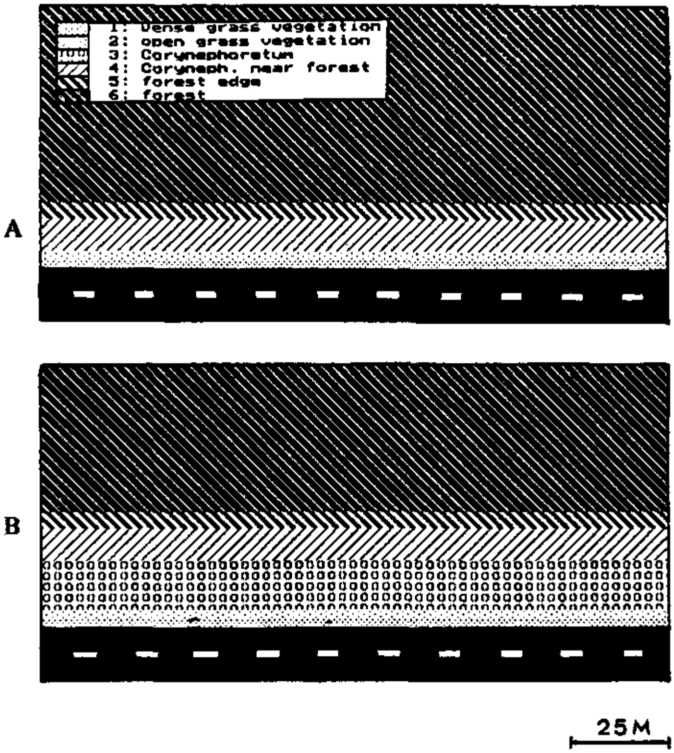

Figure 6.1. The narrow (A) and the broad (B) road verge, as tested in the simulations.

All simulations started with 1000 individuals at one starting point. The null-case was always an open situation in the preferred habitat, where the beetles could move in any direction without being hindered by other kinds of habitat. In the corridor (road verge) situation, all 1000 individuals had to move along the corridor or to enter other habitats. The *Corynephoretum*-habitat is defined as preferred habitat for the three species in the present simulations; between this and other habitats there is a certain barrier effect. In the non-*Corynephoretum* habitats they perform a lower reproduction. Only for *C. macularis*, field observations showed that this species does not reproduce at *Corynephoretum* sites close to the forest (chapter 4 and Vermeulen, 1994). Therefore, in the simulations, these sites are defined as having a low chance of reproduction for this species. All simulations were ran for 10 successive generations.

In the first set of simulations individuals of the three species were released both at a narrow (12 m), and at a broad (24 m) road verge (fig. 6.1), and an open field situation.

In the second set of simulations the reproduction on the narrow road verge was such that the successive generations had about the same number of individuals. In case of *C. macularis*, in the *Corynephoretum* near forest the chance of reproduction increased to normal (the same as in the *Corynephoretum*).

In the third set of simulations at the narrow road verge broad sites of 30 m long are introduced at intervals of respectively 40 and 75 m (fig. 6.2). The reproduction rates at these broad sites are similar to those in the open field situation.

All simulations were processed twice to check whether or not the patterns found could be generalized.

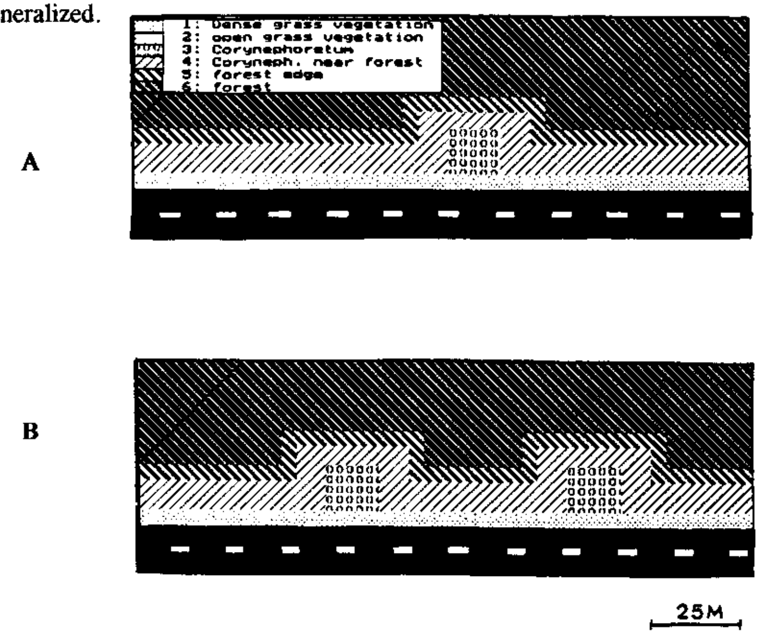

Figure 6.2. A part of the narrow road verge with broad sites at different distances , as tested in the simulations. A. broad sites of 30 m. at intervals of 75 m., B. broad sites of 30 m. at intervals of 40 m.

Simulations in open heathland, broad and narrow verges

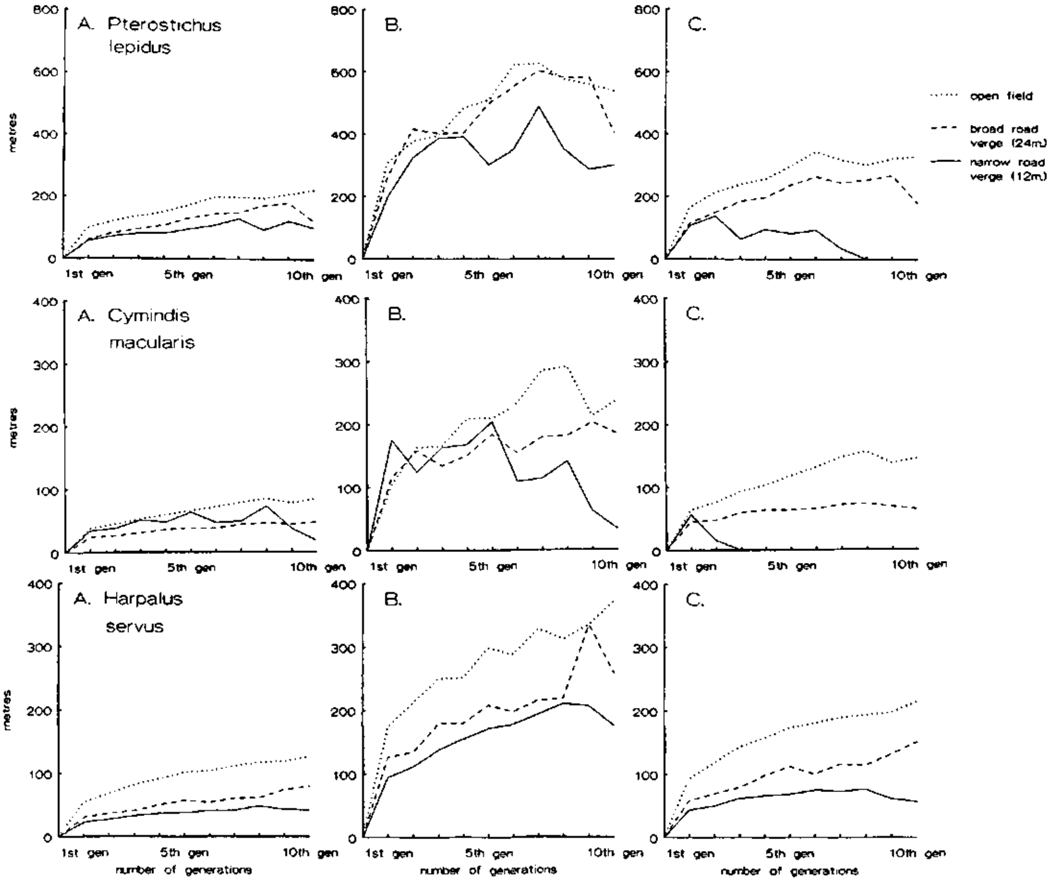

Figure 6.3. The dispersal distances covered in the successive generations in an open field situation, at a broad road verge and at a narrow road verge. A. the mean distances covered from the release point, B. The farthest distances covered, C. the distance covered by 100 individuals, which ended farthest from the release point. The reproduction rates for the separate species are similar in the three situations tested.

In both *P. lepidus* and *H. servus* the farthest mean distances were simulated for the open field, and the shortest in the narrow verge (fig 6.3a). This sequence is not found in *C. macularis*, where the results for the narrow verge are intermediate. However, the number of individuals surviving after the first generation is very small (fig. 6.4), and consequently the simulation results are open to more stochastic variation than is the case for the other species. Yet, this difference can also be explained ecologically. From Table 5.2 it can be concluded that this species moves quicker in *Corynephoretum* near forest (in the narrow verge) than in the open field *Corynephoretum*.

Interpreting mean distance values may be misleading. Because beetles choose their walking direction randomly, after some time as many beetles will disperse in a direction away from the release point as towards it. Due to this balance value the mean distance to the release point will only vary little. Depending on the circumstances this balance value will be reached within a few generations or more, and the balance distance will vary accordingly.

Therefore, we use other parameters to express the dispersal distances attained along the highway verge. Fig. 6.3b also presents the maximal distances covered by an individual of the three species. This was measured, for each generation, as the linear distance between the release point and the end position of the individual which was farthest away.

Because the directions of movement in these simulations are drawn daily from a random distribution, coincidentally individuals may disperse in a long straight line away from the release point. Sometimes the maximal distances at the road verges equal or even exceed the maxima in the open field situation. Yet, fig. 6.3b shows a tendency for the longest dispersal distances to occur in the open field, and the shortest in the narrow verge, with the broad verge in an intermediate position.

The maximal distance parameter probably is not the best parameter to indicate the distance over which recolonization might be possible. It is unknown whether one carabid beetle, even when it is a female with fertilized eggs, can found a new local population. Therefore, fig. 6.3c presents the maximal distance from the release point which is covered by 100 individuals (10% of the original 1000 individuals that started in the simulation). The limit of 10% is drawn arbitrarily. For smaller percentages the distances will be in between the maximum distance covered by one individual and the distance reached by 100 individuals. The graphs show that for all three species the narrow road verge is the least favourable corridor for dispersal. For both *P. lepidus* and *C. macularis*, after 10 generations at the broad road verge the farthest distances covered by 100 individuals decrease; at the narrow road verge these distances even drop to zero. For *H. servus* the distance at the narrow road verge decreases after 8 generations.

In the course of 10 generations the numbers of individuals in both types of roadside decrease (fig. 6.4a). At the narrow road verge this process is most dramatic. Yet, in the model *P. lepidus* and *H. servus* had a normal net reproduction at the *Corynephoretum* and *Corynephoretum*-near-forest strips (compare fig. 6.1). *H. servus*, the species with the strongest rebound at the borderline (table 5.2), suffers least from a population decline at the road verge. These observations suggest that the population decline in the corridor is caused by the losses of individuals to the adjacent areas. These losses are indeed highest at the narrow road verge (fig. 6.4b). For *C. macularis* net reproduction at the *Corynephoretum*-near-forest strip is chosen to be similar to that in the vegetation types next to the road verge. Apparently, this low reproduction level stimulates the population decrease even further.

For all three species, the losses in the broad verge are about one third of the losses in the narrow one (fig. 6.4b). *H. servus* has the smallest losses of the three species. In the broad verge, the losses for this species are so low that the numbers of individuals after one generation are close to the level in open heathland.

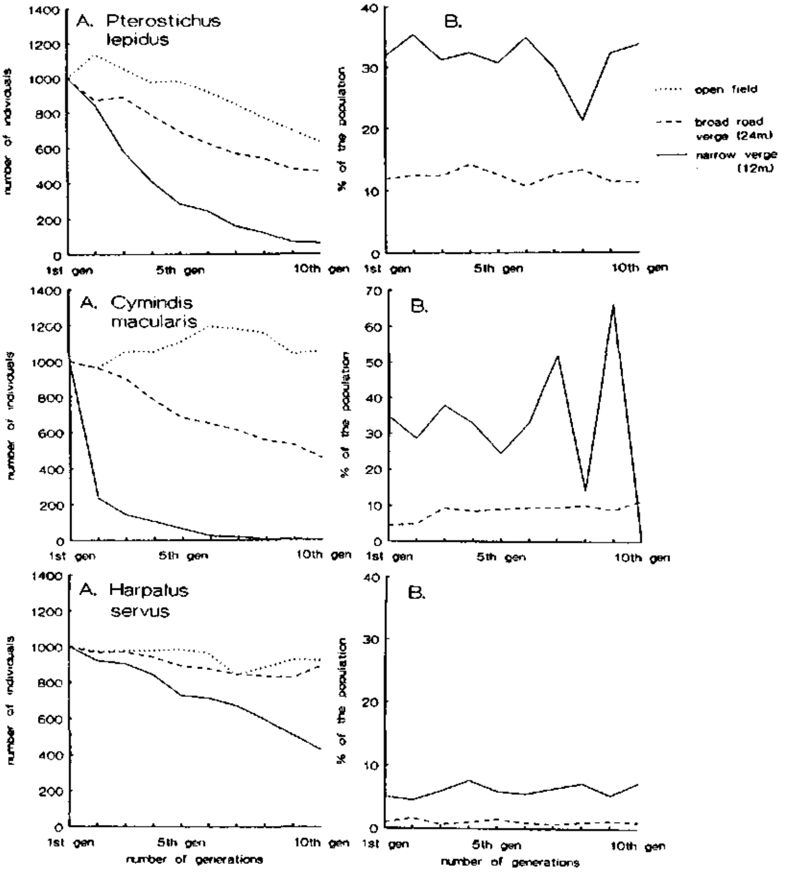

Figure 6.4. The numbers of individuals (A) and the percentage of the population lost to the adjacent areas (B) in the successive generations in an open field situation, at a broad road verge and at a narrow road verge. The reproduction rates for the separate species are similar in the three situations tested.

The role of reproduction in corridors

The above mentioned results show that the densities of beetles in road verges decrease with the passing time due to "leakage" of individuals into adjacent areas with lower net reproduction. Generation after generation the numbers of individuals dispersing diminish and consequently, the chance on long dispersal distances along the corridor decreases. However, for the species *P. lepidus* Vermeulen (1994) found evidence that a road verge may allow higher reproduction rates than the heathland it is connected to.

By increasing the reproduction rate at the narrow road verge to a level that compensates the losses, for all species tested the dispersal distances do increase compared to simulations with a reproduction rate which causes a stable population in the open field (fig. 6.5a & b). This is consistent with the higher number of individuals left after several generations (fig. 6.6a). The relative losses to the surrounding (Fig. 6.6b) do not differ. We may conclude that a higher reproduction rate leads to a higher number of long dispersing beetles.

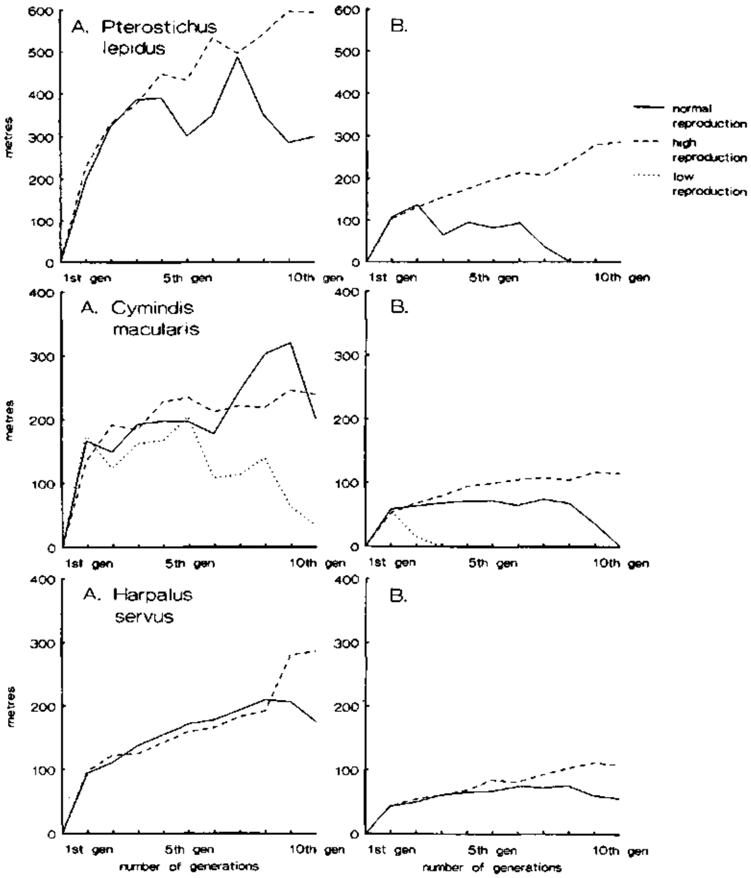

Figure 6.5. The dispersal distances covered in the successive generations at a narrow road verge, with different reproduction rates. Normal reproduction causes a stable population in an open field situation (similar to Fig. 6.3). A. The farthest distance covered, B. the distance covered by 100 individuals, which ended farthest from the release point. *C. macularis* showed in a field situation no reproduction at the road verge. Therefore, for this species also a low reproduction rate is given.

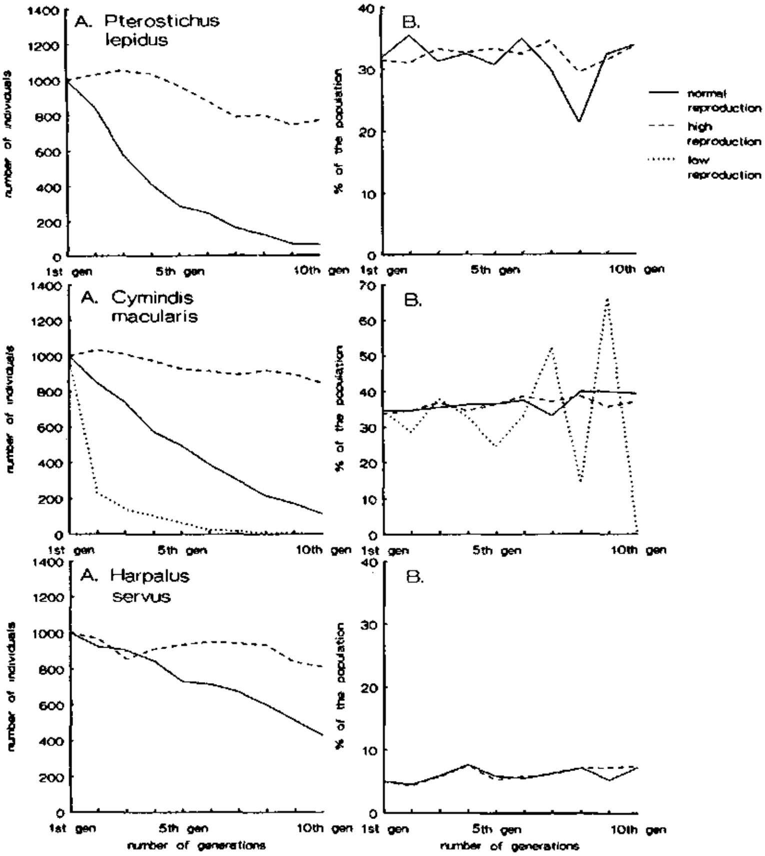

Figure 6.6. The numbers of individuals (A) and the percentage of the population lost to the adjacent areas (B) in the successive generations at a narrow road verge, with different reproduction rates. Normal reproduction causes a stable population in an open field situation. *C. macularis* showed in a field situation no reproduction at the road verge. Therefore, for this species also a low reproduction rate is given.

Broad sites in a corridor

Broad sites with suitable habitat might be introduced to a corridor to reduce the effect of a population decline on dispersal distances. Simulation results of the two cases tested (fig. 6.2) are shown in figure 6.7. The distances covered by the individual that moved farthest again gives a highly fluctuating picture (fig. 6.7a). Maximal distances covered by *P. lepidus* are longer at the road verges with broad sites, but for *C. macularis* this is only the case in the last two generations simulated at the 40-30 m. road verge. In *H. servus* distances do not increase.

In *C. macularis* dispersal distances for 100 individuals drop to only a few metres after two generations in all three situations. This is caused by the rapid decline of the population (fig. 6.8a), which leaves less than 100 individuals after 4 generations. In the other two species the decline of the population size advances more slowly. For all three species losses to the bounded areas are about similar in the three types of road verge (fig. 6.8b).

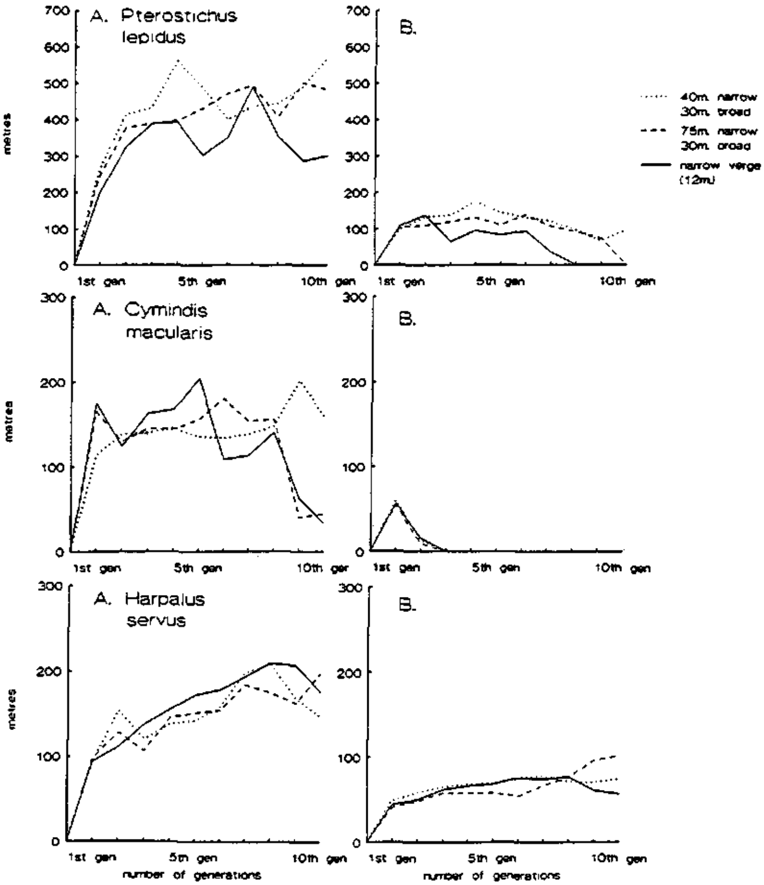

Figure 6.7. The dispersal distances covered by the successive generations at narrow road verges of a width of 12m. In two cases broad sites of a width of 24m. over a distance of 30m. were present at intervals of respectively 40 and 75m. A. The farthest distance covered, B. the distance covered by at least 100 individuals. The reproduction rates for the separate species are similar in the three situations tested.

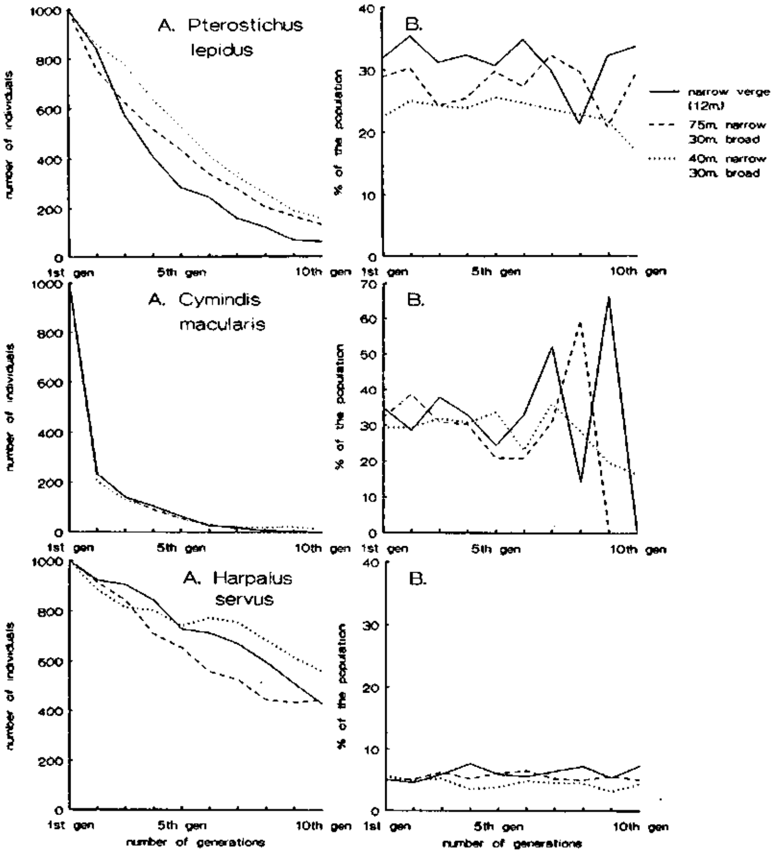

Figure 6.8. The numbers of individuals (A) and the percentage of the population lost to the adjacent areas (B) in the successive generations at narrow road verges of a width of 12m. In two cases broad sites of a width of 24m. over a distance of 30m. were present at intervals of respectively 40 and 75m. The reproduction rates for the separate species are similar in the three situations tested.

DISCUSSION

The distances covered by the beetles in these simulations are relatively short as compared to the results of Baars (1979), who for the species *Pterostichus versicolor* found a mean distance covered in one year of 160 m. The comparable species in this study, *P. lepidus*, shows a mean distance covered in one year of 76 m. This difference is probably due to the difference in collecting data for the simulations. Baars followed beetles individually by tracking radioactively marked beetles. The data used here were derived from mark-recapture experiments, in which dispersal is interrupted by repeatedly catching marked beetles in pitfall traps. This suggests that distances found in this study might be underestimations and might have to be doubled to reach more realistic levels. However, another observation counteracts this argument. Baars used eurytopic species in his experiments, whereas the species used here are regarded as rather stenotopic species (Turin et al, 1991). According to Nève de Mévergies and Baguette (1990) stenotopic species tend to walk more haphazard and therefore to move over shorter distances than eurytopic ones. If this would be a general tendency among beetles, the differences in moving distances between Baars' experiments and our simulations may be realistic.

A point of critic to the simulation model used is that it only simulates an injection of 1000 individuals at time zero at the entrance of the corridor and not more than 10 generations (10, in some species 20 years), while in the real world these numbers could very well be higher. In reality, as long as a population is present in a habitat area, there might be an inflow of individuals every year into a corridor connected to such an area. Depending on the population density in an area, this will be a small or a large inflow. Especially climatical conditions, which can differ from year to year, are thought to have a large impact on the population density (van Dijk & den Boer, 1992). In the model reproduction chances differ per habitat but stay the same through time. To avoid excessive simulation times, we have chosen for these restrictions. However, the various options simulated show relatively small effects in terms of distances over which corridors could be effective. A simulation done for 20 generations with a continuous inflow of individuals showed that the broader sites in the verge may function as local sources, supporting the dispersal flow and enlarging the distance over which the corridor functions by one order of magnitude.

This simulation study shows that corridors for ground-dwelling beetles (and invertebrates with similar habits) with poor dispersal capacities is only effective over short distances, up to an order of distances of 100 to 500 of meters. Taking into account the underestimation of distances walked in the field situation and the restrictions of the simulations these distances might be larger in reality and under more advantageous circumstances, but they will probably never exceed 1 to 2 km. These short distances are due to the haphazard way of moving, without a tendency to stick to a particular direction, in combination with the permeability of the corridor borderline. In narrow verges, up to one third of the animals is lost to the adjacent strips of land, where they have small chances to survive. In the case of *H. servus*, which has a higher tendency to return at a habitat border than the other species have (chapter 4 and Vermeulen, 1994), it can be seen that the population decline is less dramatic and the corridor is more effective (fig.'s 6.3 and 6.4). Also, encounters with habitat borders are more frequent at narrow corridors. This causes a delay in dispersal as compared to more broad corridors (chapter 5 and Vermeulen & Opsteeg, 1994). The combined effect is that narrow corridors (12 m) are less effective than broad corridors (24 m).

The model used here assumes normal reproduction in the corridor. In other words, if the habitat quality is inferior to that of the source area, the effectivity of the corridor will be even less than demonstrated here. The case of *C. macularis* shows this effect rather clearly. This study also demonstrates that improving the reproduction chance in the corridor results in longer dispersal distances. In the field study (chapter 4 and Vermeulen, 1994) was found that in the broader parts of the corridor, where the strip of the Corynephoretum vegetation widens, *H. servus* has a higher chance to reproduce than in narrower parts of the corridor. Hence, for species reproducing better in broad corridors, the effectivity may be improved as compared to the results simulated for broad corridors. Evidently, the higher the number of individuals, the higher the absolute number (not the proportion) of individuals performing long dispersal distances. This will be relevant for the chance to found a new population. Thus, a corridor which is planned to connect habitat sites in a landscape network will be more effective, the larger the population it is connected to, and the better it allows reproduction. Though in the programme it is possible to higher up the reproduction rate in a certain habitat (increasing habitat quality), sofar there is almost nothing known about this. In fact, we can only guess what the reproduction rate will be in a certain kind of corridor.

We conclude that road verges may function as corridors for carabid beetles with poor dispersal capacities only if the species is able to reproduce well in the corridor strip, and if so only up to distances of 1 till 2 km within 10 years under optimal circumstances. Such verges should be at least 20-30 m wide and contain suitable habitat in the central strip. Broader corridors are still better (because losses to adjacent areas are relatively lower), but in the case of road side verges not always realistic. Habitat patches connected by corridors are thought to form a network to eliminate regional extinction (chapter 2). In the case of ground-dwelling arthropods like carabid beetles the patches have to be situated rather close to each other or to be connected by broad corridors preferable with larger sites in it were populations can exist temporarily.

Can these conclusions be extrapolated to other kinds of corridor or to other species? We claim that similar conclusions will be obtained for studies on corridor strips in general, as long as the rebound at the borderlines is similar to the situation which has been simulated. Nothing is known about the rebound effect of agricultural fields.

The model predictions can be generalized to species with randomized walking patterns, which do not follow any particular direction ("no memory"), and have a similar rebound reaction to the borderline, and similar walking speed in the vegetation structures of the corridor, like most not flying ground-dwelling arthropods.

The consequence of our conclusions would be that corridors which are thought to connect fragments of habitat must be much broader than the average corridor which is suggested in current landscape plans. This is the more so because adverse effects of activities in adjacent land (for example fertilization) will lower the habitat quality in the border zone more than is the case for highway verges bordered by woodland. Also, such corridors will be cut in sections by various types of barriers, including roads. This will lower even further the effectiveness of the corridor as a connection.

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Chapter 7

GENERAL DISCUSSION

The role of corridors in nature conservation

In West European countries, where semi-natural habitats have become highly fragmented, much attention has centred on reconstructing links between habitat patches, often based more upon conjecture than on sound ecological evidence. A fact is that when a species is locally extinguished inside large areas of nature it can return from other places in that area without problems. Therefore Noss (1987) makes the point that nature shows considerable connectivity and that, in absence of data to the contrary, this is a compelling argument for creating and maintaining networks. Linear corridors may be seen as important components of a regional conservation strategy, with considerable resources invested in such an approach. When not based upon a critical analysis of the underlying ecological principles and processes, these efforts might be in vain.

For carabid beetles the importance of exchange of individuals between local populations for the survival of species is already demonstrated by den Boer (1990a, b & c). In networks, consisting of linear corridors connecting fragmented habitat remnants, sufficient exchange is assumed to occur by which a metapopulation should be established (see also Dawson, 1994). However, the present study does not provide evidence that in such networks the survival of carabid beetles will be extended. To demonstrate recolonization of empty habitat patches via corridors dispersal movements from one patch to another have to be monitored for a long period. As in corridors carabid beetles do not bridge distances longer than a few hundred metres per year (chapter 3) the length of the corridor may be an important obstacle for exchange between patches. However, at least some of the underlying ecological principles and processes of dispersal corridors for carabid beetles could be studied. When in network structures linear corridors should be established, the conditions under which the best results might be expected are provided by this study (chapters 5 & 6).

Road verges: dispersal corridors, refugia or both?

On British heathy road verges Eversham and Telfer (1994) recorded the presence of a divers, stenotopic carabid fauna with many teneral beetles, and suggested that those verges were suitable habitat sites. They preferred to call these road verges "refugia" rather than corridors, by which they mean a place where species can survive during adverse periods elsewhere. However, for a species which is present in high numbers along the entire verge and which reproduces there sufficiently, which indeed can be established by the presence of teneral individuals, a road verge can be more than just a refugium. When a heathy strip at a road verge is a permanent ribbon-like habitat, this may promote exchange of individuals between local populations bordering the verge. When remnants of heathland are connected with such a verge, and exchange of individuals occurs between these areas and the local populations at the verge, the latter is a kind of bridge habitat or "corridor". The results of the present field study (chapter 2 & 3) indeed confirm that heathy road verges can be permanent ribbon-like habitats for several species of heathlands. When located between two fragments of heathland, a suitable road verge can facilitate exchange between local populations of certain species as could be established by studying the movements of individuals of these species.

The road as a barrier; advantages of dispersing along the verge

Observations on carabid beetles in this study suggested that none of the marked individuals crossed the road pavement (chapter 3). Of course, the chance of crossing the pavement alive must be almost zero with a traffic pressure of 30,000 cars per day as at the A1. However, as discussed in chapter 4, most beetles probably do not even reach the road pavement, because the dense grass vegetation bordering the pavement is only occasionally entered. Furthermore, the asphalt itself seems to be a very hostile environment: during this study beetles thrown upon the pavement immediately started to run back to the verge. So even beetles penetrating the dense grass strip, 1 to 2 m. wide and bordering almost all road pavements, will only rarely enter the road pavement. Therefore, for small ground-dwelling animals like carabid beetles the road pavement itself can be regarded as an absolute barrier. The simulations in chapter 6 showed that when losses to areas surrounding corridors are diminished, dispersal through a corridor will be improved in the long term. In this respect, it can be expected that the broad road verges which are often present in the centre of highways, and which are bordered at both sides by roads, could be highly effective dispersal corridors for small ground-dwelling animals, if there would be some connection with suitable habitat fragments (e.g. via small underpasses, made suitable for such animals).

Though small ground-dwelling animals might profit from corridors bordered by roads, this might not apply to small flying animals. During this study at the area of drift sand, about 10 times more small flying animals were caught in a window trap than in a window trap placed at the road verge at only 200m. away. The cause of this large difference is not known, but it is supposed that the passing traffic is killing a lot of these flying animals.

Other animals than carabids that might profit from corridors

Animals characteristic for the kind of habitat presented by a certain corridor structure and actually observed there, might indeed use this structure as a corridor (Ferris-Kaan, 1995). During my field work various kinds of animals, which were not entering from the surrounding habitats, were observed at the road verges. Some of them, like adults of ant lions and grasshopper species from heathlands, could have flown in. Nevertheless, they settled and reproduced at the road verge. Therefore, such sites might support dispersal to areas further away, i.e. it might be a stepping stone. Many of the species found in the verges were ground-dwelling animals such as carabid beetles, so they could not have flown in. Among them were also vertebrate species such as *Lacerta vivipara* (three locations) and *Lacerta agilis* (one location). In the Netherlands the latter species is considered to be very rare, but it was rather numerous along the entire south exposed verge of the A1, near the Caitwickerzand: at least 21 different individuals were counted at half a kilometre of verge in a single year. At the same road verge, a few kilometres away from the study area, some specimens of *Vipera berus* were observed as well (Anon., 1993). Therefore, it seems adequate to study the benefits/costs balance between the advantages of road verges as extra habitats for reptiles such as lizard and snakes and the risk that these animals are killed by traffic when entering the road pavement. Also some rare spider species, characteristic for areas of drift sand, like *Eresus niger*, and some wolf spiders, were found at this road verge (cf. Baert & Maelfait, 1988, Maelfait & de Keer, 1990)

Species that prefer to live in ecotones might profit from road verges in a different way. For instance, nests of different species of wood ants were found at the borders of poor sandy road verges running through an area of woodland.

Heathy road verges in the Netherlands

Before the start of this study all poor sandy, open road verges in the North-East part of the Netherlands were visited. The ten supposedly most suitable verges were selected for this study. Only three of them were connected to a more or less heathy area, but without a connection to a second one (chapter 2). Until now, 1994, such road verges, i.e. real corridors, do not exist, though the number of poor sandy road verges did increase and these are certainly suitable as a habitat for stenotopic species (Vermeulen *et al.*, 1994). One of the reasons for not connecting road verges to areas of heathland might be that certain people deliberately avoided this. From discussions with managers of heathland areas adjacent to roads it became obvious that many of them regard roads as hostile and as badly looking objects in the landscape. In most instances they try to isolate the view of roads by strips of forest.

In the Netherlands, the new style of managing road verges as exhibited by the Ministry of Transport, Public Works and Water Management, is rather comprehensive. The so created poor sandy, open road verges provide often a high quality of heathy habitat where stenotopic species can survive and reproduce sufficiently. When not separated from a heathy fragment by strips of forest or other kinds of barrier, such road verges might enlarge the amount of heathland , even without connections to other fragments. However, most heathy road verges are far away from areas of heathland or drift sand. Therefore, the characteristic fauna of such areas is absent from these road verges. Nevertheless, an introduction experiment showed that many of these verges can already support local populations of even very stenotopic carabid species with low powers of dispersal (Vermeulen *et al.*, 1994). The fact that the quality of a road verge might be sufficient for stenotopic heathland species in general is indicated by the presence of stenotopic species with high powers of dispersal, *Bradycellus ruficollis*, *Trichocellus cognatus*, *Pterostichus diligens* and *Olistophus rotundatus*.

When a road verge is a permanent habitat it also can get the status of a refugium in case of adjacent habitat areas becoming unsuitable or are cut off. Animals can survive in such sites for a certain period to repopulate the adjacent habitat areas after conditions have improved there. In the Netherlands an example of this was found at the A1 near Rijssen. Here a nice heathy verge of about 50-60m. wide in excellent condition is present. Two more or less heath-like areas were connected by this verge. In better times these two fragments must have been covered with heath but now they are dominated by *Molinia*. Only three stenotopic species of heathlands were caught in these fragments, whereas at the verge 13 stenotopic species were present. Because many of these species are not able to fly, the verge is created rather recently, and as no other areas of heathland were connected with it, these species at the road verge must have originated from these two fragments when these were still suitable. When these fragments are managed well the heathland species will recolonize it from the verge.

Recommendations for corridor management and nature conservation

First, it is necessary to state that the best way of connecting heathy fragments will be, of course, integration of several fragments into a newly developed heathland area, as will be done in the project "Goudplevier" (golden plover) of the Dutch nature conservation organization "Natuurmonumenten". In such a continuous area the loss of dispersing individuals to unsuitable surrounding areas is much smaller, resulting in increasing effectiveness of (re)colonizing reproduction sites. However, as such projects consume a lot of territory, only in a few cases such projects will be possible. Therefore, as a second solution corridors can be used to connect isolated habitat fragments.

An effective corridor must include a strip of habitat similar to the habitat sites it is supposed to connect. So two heathland areas can only be connected by a heathy strip and not by a hedgerow, as has been proposed in some nature developing plans. In farmland landscapes with a highly intensive agriculture, strips of heathy habitat have to be buffered by broad zones in which the in flow of nutrients from adjacent fields is deposited. Moreover, such corridors must kept free from shrubs, while the excess nutrient inflow in the heathy strip must be removed by yearly mowing or occasional sod removal. Such corridors are expensive to keep effective. When large strips of habitat are available near valuable habitat fragments it is advised to remove the barriers between them. Even if such strips can not connect other habitat fragments, under certain conditions they might enlarge the amount of habitat available for animals living in and depending on habitat fragments. For instance, it would be advisable to remove all trees separating areas of heathland from broad heathy road verges. This will increase the chance of survival of heathland species, as mentioned above in the example of the A1, near Rijssen. However, when trees have to be removed also the significance of those trees for other animals have to be taken into consideration. For forest species they may have a corridor function too (Plat *et al.*, 1995) and to recover such function by newly planted trees will take at least several decades (Szyszko, 1978, Gruttke & Willecke, 1993 and Gruttke, 1994).

To find out whether a proposed corridor is effective, the simulation programme, presented and used in chapters 5 and 6, might be a helpful tool. It gives exact information about expected dispersal distances and dispersing numbers of individuals in different kinds of corridor. This can be misleading because the simulation programme "imitates" the actions of individuals of species that are thought to be involved in dispersal. Although the results obtained by the programme were similar to those from the field study, it can not be excluded that some properties of the organism, affecting their dispersal, are neglected (see chapter 5 & 6). Also, when a corridor is suitable for a certain species, it need not be for another species. The best procedure will be to plan corridors as broad and short as possible. When this is done, simulations can provide both useful information about dispersal in such corridors, and about the kind of problems that can be expected. It will also indicate where broader reproduction sites should be planned. It is advisable to test this in the first place for the most vulnerable species that are supposed to profit from the corridor.

REFERENCES

Anon. (1988) DWW wegwijzer nr 1. Ecological perspectives of grazy road-verge vegetation, Rijkswaterstaat, The Netherlands.

Anon. (1990) *Natuurbeleidsplan, regeringsbeslissingen*. Min. v. Landbouw, Natuurbeheer en Visserij, Tweede kamer der Staten-Gen., The Netherlands, 21 149, 2-3: 1-272.

Anon. (1993) Addergebroed maakt veel pennen los, Boomblad 5, IBN-DLO, Wageningen.

Apeldoorn, R.C. van, Oostenbrink, W.T., Winden, A. van & Zee, F.F. van der (1992). Effects of habitat fragmentation on the bank vole, *Clethrionomys glareolus*, in an agricultural landscape. Oikos, **65**, 265 - 274.

Aukema, B. (1986) Winglength determination in relation to dispersal by fligth in two wing dimorphic species of Calathus Bonelli (Coleoptera, Carabidae) In P.J. den Boer, M.L. Luff, D. Mossakowski & F. Weber (eds.) *Carabid beetles, their adaptations and dynamics*. Gustav Fisher, Stuttgart, 91 - 99

Baars, M.A. (1979) Patterns of movement of radioactive carabid beetles. Oecologia, Berl., **44**, 125 - 140

Beart, L & Maelfait, J-P. (1988) Araignees des versants d'exposition nord et sud d'une autoroute en tranchee dans une colline sablonneuse. C.R. Xème Coll. europ. Arachnol., Bull. Soc. sci. Bretagne, **59**, I, 17 - 24

Batschelet, E. (1981). *Circular statistics in biology*. Academic Press, London pp. 1-58.

Bauer, L.J. (1989) Moorland beetle communities on limestone habitat islands. I. Isolation, invasion and local species diversity in Carabids and Staphylinids. Journal of Animal Ecology, **58**, 1077 - 1098.

Blab, J., Nowak, E., Trautmann, W. & Sukopp, H., 1984. *Rote Liste der gefährdeten Tiere und Pflanzen in der Bundesrepublik Deutschland*. Kilda-Verlag: 75 - 83.

Boeken, M. (1987) *De loopkevers (Cicindelidae en Carabidae) van Nederland*. Jeugdbondsuitgeverij, Utrecht.

Boer, P.J. den (1968). Spreading of risk and stabilization of animal number. *Acta Biotheor. (Leiden)*, **18**, 165-94.

Boer P.J. den (1971) On the dispersal power of carabid beetles and its possible significance. In P.J. den Boer (ed.) *Dispersal and dispersal power of carabid beetles*. Misc. Pap. 8 Landbouwhogeschool Wageningen, The Netherlands.

Boer, P.J. den (1977) *Dispersal power and survival. Carabids in a cultivated countryside*. Misc. Pap. LH Wageningen **14**, II+190 the Netherlands.

Boer, P.J. den (1979) The significance of dispersal power for the survival of species, with special reference to the carabid beetles in a cultivated countryside. Fortschr. Zool. **25**, 79 - 94. Gustav Fischer, Stuttgart.

Boer, den P.J. (1981) On the survival of populations in a heterogeneous and variable environment. Oecologia, Berl., **50**, 39 - 53.

Boer, P.J. den (1985) Fluctuations of density and survival of carabid beetles. Oecologia **67**, Springer-Verlag, Berlin: 322 - 330.

Boer, P.J. den (1986) What can carabid beetles tell us about dynamics of populations? In P.J. den Boer, M.L. Luff, D. Mossakowski & F. Weber (eds.) *Carabid beetles, their adaptations and dynamics*. Gustav Fisher, Stuttgart, 315 -330.

Boer, P.J. den (1990a) Density limits and survival of local populations in 64 carabid species with different powers of dispersal. J. evol. Biol. **3**, 19 - 48.

Boer, P.J. den (1990b) The survival value of dispersal in terrestrial arthropods. Biol. Conserv., **54**, 175 - 192.

Boer, P.J. den (1990c) Isolatie en uitsterfkans. Landschap **6** (2). 101 - 119

Burel, F. (1989) Landscape structure effects on carabid beetles spatial patterns in western France. Landscape ecol. 2, 215 - 226

Butovsky, R.O. (1994). Carabids in roadside ecosystems: perspectives of bioindication. In K. Desender, M. Dufrêne, M. Loureau, M. Luff & J-P. Mealfait (eds.) *Carabid beetles: ecology and evolution*. Kluwer academic press, the Netherlands, pp. 241 - 246.

Dawson, D. (1994) Are habitat corridors conduits for animals and plants in a fragmented landscape? Areview of the scientific evidence. English Nature Research Report 94, English Nature, Peterborough.

Desender, K. & Turin, H. (1986) Overeenkomsten en verschillen bij recente veranderingen in de samenstelling van de loopkeverfauna in vier West-Europese landen (Coleoptera, Carabidae). Nieuwsbrief European Invertebrate Survey Nederland **17**, 23 - 32.

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, Cincindelidae). Biol. Conserv., **48**, 277 - 294.

Diamond, J.M. (1975) The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. Biol. Conserv. **7**, 129 - 146.

Dijk, van Th.S (1986) Changes in the carabid fauna of a previously agricultural field during the first twelve years of impoverishing treatments. Neth. J. of Zool. **36**, 413 - 437

Dijk, van Th.S. and den Boer, P.J., 1992. The life histories and population dynamics of two carabid species on a Dutch heathland. 1. Fecundity and the mortality of immature stages. Oecologia Berl., **90**, 340 - 352.

Elton, C.S. (1958). The ecology of invasions by animals and plants. London: Methuen & Co Ltd, New York: John Wiley & Sons Inc.

Ent, van der L.J. & Dijk, van Th.S (1991). Individual walking behaviour of *Carabus Problematicus* in a dutch forest as recorded by a portable radar-detection system. *Proc. Fourth European Congr. Entomol. XIII, Int. Symp. für die Entomofaunistik Mitteleuropas.* Hungarian Nat. Hist. Mus., Budapest, pp. 115 - 121.

Essen, van S. (1993) *Loopkeverinventarisatie Dwingelerveld 1991*. Grafish service centrum, Wageningen.

Eversham, B.C. & Telfer M.G. (1994) Conservation value of roadside verges for stenotopic heathland *Carabidae*: corridors or refugia? Biodiv. and Conserv., **3**, 538 - 545

Everts, E. (1898) Coleoptera Neerlandica de schildvleugelige insecten van Nederland en het aangrenzend gebied, deel 1, M. Nijhoff, 's Gravenhage. 25 - 107

Faber, F.J. (1942) *Nederlandse Landschappen, bodem, grond en geologische bouw.* J.Noordrijn en zn N.V., Gorinchem.

Ferris-Kaan, R. (1995) Management of linear habitats for wildlife in british forests. In D. Saunders (ed) *Nature Conservation 4: The role of Networks*. Surrey Beatty and Sons, Chipping Norton.

Gardner, S.M. (1991) Ground beetle (Coleoptera: Carabidae) communities on upland heath and their association with heathland flora. Journ. of Biogeogr. **18**, 281 - 289

Getz L.L., Cole, F.R. & Gates, D.L. (1978) Interstate roadsides as dispersal routes for *Microtus pennsylvanicus*. J. Mammal. **59**. 208 - 212

GENSTAT 5 Committee (1987) Genstat 5. reference manual. Clarendon Press, Oxford.

Gilpin, M. & Hanski, I (1991) *Metapopulation Dynamics: Empirical and Theoretical Investigations*. Linn. soc. of London, Ac. press Hartcourt Brace Janavovich Publishers, London.

Grüm, L. (1971a) Spatial differentiation of the *Carabus* L.(Carabidae, Coleoptera) mobility. Ekol. Polska, **19** (1), 1 - 34.

Grüm, L. (1971b) Remarks on the differentiation in Carabidae mobility. Ekol. Polska, **19** (3), 1 - 10.

Gruttke, H. (1994) Dispersal of carabid species along a linear sequence of young hedge plantations. In K. Desender, M. Dufrêne, M. Loureau, M. Luff & J-P. Mealfait (eds.) *Carabid beetles: ecology and evolution*. Kluwer academic press, The Netherlands, pp. 299 - 303.

Gruttke, H. & Willecke, S. (1993) Tierökologische Langzeitstudie zur Besiedlung neu angelegter Gehölzanpflanzungen in der intensiv bewirtschafteten Agrarlandschaft - ein E+E-Vorhaben. Natur und Landschaft **68** nr. 7/8, Verlag W.Kohlhammer Gmbh, Stuttgart. 367 - 376.

Heydemann, B. (1957). Die Biotopstruktur als Raumwiderstand und Raumfülle für die Tierwelt. Verh. Deut. Zool. Ges. Hamburg, **50**, 332 - 47.

Hobbs, R.J. (1992). The role of corridors in conservation: solution or bandwagon? Tree, **7** (11), 389 - 392.

Hopkins, P.J. & Webb, N.R. (1984) The composition of the beetle and spider faunas on fragmented heathlands. Journ. of appl. ecol., 935 - 946

Huizen, T.H.P. van (1980). Bouw van loopkevers en algemene technieken van onderzoek.

Huizen, T.H.P. van (1980) Species of Carabidae (Coleoptera) in which the occurrence of dispersal by flight of individuals has been shown. Ent. Ber., Amst. **40**. 166 - 168

Huizen, T.H.P. van (1990) "Gone with the wind":Fligth activity of carabid beetles in relation to wind direction and reproductive state of females in flight. In N.E. Stork (ed.), *The role of ground beetles in ecological and environmental studies*. Intercept, Andover, 289 - 293

Huizen, T.P.H. van & Aukema, B. (1992) Additional records of carabids caught in window traps in Drenthe and Oost-Flevoland (Coleoptera: Carabidae). Ent. Ber., Amst. **52**. 12

Johnson, A.R., Milne, B.T. & Wiens, J.A. (1991) Diffusion in fractal landscapes simulations and experimental studies of tenebrionid beetle movements. Ecology **73**, 1968 - 1983

Kam, J. van de (1984) *Spectrum atlas van de beschermde natuurgebieden Nederland & België*. Uitgeverij Het Spectrum, Utrecht.

Klazinga, N. & Vries, H.H. de (1994) Walking distances of five differently sized ground beetle species. In M.J. Sommeijer and J. van der Blom (eds), *Proceedings of the section expermental and applied entomology*. Vol. 5. Netherlands Entomological Soceity, Amsterdam, pp. 99 - 100

Levins, R. (1970) Extinction. In Gerstenhaber, M. (ed.) *Some mathematical problems in biology*. Am. Mathemat. Soc., Providence, RI, 77 - 107

Lindroth, C. (1974) *Handbooks for the identification of British insects Coleoptera Carabidae*, Vol.IV. Part 2, Royal Entomological Society of London.

Mabelis, A.A. & Velden, van M.C. (1992) Bosjes in het cultuurlandschap als ecologische eilanden voor ongewervelden; de rol van oppervlakt en isolatie. RIN-rapport 92/9, Instituut voor Bos- en Natuuronderzoek, Leersum, The Netherlands.

MacArthur, R.H. & Wilson, E.O. (1967) The theory of island biogeography. Princeton University Press, New Jersey.

Mader, H.J. (1979) Biotopisolierung durch Straßenbau am Beispiel ausgewählter Arten - Folgerungen für die Trassenwahl, Ber. Akad. für Naturschutz und Landschaftspflege, 56 - 63

Mader, H.J. (1984) Animal habitat isolation by roads and agricultural fields. Biol. Conserv. 29, 81 - 96

Mader, H.J. (1987) Straßenränder, Verkehrsnebenflächen -Elemente eines Biotopverbundsystems? Natur und Landschaft 62 nr. 7/8, Verlag W.Kohlhammer Gmbh, Stuttgart. 296 - 299

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

Maelfait, J-P & de Keer, R. (1990) The border zone of an intensively grazed pasture as a corridor for spiders (Araneae). Biol. Conserv. 54, 223 - 238

Mols, P.J.M. (1986) Predation in the carabid beetle *Pterostichus coerulescens* L. In P.J. den Boer, L. Grüm & J. Szyszko (eds.) *Report of the fifth meeting of Europen Carabiodologists*, Warsaw Agricultural University SGGW-AR, Warsaw. pp. 49 - 58

Neve de Mévergies, G. & Baguette, M. (1990) Spatial behaviour and microhabitat preferences of *Carabus auronitens* and *Carabus problematicus* (Coleoptera, Carabidae). Acta Oecologica 11 (3), 327 - 336.

Neumann, U. (1971) Die Ausbreitungsfähigkeit von Carabiden in den Forstlichen Rekultivierungen des Rheinischen Braunkohlenreviers. In P.J. den Boer (ed.) *Dispersal and dispersal power of carabid beetles*. Misc. Pap. 8, Landbouwhogeschool Wageningen pp. 89 - 103

Norusis, M.J. (1988) SPSS/PC+ V2.0 Base Manual for the IBM PC/XT/AT and PS/2, SPSS Inc. Chicago.

Noss, R.F. (1987) Corridors in real landscapes: a reply to Simberloff and Cox. Conserv. Biol. 1, 159 - 164.

Nijdam, B. & Van Buren, H. (1983) *Statistiek voor de sociale wetenschappen. deel 2 Kansverdelingen, toetsings- en schattingstheorie*. Samson uitgeverij, Alphen aan de Rijn/Brussel.

Opdam, P. (1987) De metapopulatie: model van een populatie in een versnipperd landschap. Landschap 4, 289 - 306, the Netherlands

Opdam, P. (1990) Dispersal in fragmented populations: the key to survival. In R.G.H. Bunce and D.C. Howard (eds.), *Species dispersal in agricultural habitats*. Belhaven Press London, New York. 3 - 173.

Opdam, P. & Hengeveld, R. (1990) De versnippering van het Nederlandse landschap. Effecten op planten- en dierpopulaties. Publicatie RMNO 45, pp. 95 - 158.

Opdam, P., Van Apeldoorn, R., Schotman, A. and Kalkhoven, J., (1993) Population responses to landscape fragmentation. In C. C. Vos and P. Opdam (Eds.), *Landscape ecology of a stressed environment*. Chapman and Hall, London,pp. 147 - 171.

Petit, S. (1994) Diffusion of forest carabid beetles in hedgerow network landscapes. In K. Desender, M. Dufrêne, M. Loureau, M. Luff & J-P. Mealfait (eds.) *Carabid beetles: ecology and evolution*. Kluwer academic press, the Netherlands, pp. 339 - 343.

Plat, S., Vermeulen, H.J.W. & Kuivenhoven, P. (1995) Verbindingsbanen voor loopkevers in versnipperd Nederland. De levende Natuur (in press).

Pulliam, H.R. (1988) Sources, sinks, and population regulation. Am. Nat. 132, 652 - 661

Saunders, D.A. & Hobbs, R.J. (eds) (1991). *Nature Conservation 2: The role of corridors*. Surrey Beatty and Sons, Chipping Norton.

Rijnsdorp, A.D. (1980) Pattern of movement in and dispersal from a dutch forest of *Carabus problematicus* Hbst. (Coleoptera, Carabidae). Oecologia **45**, 274 - 281

Schuring, H., Beemt, F. van den & Ruiten, T. van (1992) Veranderend landschap, Min. van Landbouw, Natuurbeheer en Visserij, the Netherlands.

Schøtz-Christensen, B. (1965). Biology and population studies of Carabidae of the Corynephoretum. Natura Jutlandica, **11**. pp. 15 - 18.

Sluijs, J. van der & Vissers, J. (1991) Wegbermbeheer bij Rijkswaterstaat. In: Wegbermen, betekenis voor vegetatie en fauna, H.Heemsbergen et al. Vakgroep Vegetatiekunde, Plantenoecologie en Onkruidkunde; L.U.W., Wageningen. 71 -78.

Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*, Freeman and comp. New York, 128 - 683.

Soulé, M.E. & Gilpin, M.E. 1991. The theory of wildlife corridor capability. Pages 3-8 *in* D.A. Saunders & R.J. Hobbs (eds.) *Nature Conservation 2. The Role of Corridors.* Surrey Beatty & Sons, Chipping Norton, Australia.

Szyszko J. (1978) Some remarks on the biometric characteristics of populations of selected *Carabidae (Coleoptera)* species in various forest habitats. Pol. Pismo entomol. **48**, 49 - 65

Turin, H. (1989) De toestand van de loopkeverfauna in N.B.P.-regio's. Nieuwsbrief European Invertebrate Survey Nederland **19**. 11 - 22.

Turin, H. (1990) Naamlijst voor de Nederlandse loopkevers (Coleoptera: Carabidae). Ent. Ber., Amst. **50**. 61 - 72.

Turin, H., J. Haeck, and R. Hengeveld (1977) *Atlas of the carabid beetles of The Netherlands*. Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Reeks 86, Amst.

Turin, H and Peters, H., (1986) Changes in the distribution of carabid beetles in The Netherlands since about 1880. I: Introduction. In: P.J. den Boer, M.L. Luff, D. Mossakowski and F. Weber (eds), *Carabid beetles, Their adaptations and dynamics*. Fischer, Stuttgart,pp. 489-495.

Turin, H. & Boer, P.J. den (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). Biol. Conserv. **44**. 179 - 200.

Turin, H., Alders, K., Boer, P.J. den, Essen, S. van, 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

Usher, M.B. (1992) Management and diversity of arthropods in *Calluna* heathland. Biodiv. and Conserv., 1, 63 - 79

Verboom, B. & Van Apeldoorn, R. (1990). Effects of habitat fragmentation on the red squirrel, *Sciurus vulgaris* L. Landscape ecology vol. **4**, 171 - 176.

Vlerk, I.M. van der & Florschütz, F. (1949) Nederland in het ijstijdvak. Uitgeversmaatschappij W. de Haan N.V. Utrecht.

Vermeulen, R. (1994). The effects of different vegetation structures on the dispersal of carabid beetles from poor sandy heath- and grasslands. In K. Desender, M. Dufrêne, M. Loureau, M. Luff & J-P. Mealfait (eds.) *Carabid beetles: ecology and evolution*. Kluwer academic press, the Netherlands, pp. 389 - 394.

Vermeulen, H.J.W. & Veenbaas, G. (1991). The effect of connections between heathy habitat fragments on the survival of stenotopic ground-dwelling arthropods. *Proc. Fourth European Congr. Entomol. XIII, Int. Symp. für die Entomofaunistik Mitteleuropas.* Hungarian Nat. Hist. Mus., Budapest, pp. 387-92.

Vermeulen, R. & Opsteeg, T. (1994). Movements of some carabid beetles in road-side verges. In K. Desender, M. Dufrêne, M. Loureau, M. Luff & J-P. Mealfait (eds.) *Carabid beetles: ecology and evolution.* Kluwer academic press, the Netherlands, pp. 395 - 400.

Vermeulen, H.J.W., Spee, A.J., Mealfait, J-P. & Butowski, R.O. (1994) Road-side verges as a new habitat for carabid beetles of heathlands. In M.J. Sommeijer and J. van der Blom (eds), *Proceedings of the section expermental and applied entomology.* Vol. 5. Netherlands Entomological Soceity, Amsterdam, pp. 101 - 108

Vries, H.H. de (1994) Size of habitat and presence of ground beetle species. In K. Desender, M. Dufrêne, M. Loureau, M. Luff & J-P. Mealfait (eds.) *Carabid beetles: ecology and evolution.* Kluwer academic press, the Netherlands, pp. 255 - 261.

Vries, H.H. de & Boer, P.J. den (1990) Survival of populations of *Agonum ericeti* Panz. (Col., Carabidae) in relation to fragmentation of habitats. Neth. Journ. of Zool. **40** (3). 484 - 498.

Wallin, H. (1986) Habitat choice of some field-inhabiting carabid beetles (Coleoptera: Carabidae) studied by recapture of marked individuals. Ecol. Entom. **11**, 387 - 392

Webb, N.R. & Hopkins, P.J. (1984) Invertebrate diversity on fragmented Calluna heathland. Journ. of Appl. Ecol. **21**, 921 - 933.

Wiens, J.A. & Milne, B.T. (1989) Scaling of landscape in landscape ecology, or, Landscape ecology from a beetle's perspective. Landscape Ecology **3**, 87 - 96

Zanden, J.L. van & Verstegen, S.W. (1993) Groene geschiedenis van Nederland. Het Spectrum, the Netherlands.

Zerbe, S. (1989). Untersuchung artspezifischer Bewegungsmuster entlang von Korridoren am beispiel von Laufkäfern (Carabidae) und Heuschrecken (Acrididae). Landschaft und Stadt, 21, 3. Stuttgart 100-103.

CURRICULUM VITAE

* 9 december 1957	Geboren te Coevorden
* 1975	Eindexamen HAVO, Rijksscholengemeenschap te Leeuwarden
* 1982	Examen 2de graads leraar aan de lerarenopleiding Ubbo Emmius te Groningen - Hoofdvak : biologie - Bijvakken: huishoudkunde en onderwijskunde
* 1987	Doctoraalexamen Biologie (met veel genoegen), Rijks Universiteit Groningen - Hoofdvak : Dieroecologie - Bijvakken: Toegepaste oecologie en Mariene Biologie - 1ste graads leraar biologie
* 1988	Diploma Assistant to the Manager bij Nieuw Elan/ VNO de baak. - Personeel en organisatie - Trainer/opleider
* 1989	Onderzoeker bij de afdeling landschapsecologie van het Instituut voor Bos en Natuuronderzoek te Leersum. Gedurende deze periode is er gewerkt aan dit promotieonderzoek bij het Biologisch Station van de Landbouw Universiteit Wageningen te Wijster.
* 1993 - heden	Vrijwillig medewerker bij het Biologisch Station te Wijster
* 1994 - heden	Leraar biologie aan de Regionale scholengemeenschap Stad en Esch te Meppel

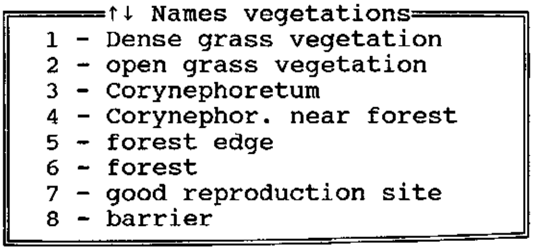
APPENDIX 1

General conditions for the simulations

A. Seasons (periods of time) and number of days per season as used in the simulations

Name season	Number of days
januari	31
februari	28
maart	31
april	30
mei	31
juni	30
juli	31
augustus	31
september	30
oktober	31
november	30
december	31

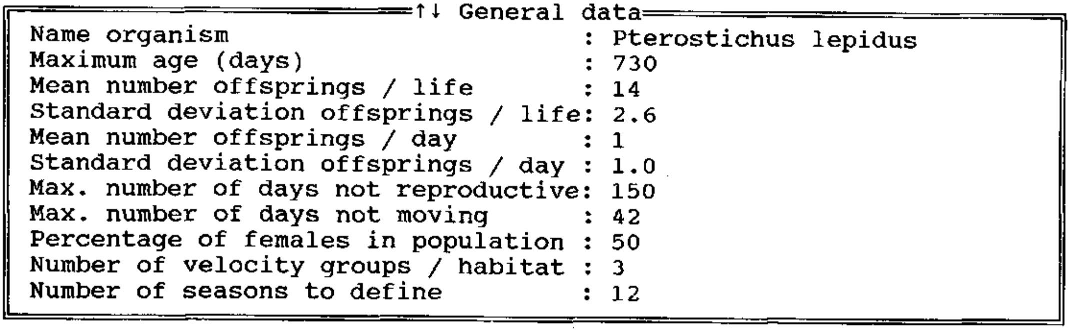
B. The kind of vegetation (habitat areas) as used in the simulations. 7 - good reproduction site = the same as Corynephoretum but with 1.5 times the normal reproduction. 8 - barrier = kind of habitat which beetles are not allowed to enter.



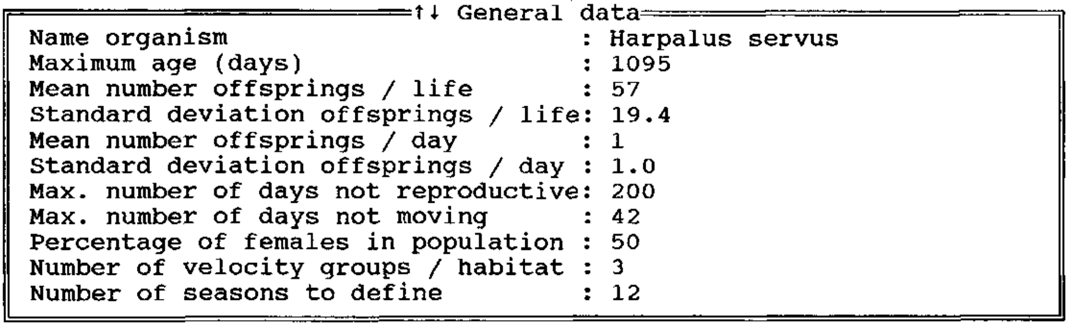
```
↑↓ Names vegetations
1 - Dense grass vegetation
2 - open grass vegetation
3 - Corynephoretum
4 - Corynephor. near forest
5 - forest edge
6 - forest
7 - good reproduction site
8 - barrier
```

APPENDIX 2

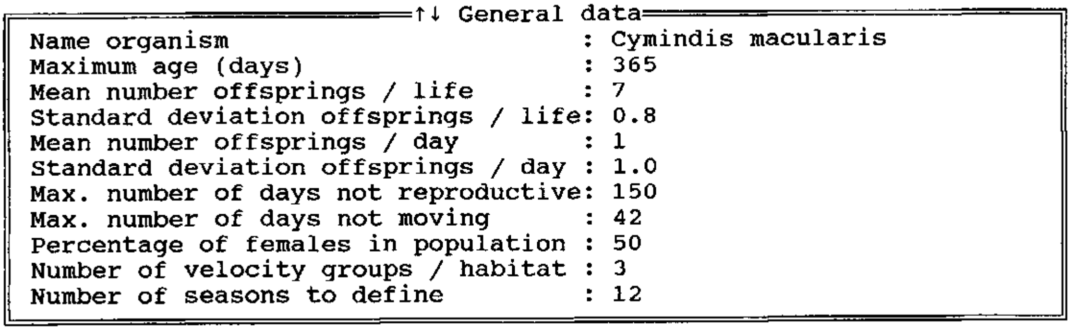
General data of the three beetle species as used in the simulations.



```
Name organism                        : Pterostichus lepidus
Maximum age (days)                   : 730
Mean number offsprings / life        : 14
Standard deviation offsprings / life: 2.6
Mean number offsprings / day         : 1
Standard deviation offsprings / day : 1.0
Max. number of days not reproductive: 150
Max. number of days not moving       : 42
Percentage of females in population : 50
Number of velocity groups / habitat : 3
Number of seasons to define          : 12
```



```
Name organism                        : Harpalus servus
Maximum age (days)                   : 1095
Mean number offsprings / life        : 57
Standard deviation offsprings / life: 19.4
Mean number offsprings / day         : 1
Standard deviation offsprings / day : 1.0
Max. number of days not reproductive: 200
Max. number of days not moving       : 42
Percentage of females in population : 50
Number of velocity groups / habitat : 3
Number of seasons to define          : 12
```



```
Name organism                        : Cymindis macularis
Maximum age (days)                   : 365
Mean number offsprings / life        : 7
Standard deviation offsprings / life: 0.8
Mean number offsprings / day         : 1
Standard deviation offsprings / day : 1.0
Max. number of days not reproductive: 150
Max. number of days not moving       : 42
Percentage of females in population : 50
Number of velocity groups / habitat : 3
Number of seasons to define          : 12
```

Max. number of days not reproductive refers to the period between egg-laying and the next reproduction season.

Max. number of days not moving refers to the period between egg-laying and hatching of the eggs.

Number of velocity groups/habitats refers to the three groups in which direct walk, intermediate walk and random walk occur.

APPENDIX 3

Velocity groups and relative velocity per species

A. Frequency distribution in which direct walk, intermediate walk and random walk occurs per species expressed as percentage. Distributions are based on data collected in enclosures (chapter 4). Horizontal: kinds of habitat (appendix 1), vertical: kinds of walk and their frequency to occur. Per kind of habitat the sum of these behaviours is always 100.

```
↑↓↔ Ratio velocity groups of Pterostichus lepidus

                         Name habitat: Dense grass vegetation
group 1      2      3      4      5      6      7      8
  1  67.6   67.6   76.4   76.4   71.9   71.0   67.6  100.0
  2  24.1   24.1   16.3   15.3   18.5   13.0   24.1    0.0
  3   8.3    8.3    7.3    8.3    9.6   16.0    8.3    0.0

Sum 100.0  100.0  100.0  100.0  100.0  100.0  100.0  100.0

Ratio velocity group 1 (%): 67.6     (0.0 .. 67.6)
```

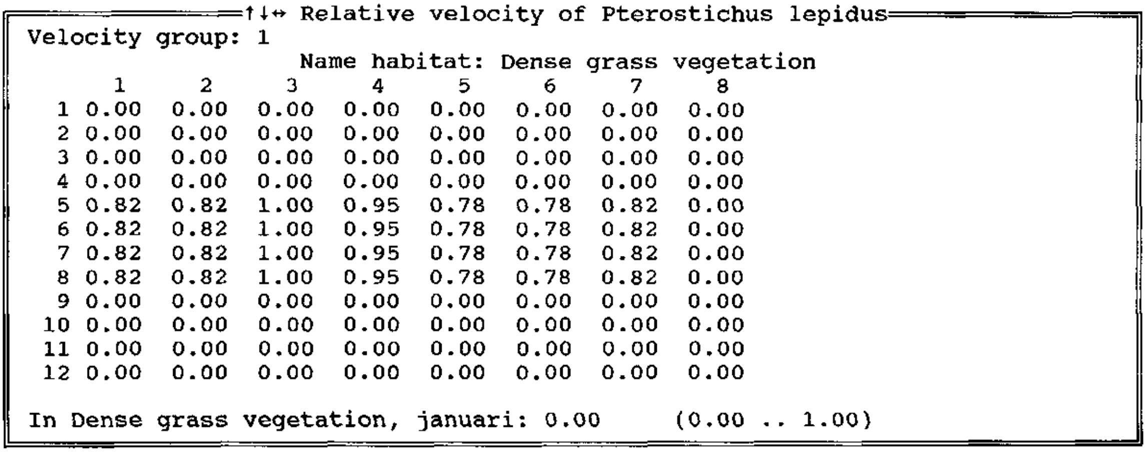
```
↑↓↔ Ratio velocity groups of Harpalus servus

                         Name habitat: Dense grass vegetation
group 1      2      3      4      5      6      7      8
  1  13.0   13.0   35.0   18.0   24.0   24.0   35.0  100.0
  2  49.0   49.0   33.0   37.0   28.0   28.0   33.0    0.0
  3  38.0   38.0   32.0   45.0   48.0   48.0   32.0    0.0

Sum 100.0  100.0  100.0  100.0  100.0  100.0  100.0  100.0

Ratio velocity group 1 (%): 13.0     (0.0 .. 13.0)
```

```
↑↓↔ Ratio velocity groups of Cymindis macularis

                         Name habitat: Dense grass vegetation
group 1      2      3      4      5      6      7      8
  1  35.0   35.0   36.0   50.0    0.0    0.0   36.0  100.0
  2  15.0   15.0   28.0   33.0   33.0   33.0   28.0    0.0
  3  50.0   50.0   36.0   17.0   67.0   67.0   36.0    0.0

Sum 100.0  100.0  100.0  100.0  100.0  100.0  100.0  100.0

Ratio velocity group 1 (%): 35.0     (0.0 .. 35.0)
```

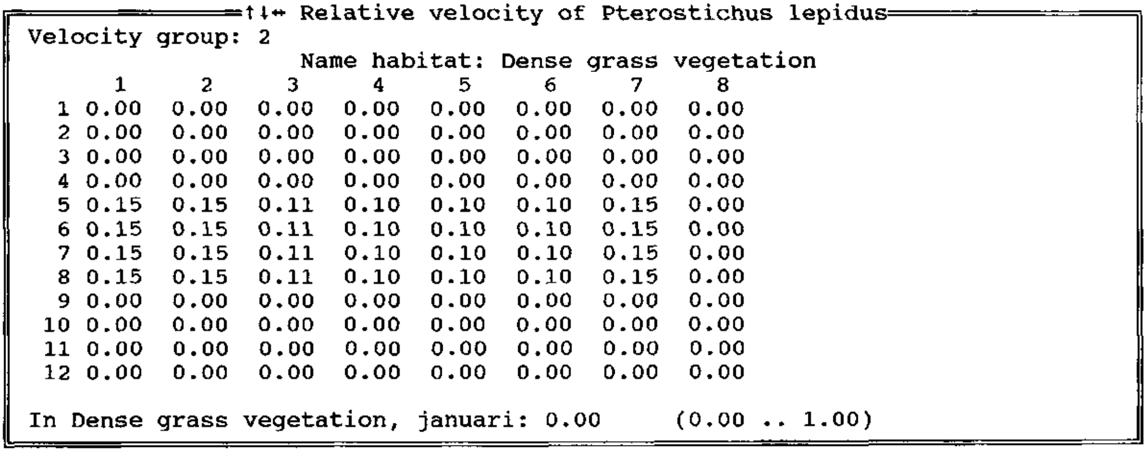
APPENDIX 3

B *Velocity groups and relative velocity per species as used in the simulations*

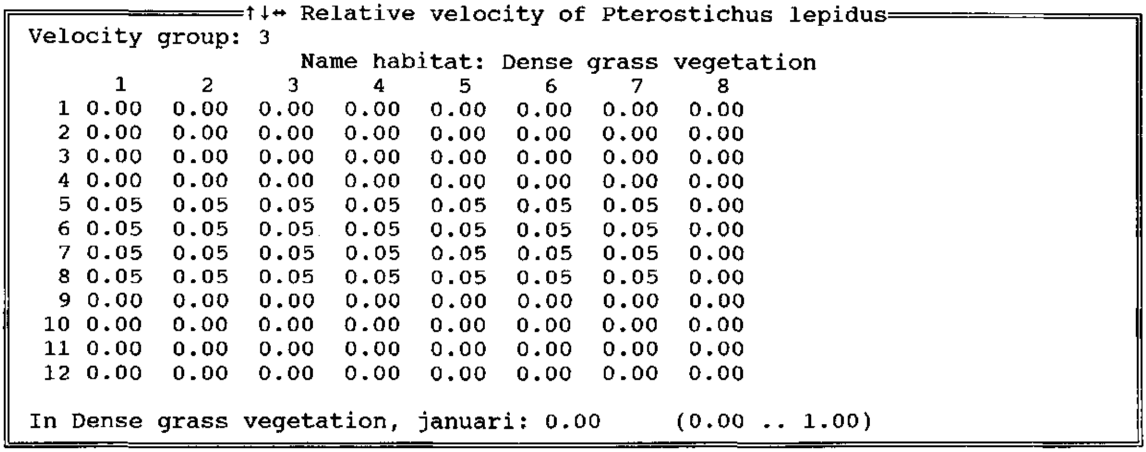
A. Frequency distribution in which direct walk, intermediate walk and random walk occurs per species expressed as percentage. Distributions are based on data collected in enclosures (chapter 4). Horizontal: kinds of habitat (appendix 1), vertical: kinds of walk and their frequency to occur. Per kind of habitat the sum of these behaviours is always 100.



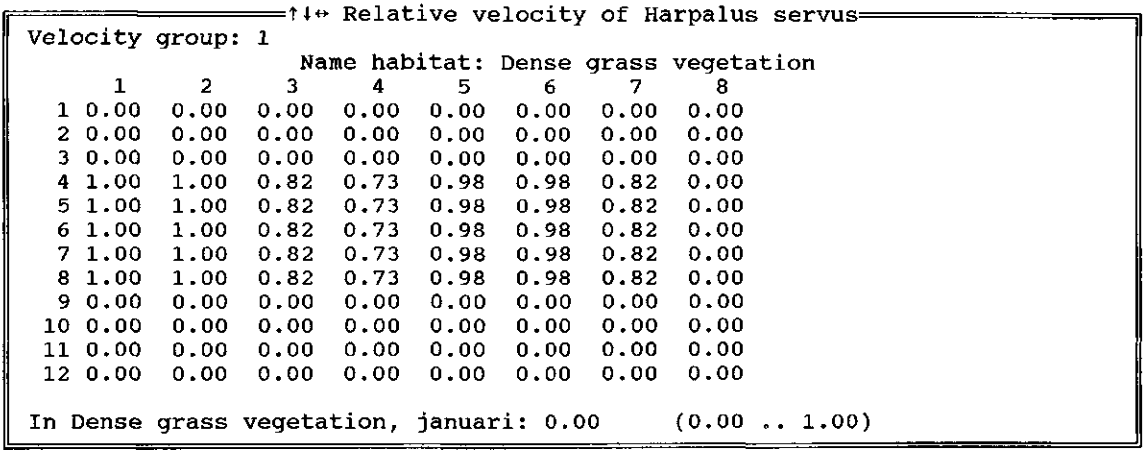
```
═══════════↑↓↔ Relative velocity of Pterostichus lepidus═══════════
Velocity group: 1
                         Name habitat: Dense grass vegetation
       1      2      3      4      5      6      7      8
   1 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   2 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   3 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   4 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   5 0.82   0.82   1.00   0.95   0.78   0.78   0.82   0.00
   6 0.82   0.82   1.00   0.95   0.78   0.78   0.82   0.00
   7 0.82   0.82   1.00   0.95   0.78   0.78   0.82   0.00
   8 0.82   0.82   1.00   0.95   0.78   0.78   0.82   0.00
   9 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  10 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  11 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  12 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00

In Dense grass vegetation, januari: 0.00     (0.00 .. 1.00)
```



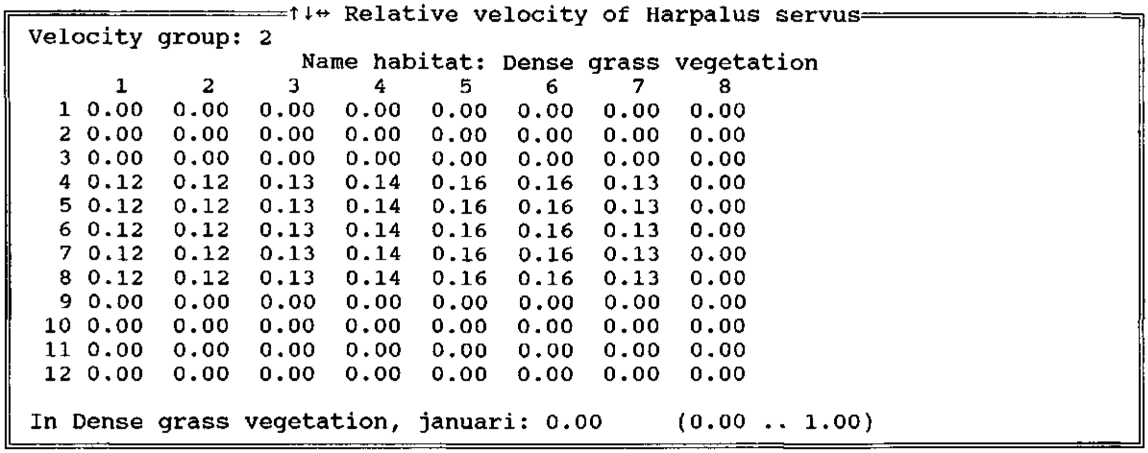
```
═══════════↑↓↔ Relative velocity of Pterostichus lepidus═══════════
Velocity group: 2
                         Name habitat: Dense grass vegetation
       1      2      3      4      5      6      7      8
   1 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   2 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   3 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   4 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   5 0.15   0.15   0.11   0.10   0.10   0.10   0.15   0.00
   6 0.15   0.15   0.11   0.10   0.10   0.10   0.15   0.00
   7 0.15   0.15   0.11   0.10   0.10   0.10   0.15   0.00
   8 0.15   0.15   0.11   0.10   0.10   0.10   0.15   0.00
   9 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  10 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  11 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  12 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00

In Dense grass vegetation, januari: 0.00     (0.00 .. 1.00)
```



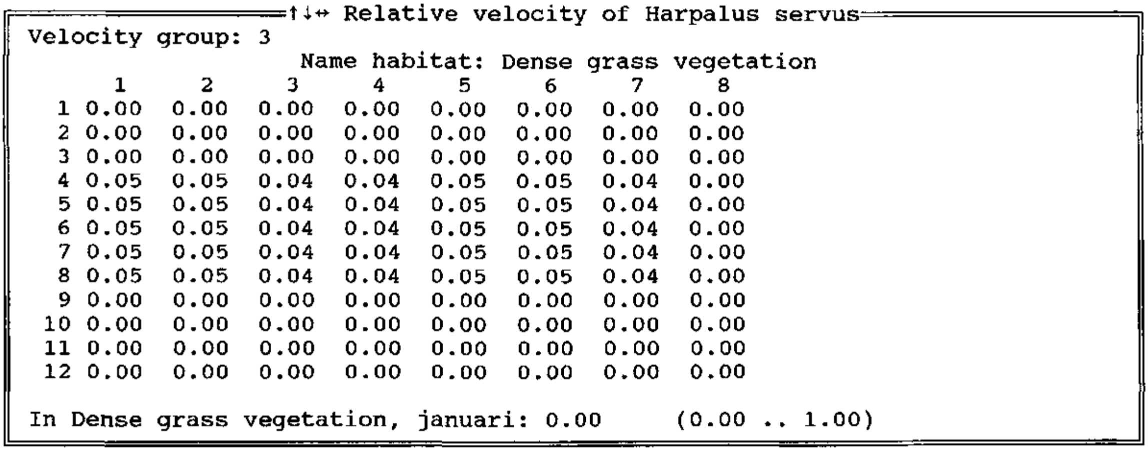
```
↑↓↔ Relative velocity of Pterostichus lepidus
Velocity group: 3
                         Name habitat: Dense grass vegetation
      1      2      3      4      5      6      7      8
   1 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   2 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   3 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   4 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   5 0.05   0.05   0.05   0.05   0.05   0.05   0.05   0.00
   6 0.05   0.05   0.05   0.05   0.05   0.05   0.05   0.00
   7 0.05   0.05   0.05   0.05   0.05   0.05   0.05   0.00
   8 0.05   0.05   0.05   0.05   0.05   0.05   0.05   0.00
   9 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  10 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  11 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  12 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00

In Dense grass vegetation, januari: 0.00     (0.00 .. 1.00)
```



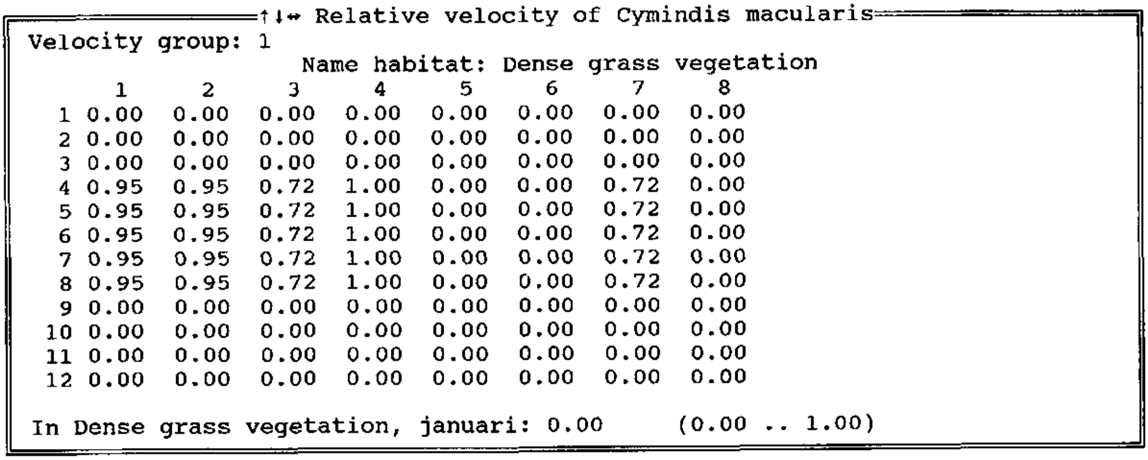
```
↑↓↔ Relative velocity of Harpalus servus
Velocity group: 1
                         Name habitat: Dense grass vegetation
      1      2      3      4      5      6      7      8
   1 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   2 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   3 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   4 1.00   1.00   0.82   0.73   0.98   0.98   0.82   0.00
   5 1.00   1.00   0.82   0.73   0.98   0.98   0.82   0.00
   6 1.00   1.00   0.82   0.73   0.98   0.98   0.82   0.00
   7 1.00   1.00   0.82   0.73   0.98   0.98   0.82   0.00
   8 1.00   1.00   0.82   0.73   0.98   0.98   0.82   0.00
   9 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  10 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  11 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  12 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00

In Dense grass vegetation, januari: 0.00     (0.00 .. 1.00)
```



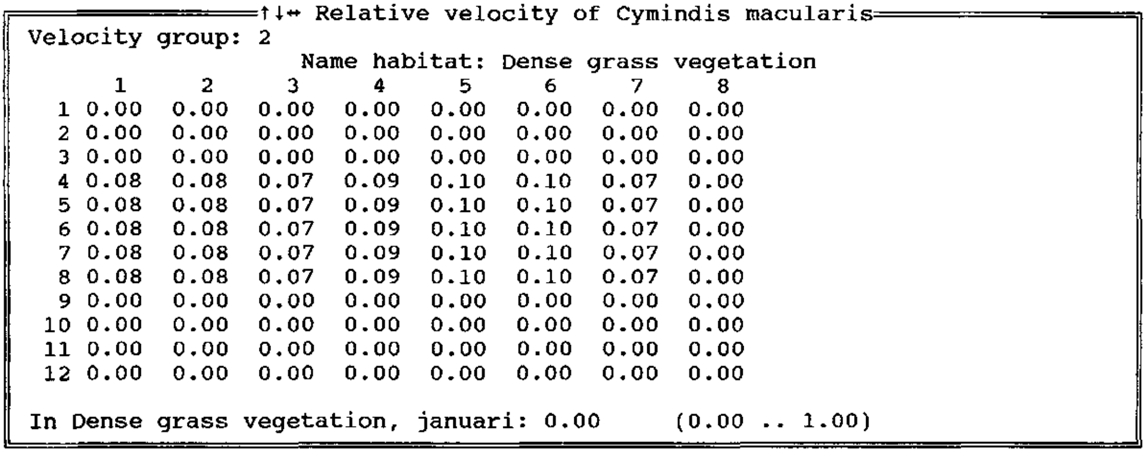
```
↑↓↔ Relative velocity of Harpalus servus
Velocity group: 2
                         Name habitat: Dense grass vegetation
      1      2      3      4      5      6      7      8
   1 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   2 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   3 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   4 0.12   0.12   0.13   0.14   0.16   0.16   0.13   0.00
   5 0.12   0.12   0.13   0.14   0.16   0.16   0.13   0.00
   6 0.12   0.12   0.13   0.14   0.16   0.16   0.13   0.00
   7 0.12   0.12   0.13   0.14   0.16   0.16   0.13   0.00
   8 0.12   0.12   0.13   0.14   0.16   0.16   0.13   0.00
   9 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  10 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  11 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  12 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00

In Dense grass vegetation, januari: 0.00     (0.00 .. 1.00)
```



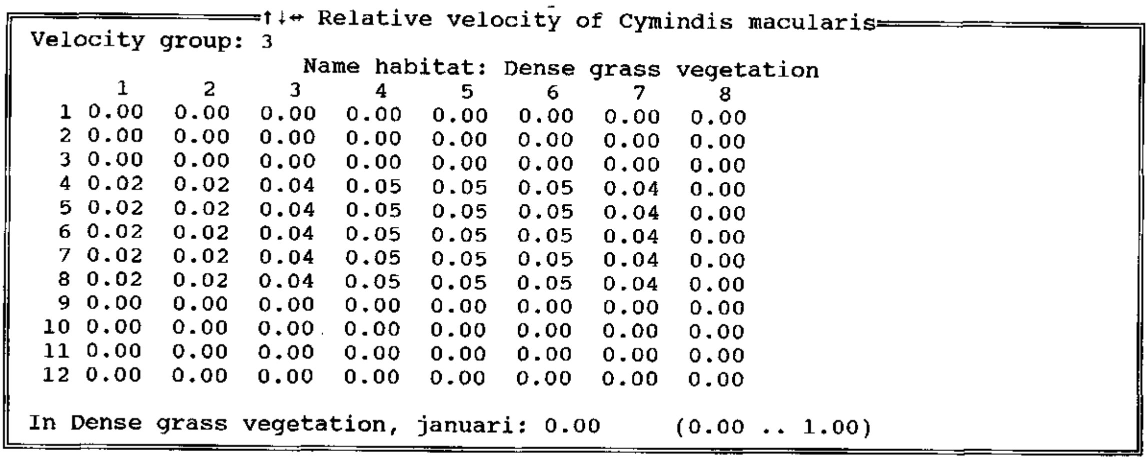
```
↑↓↔ Relative velocity of Harpalus servus
Velocity group: 3
                         Name habitat: Dense grass vegetation
      1      2      3      4      5      6      7      8
   1 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   2 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   3 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   4 0.05   0.05   0.04   0.04   0.05   0.05   0.04   0.00
   5 0.05   0.05   0.04   0.04   0.05   0.05   0.04   0.00
   6 0.05   0.05   0.04   0.04   0.05   0.05   0.04   0.00
   7 0.05   0.05   0.04   0.04   0.05   0.05   0.04   0.00
   8 0.05   0.05   0.04   0.04   0.05   0.05   0.04   0.00
   9 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  10 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  11 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  12 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00

In Dense grass vegetation, januari: 0.00     (0.00 .. 1.00)
```



```
═════════════↑↓↔ Relative velocity of Cymindis macularis═════════════
Velocity group: 1
                        Name habitat: Dense grass vegetation
       1      2      3      4      5      6      7      8
   1 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   2 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   3 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   4 0.95   0.95   0.72   1.00   0.00   0.00   0.72   0.00
   5 0.95   0.95   0.72   1.00   0.00   0.00   0.72   0.00
   6 0.95   0.95   0.72   1.00   0.00   0.00   0.72   0.00
   7 0.95   0.95   0.72   1.00   0.00   0.00   0.72   0.00
   8 0.95   0.95   0.72   1.00   0.00   0.00   0.72   0.00
   9 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  10 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  11 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  12 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00

In Dense grass vegetation, januari: 0.00     (0.00 .. 1.00)
```



```
═════════════↑↓↔ Relative velocity of Cymindis macularis═════════════
Velocity group: 2
                        Name habitat: Dense grass vegetation
       1      2      3      4      5      6      7      8
   1 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   2 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   3 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   4 0.08   0.08   0.07   0.09   0.10   0.10   0.07   0.00
   5 0.08   0.08   0.07   0.09   0.10   0.10   0.07   0.00
   6 0.08   0.08   0.07   0.09   0.10   0.10   0.07   0.00
   7 0.08   0.08   0.07   0.09   0.10   0.10   0.07   0.00
   8 0.08   0.08   0.07   0.09   0.10   0.10   0.07   0.00
   9 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  10 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  11 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  12 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00

In Dense grass vegetation, januari: 0.00     (0.00 .. 1.00)
```



```
═════════════↑↓↔ Relative velocity of Cymindis macularis═════════════
Velocity group: 3
                        Name habitat: Dense grass vegetation
       1      2      3      4      5      6      7      8
   1 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   2 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   3 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
   4 0.02   0.02   0.04   0.05   0.05   0.05   0.04   0.00
   5 0.02   0.02   0.04   0.05   0.05   0.05   0.04   0.00
   6 0.02   0.02   0.04   0.05   0.05   0.05   0.04   0.00
   7 0.02   0.02   0.04   0.05   0.05   0.05   0.04   0.00
   8 0.02   0.02   0.04   0.05   0.05   0.05   0.04   0.00
   9 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  10 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  11 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
  12 0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00

In Dense grass vegetation, januari: 0.00     (0.00 .. 1.00)
```