4 Restoring habitat connectivity across roads: where to begin?[3]

4.1 Abstract

We studied the potential effect of mitigation measures on the viability of wildlife populations to prioritize the construction of wildlife passages and restore habitat connectivity across roads in The Netherlands. We used the model LARCH to assess potential habitat configuration and network population viability for five indicator species, sensitive to roads as barriers. High-priority locations for defragmentation were distinguished at road transects where network population viability shifted either from non-viable (extinction probability >5% in 100 years) or vulnerable (extinction probability 1-5% in 100 years) towards highly viable (extinction probability <1% in 100 years) solely due to the removal of roads as barriers. Furthermore, high-priority locations were distinguished where roads block either the forming or re-enforcement of key populations or Robust Ecological Corridors. Analyses showed that 12,281 km (52%) of roads can be classified as critical road transects of which 1,888 km (15%) were determined high priority locations for defragmentation. Due to the removal of road barriers total number of network populations will decrease 33-51%. The area with highly viable network populations will increase about 20-30% for small species with low dispersal capacity, and over 90% for medium-sized to large species with high dispersal capacity. Because the loss of network population viability is sometimes exclusively the result of the presence of roads, restoring habitat connectivity across roads should be given high priority by both policy makers and road managers.

Keywords: *Habitat fragmentation, Infrastructure, Network population, Population viability, Defragmentation, Mitigation measures, Wildlife passages.*

4.2 Introduction

Rapid expansion of urban areas and infrastructure is the most important recent change in land use in The Netherlands. In 1996 about 9.5% of the country was covered by developed areas, which was twice as much as in 1960 (Natuurplanbureau, 2001). Between 1985 and 1998 the length of paved roads increased almost 20%, resulting in an average of 3.4 km of paved road per square kilometer (CBS, 2000; CBS, 2001). In the same period traffic volume increased about 60% (CBS, 2000). And there is no indication that the growth rate of both urban areas, road density and traffic intensity is levelling off.

Ever expanding urban areas, and the continuous construction of new infrastructure in between, reduces both the quantity and quality of wildlife habitat. Formerly continuous habitat becomes highly fragmented, leaving small habitat patches scattered throughout the landscape. Populations in such small habitat patches have a higher risk of extinction due to demographic and environmental stochasticity (Verboom *et al.*, 1993). At the same time the chance of recolonizations is reduced due to an increase in both distance between populations

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and number of barriers, such as roads (Opdam *et al.*, 1993). At present, most nature areas in The Netherlands are too small or too isolated to sustain viable wildlife populations (Kalkhoven *et al.*, 1996).

This problem may be overcome if scattered habitat patches are connected into habitat networks. A habitat network could be defined as a cluster of habitat patches, in which animals are able to exchange between (local) populations that inhabit the different patches (Opdam *et al.*, 1993). Animal movements between patches may be facilitated by connecting corridors or stepping stones (Bennett, 1999). Together, the local populations in a habitat network form a network population (Levins, 1970; Opdam, 1987). Although local population viability in an isolated habitat patch may be low, the chance of survival increases if the local population is linked to other populations in nearby habitat patches. Still, local populations may be extirpated, but recolonisation is facilitated by the network population. Viability of the network population itself depends on size, quality and spatial cohesion of the habitat patches in the network (Opdam *et al.*, 1993; Verboom *et al.*, 2001).

To improve network population viability, the Dutch Ministry of Agriculture, Nature management and Fisheries developed a plan for a National Ecological Network (NEN) in the late 1980s (Ministerie LNV, 1990). This NEN consists of existing nature areas, nature areas still to be developed, and ecological corridors between these nature areas. The NEN is scheduled to be completed by 2018. After evaluating expected effectiveness and progress of the NEN plans, seven additional ecological corridors were proposed, that have significantly larger dimensions than the original linkages of the NEN (Natuurplanbureau, 2000; Pelk *et al.*, 2000; Ministerie LNV, 2000). Main objectives of these Robust Ecological Corridors (REC) are to improve the spatial cohesion within the NEN and to conserve biodiversity (Ministerie LNV, 2000). Improving connectivity between habitat patches of species with high dispersal capacity, providing access to new habitats for species with medium dispersal capacity, and creating wildlife refuges to limit the impacts of unexpected events (e.g. climatic changes), are the main actions through which these objectives are to be achieved (Broekmeyer, 2001).

For many wildlife species roads are a barrier to movements between local populations (Bennett, 1991; Forman & Alexander, 1998). In some cases this is caused by the physical appearance of the road and roadside, or the disturbance associated with road use or road management, causing animals to avoid the vicinity of roads (Trombulak & Frissell, 2000). Barrier effects may also result from a decrease in successful wildlife crossings due to high traffic densities. In some cases animal-vehicle collisions are the leading cause of animal mortality, effectively fragmenting otherwise connected populations (Van der Zee *et al.*, 1992; Clarke *et al.*, 1998).

In The Netherlands much effort has been put into restoring habitat connectivity across roads over the last two decades (Bekker *et al.*, 1995). Wildlife overpasses and underpasses have been designed to facilitate the movement of wildlife at several hundred locations throughout the country (Bekker *et al.*, 2001). However, at many locations roads are still a major cause of habitat fragmentation (Reijnen *et al.*, 2000; van der Grift *et al.*, 2001). To prioritize actions to restore habitat connectivity across roads through wildlife passages, we studied the potential effect of these mitigation measures on the viability of wildlife populations. Our specific objectives were to: (1) determine at which locations mitigation measures at roads would result in a significant increase in population viability, (2) determine locations where, apart from the construction of wildlife passages, additional measures are necessary to increase population viability, and (3) provide recommendations for planning defragmentation initiatives in transportation corridors.

4.3 Methods

4.3.1 Introduction

We distinguished five steps in our research: (1) the selection of indicator species, (2) population viability analysis for each indicator species, according to the present major road network, (3) population viabilty analysis for each indicator species, with the barrier effect of roads fully mitigated, (4) the assessment of critical road transects for each indicator species, and (5) the assessment of high-priority locations for defragmentation for each indicator species.

4.3.2 Indicator species

We selected five terrestrial indicator species for analysis, all sensitive to fragmentation and the barrier effect of roads. The indicator species differ in their habitat preference and, in case of forest habitats, their ability to disperse (Table 4.1). This way species groups with both low and high dispersal capacity were represented and all major wildlife habitats of The Netherlands are covered (see also discussion).

Table 4.1. Selected indicator species per habitat type and dispersal capacity.

Habitat	Dispersal capacity low (< 10 km)	high (> 10 km)
forest	bank vole (Clethrionomys glareolus)	pine marten (Martes martes)
heathland/moorland	sand lizard (Lacerta agilis)	viper (Vipera berus)
wetland	root vole (Microtus oeconomus)	-

4.3.3 Population viability analysis

We assessed potential habitat configuration and network population viability for the five indicator species, in the situation with and without roads, using the GIS-based decision support system LARCH (Landscape ecological Analyses and Rules for the Configuration of Habitat; Pouwels *et al.*, 2002). A full description of LARCH is given by Pouwels *et al.* (2002) and Verboom & Pouwels (in press). For each indicator species LARCH assesses (1) the spatial pattern of habitat patches, (2) carrying capacity of each habitat patch, i.e. maximum population density per patch, and spatial pattern of local populations, i.e. clusters of habitat patches, (3) spatial pattern of network populations, i.e. clusters of local populations, and (4)viability of the network populations (see Figure 4.1).

To assess spatial configuration of actual and potential habitat we used the grid cell based vegetation map Begroeiingstypenkaart LARCH Vogels Nationaal (grid cell size 250x250 m) (Griffioen *et al.*, 2000; Reijnen *et al.*, 2001). For each grid cell the coverage of vegetation types that are present in that particular cell is given as a percentage. A habitat map was extracted from this vegetation map by selecting vegetation types which are considered suitable habitat for the indicator species concerned. For each selected vegetation type carrying capacity was calculated for each grid cell, using population density standards based on empirical studies (Pouwels *et al.*, 2002). Successively, the carrying capacity of each grid cell was calculated by adding up carrying capacity of the vegetation types. Bordering grid cells in which suitable habitat occured were joined into habitat patches. The carrying capacity of each habitat patch was calculated by adding up the carrying capacity of the grid cells that make up the habitat patch (see also Reijnen *et al.*, 2001).

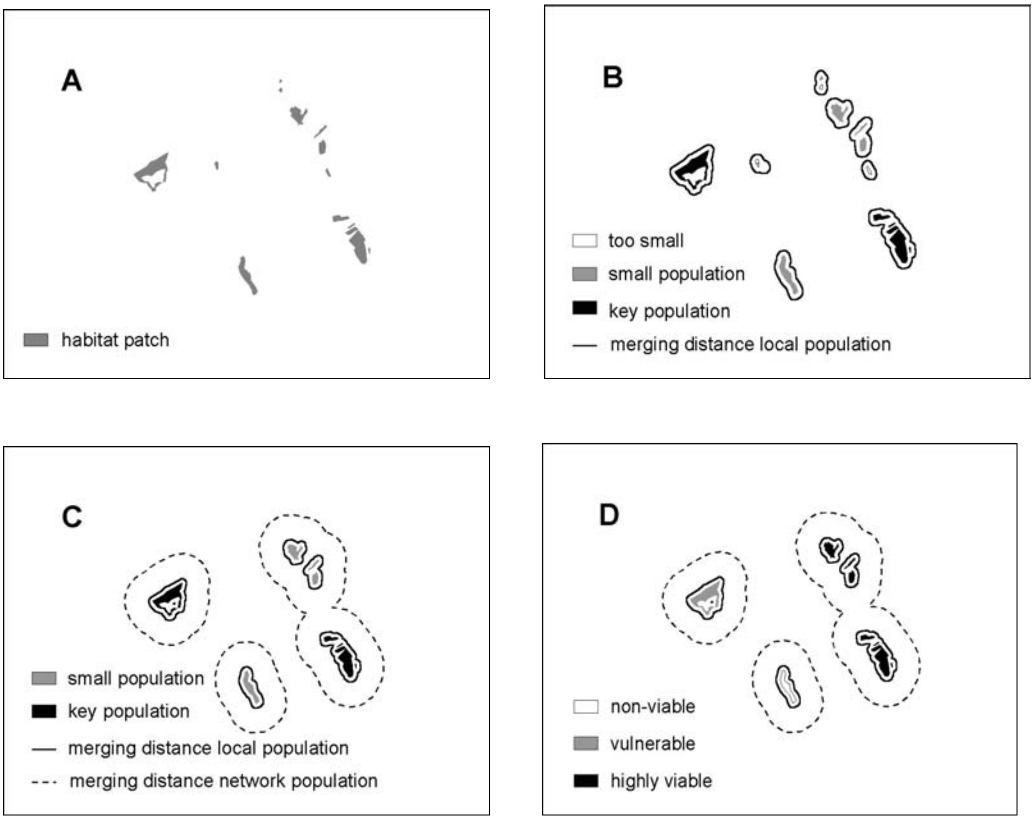

Figure 4.1. Outline of the assessment of network population viability with LARCH: A. creating habitat map, B. assessment spatial pattern and carrying capacity of local populations, C. assessment spatial pattern of network populations, and D. assessment of network population viability.

To assess whether habitat patches belong to the same local population LARCH uses a species-specific merging distance, i.e. the distance below which about 90% of all animal movements within the local population take place (Table 4.2). When barriers (roads) were present between two patches, the patches were considered to be part of different local populations, regardless of the distance between the patches. Successively, the distance between local populations and the presence of barriers determined whether local populations belonged to the same network population. The merging distance standards used in LARCH to assess spatial configuration of both local populations and network populations, are based on empirical data of home range size and dispersal capacity respectively (Pouwels *et al.*, 2002).

Whether or not roads are barriers is species specific. Typically, roads with low traffic volumes are not a significant barrier to species with high dispersal capacity. The classification of roads as barriers is based on empirical studies (Pouwels *et al.*, 2002). Furthermore, for each indicator species roads are classified as local barriers, network barriers, or both (see Table 4.3). Roads labeled as local barriers are roads that act as a barrier to wildlife movements between local populations. Similarly, roads labeled as network barriers are roads that act as a barrier to dispersal movements between network populations. This distinction is important since certain road types may form a barrier for home range movements of some species, but they are not a barrier when an animal leaves the area to disperse (Pouwels *et al.*, 2002). The presence of existing mitigation measures were not included in the analyses.

Table 4.2. Merging distance standards used in LARCH to asses spatial configurations of local populations and network populations per indicator species.

LARCH parameter	Values used (in meters)				
	sand lizard	viper	bank vole	root vole	pine marten
Merging distance local population	250	250	250	50	2000
Merging distance network population	1000	1000	1000	4800	10000

Table 4.3. Classification of roads as local barriers (lb), network barriers (nb), or both, per indicator species.

Indicator species	Road type (traffic speed)				
	national motorway (100-120 km/h)	provincial highway (80-100 km/h)	provincial main road (80 km/h)	provincial road (80 km/h)	local main road (80 km/h)
Sand lizard	lb/nb	lb/nb	lb/nb	lb/nb	lb/nb
Viper	lb/nb	lb/nb	lb/nb	lb/nb	lb/nb
Bank vole	lb/nb	lb/nb	lb/nb	lb	lb
Root vole	lb/nb	lb/nb	lb/nb	lb	Lb
Pine marten	lb	lb	-	-	-

For each habitat network total carrying capacity was compared with standards for minimal viable network populations (MVNP's). If these standards were met the network populations were considered viable. The standards for MVNP's in LARCH are based on simulations with dynamic (meta)population models (see Verboom *et al.*, 1997; Verboom *et al.*, 2001). In assessing network population viability we took the configuration of habitat into account, in particular the presence of key patches. A key patch is defined as a habitat patch with a carrying capacity large enough to sustain a key population (KP), i.e. a relatively large local population in a network, which is persistent under the condition of one immigrant per generation (Verboom *et al.*, 2001). If a key population is present, lower standards apply for MVNP sizes (see Verboom *et al.*, 2001). Table 4.4 summarizes the standards used in this study for KP size, and MVNP sizes in configurations with and without a key population for each indicator species. Population sizes are expressed in reproductive units. For the selected indicator species a reproductive unit can be defined as one male, one female, and the proportional part of the non-breeding population.

Table 4.4. Used standards in population viability analyses for key population size (KP) and for Minimal Viable Network Population (MVNP) sizes in configurations with and without a key population, expressed in number of reproductive units.

Indicator species	KP	MVNP with KP	MVNP without KP
Sand lizard	100	250	400
Viper	100	300	500
Bank vole	100	150	200
Root vole	100	150	200
Pine marten	40	160	240

We classified network populations as non-viable, vulnerable, or highly viable. A network population is considered non-viable when survival probability is less than 95% in 100 years. For vulnerable network populations the extinction probability is 1-5% in 100 years. Although the threshold for viability is met, these network populations will still be rather sensitive to changes in habitat size or quality (see Verboom & Pouwels, in press). Highly viable network populations are populations in habitat networks of which carrying capacity exceeds the standard for a MVNP five times or more, i.e. an extinction probability of < 1% in 100 years.

4.3.4 Assessing critical road transects

Per indicator species critical road transects, i.e. road barriers that may potentially impact network population viability, were mapped. A critical road transect was defined as a road transect that intersects or directly borders a habitat patch. Because the habitat map we used is grid-based with a grid cell size of 250x250 m, minimum length of critical road transects is 250 m. However, in large habitat patches critical road transects may have a length of many kilometers. Only roads that are considered barriers to animal movements for the species concerned are included (see Table 4.3).

4.3.5 Assessing high-priority locations for defragmentation

We determined high-priority locations in critical road transects for indicator species with low dispersal capacity in two steps. First, we compared survival probability of network populations with and without roads. High-priority locations were distinguished at road transects where mitigation measures will have an immediate positive effect on the persistance of network populations. Therefore locations were labeled high-priority where network population viability shifted from either non-viable or vulnerable towards highly viable, solely due to mitigation of road-barrier impacts.

Secondly, we determined which of the above mentioned network populations show a shift in viability, due to planned expansion of nature areas and improvement of habitat quality. In this analysis we used the final spatial configuration of NEN, and habitat quality aimed for within this NEN, to assess spatial pattern and carrying capacity respectively of habitat patches, local populations, and network populations (Natuurplanbureau, 2000). Locations where network population viability shifts from non-viable or vulnerable to highly viable as a result of NEN plans, regardless of changes in road network, were no longer distinguished high-priority locations.

When no road network is present, all local populations of the indicator species with high dispersal capacity (pine marten) belong to a very limited number of network populations. As a consequence, high-priority locations cannot easily be detected by comparing network population viability in the situation with and without roads. However, within a network population the presence or absence of key populations (KP's; see Section 2.3) greatly determine network population viability. Therefore high-priority locations for indicator species with high dispersal capacity were determined by detecting road transects which block the forming of new KP's, or hinder the re-enforcement of existing KP's.

In addition, all major roads that intersect a REC are considered high-priority locations for defragmentation.

4.4 Results

For all species the removal of road barriers results in a considerable shift in both number and viability of network populations, as illustrated for the bank vole in figure 4.2. The total number of network populations decreases 33% to 51% (Table 4.5). At the same time network population size increases, at many locations resulting in a shift in network population viability from non-viable or vulnerable to highly viable network populations. The area with highly viable network populations increases about 20-30% for species with low dispersal capacity (Figure 4.3). For the pine marten mitigation of road barriers will result in one highly viable network population, covering almost all suitable habitat patches within The Netherlands (Table 4.5 and Figure 4.3).

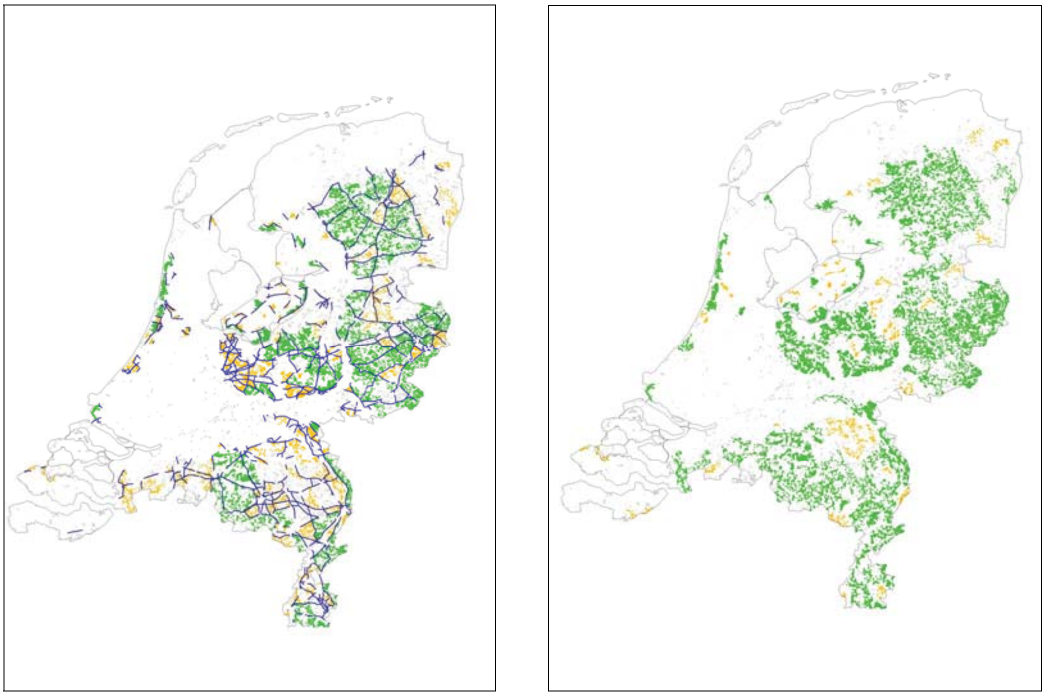

Figure 4.2. Network population viability of the bank vole in The Netherlands in the situation with and without major roads. Network populations are marked as non-viable (grey), vulnerable (yellow) or highly viable (green). Critical road transects are marked blue.

Table 4.5. Number of non-viable (nv), vulnerable (v) and highly viable (hv) network populations in the situation with and without roads for each indicator species, and the decline in network population numbers between the situation with and without roads.

Indicator species	With roads				Without roads				Decline
	hv	v	nv	total	hv	v	nv	total	
Sand lizard	26	47	775	848	21	37	391	457	46%
Viper	8	18	556	582	6	14	291	311	47%
Bank vole	63	126	1206	1395	22	46	612	680	51%
Root vole	29	55	234	318	21	23	128	172	46%
Pine marten	0	2	7	9	1	0	5	6	33%

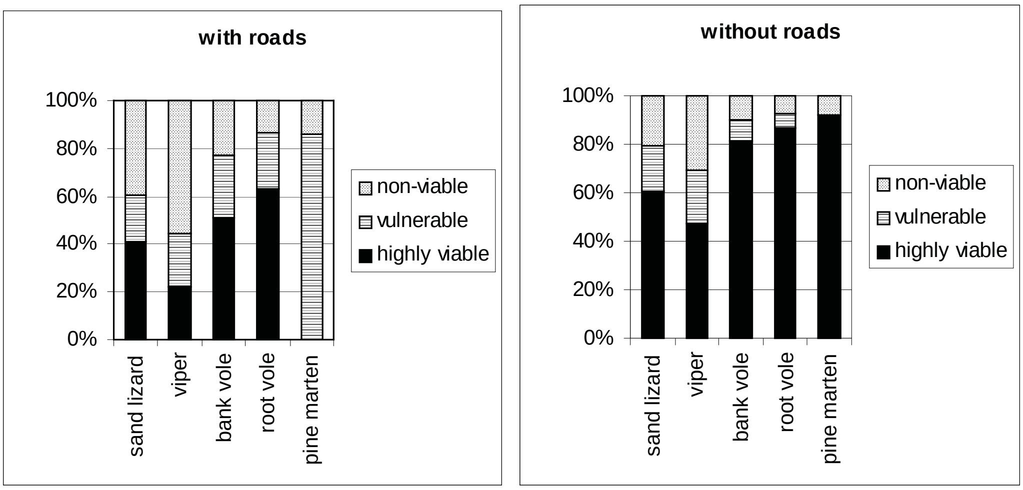

Figure 4.3. Total area of non-viable, vulnerable and highly viable network populations in the situation with and without roads for each indicator species.

Of all roads considered barriers for one or more of the indicator species (see Table 4.3), 12,281 km of roads (52%) are classified as critical road transects. Of these road transects 1,888 km (15%) were determined high priority locations for defragmentation (Figure 4.4). The impact of planned NEN expansion and NEN habitat quality improvement was limited on both number and length of high priority defragmentation locations.

Most critical road transects and high-priority locations are found in forested habitat. In wetlands the length of both critical road transects and high priority locations for defragmentation is smallest. We identified 711 road transects intersecting Robust Ecological Corridor's (REC's), with a total length of 911 km (Figure 4.5). Approximately 136 km of these road transects within REC's are also labeled high priority locations by one or more of the indicator species.

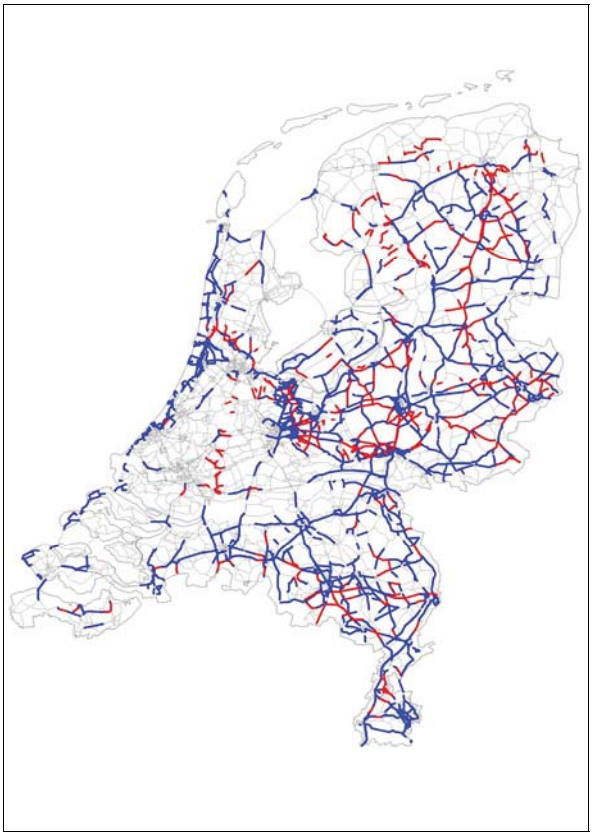

Figure 4.4. Critical road transects (blue) and high priority defragmentation locations (red) within these transects in The Netherlands, based on LARCH-analyses of five indicator species. Total length of major road network (grey) is about 23,600 km.

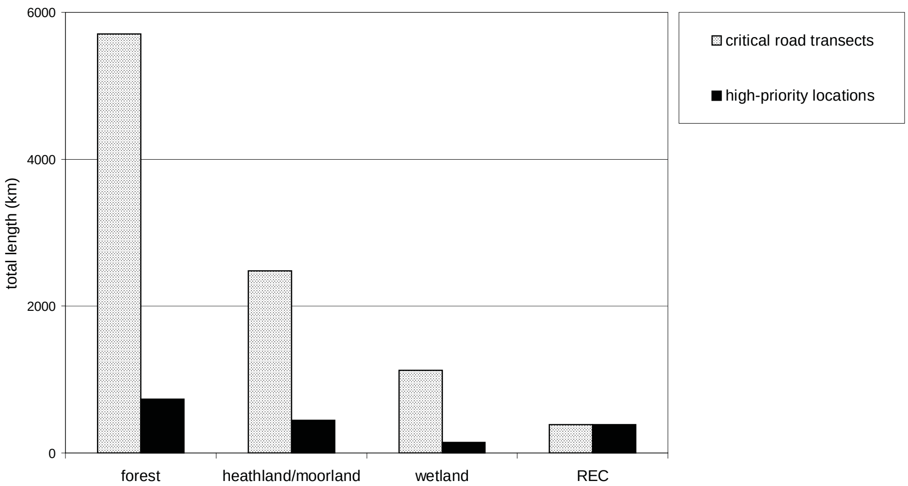

Figure 4.5. Length of critical road transects and high priority defragmentation locations per habitat type and within REC's.

4.5 Discussion

4.5.1 Selection of indicator species

Not all natural habitat types present in The Netherlands were included in our study. However, the selected indicator species represent the main ecosystems in Dutch nature conservation areas, i.e. forest (coniferous/deciduous/mixed), heathland/moorland, and wetland. These habitat types cover about 89% of the area covered by natural ecosystems in The Netherlands, excluding large freshwater bodies (RIVM, 2001). No indicator species were selected for the habitat types large freshwater bodies, salt marshes, and beaches. However, results are not likely to change much if these habitat types are included since there are very few roads within these habitat types.

The selection of indicator species was further limited because of our choice to focus on defragmentation within more or less continuous nature areas. Species indicative to small habitat patches or linear habitat elements within agricultural areas, so called ‘green veins’, were not included. Improving spatial cohesion of these small habitat fragments in agricultural landscapes may significantly re-enforce spatial cohesion of the NEN, and thus viability of network populations (Verboom *et al.*, 1991; Opdam *et al.*, 2000). Similar to situations within continuous nature areas, roads may block connectivity within green vein networks. The assessment of critical road transects outside NEN areas is therefore recommendable, especially because agricultural areas still cover about 70% of the country.

4.5.2 Assessing critical road transects

In our study critical road transects are identified whenever (potential) habitat is intersected. However, in some situations a shift in network population viability may be the result of roads which do not intersect habitat, but are located within the dispersal distance of the species concerned. We suggest that in further analysis a buffer zone along roads should be used to assess critical road transects, at which buffer size is based on species specific dispersal capacity. In further analyses it may also be desirable to include the presence of existing wildlife passages, decreasing the number of critical road transects.

4.5.3 High-priority locations

Our results show that loss of network population viability is sometimes exclusively the result of the barrier effect of the road itself. Construction of effective wildlife passages at these locations will result in immediate success, i.e. improvement of network population viability. At other locations restoring habitat connectivity across roads is only part of the solution. The reason for this is that the distance between habitat patches on either side of the road is too large. In these situations the construction of wildlife passages at the road should be accompanied by additional measures in the vicinity of the road, i.e. restoring or creating wildlife corridors and ecological stepping stones, enlarging existing habitats or improving habitat quality, to reach the same positive changes in network population viability.

It should be noticed that locations labelled ‘high-priority’ in our study are labelled so solely because at these locations mitigative measures will result in an immediate improvement of network population viability. No conclusions can be drawn about the ecological importance of defragmentation locations, based on this label. Road transects bordering rather insignificant, non-viable or vulnerable local populations on one side, and a highly viable network population on the other side will be identified as high-priority location. Conversely, road transects that isolate large non-viable or vulnerable network populations may not be detected as high-priority, only because the distance between a highly viable network population on the other side of the road extends the dispersal capacity of the species. However, because it takes time to plan and construct the additional measures (habitat, corridors, stepping stones) at such locations, efforts by road managers could be best focussed on locations where immediate results are expected.

4.5.4 Additional barriers

Major roads are not the only barriers to wildlife movement. Small local roads, railroads, or large waterways may also prohibit the exchange of animals between local populations, or network populations (Van Langevelde & Jaarsma, 1997; Van der Grift & Kuijsters, 1998; Van der Grift *et al.*, 2001). The effectiveness of wildlife passages at major roads is partly determined by defragmentation measures at such other transportation barriers, especially when these additional barriers are located in the vicinity of major roads. Therefore, we suggest further studies to determine impact of these barriers on persistance of network populations in relation to the impacts of major roads, and identify mitigation measures necessary to restore habitat connectivity across such additional barriers.

4.5.5 Identifying defragmentation locations

Literature shows that a variety of methods have been used to assess defragmentation locations. Most often placement of mitigation measures is based on data of wildlife-vehicle collisions, or prior knowledge of animal movements and the location of actual travel paths (Singer & Doherty, 1985; Van Apeldoorn *et al.*, 1995; Lehnert *et al.*, 1996; Foster & Humphrey, 1995; Scheick & Jones, 1999). An important advantage of these methods is the preciseness with which recommendations for mitigation measures can be made, due to the direct link between mitigative measure and road impact, i.e. mortality and barrier effect. However, to gather mortality or animal movement data requires a considerable effort. Therefore, these methods are primarily useful in case of defragmentation studies on a local or regional scale, with a limited number of species. Furthermore, with these methods defragmentation locations in areas where populations have already become extinct will not be detected. The same applies when mitigation sites are identified using knowledge of actual spatial distribution of (threatened) species (Den Held & Van Rij, 1994; Kobler & Adamic, 1999).

In other cases defragmentation locations are identified by mapping road transects that intersect (1) potential key linkage areas, based on analyses of landscape characteristics and ecological features of natural areas, (2) areas with some sort of nature conservation designation, or (3) proposed ecological networks, or ecological corridors (Morel & Specken, 1992; Carr *et al.*, 1998; Ruediger *et al.*, 1999; Singleton & Lehmkuhl, 1999; Smith, 1999). Most of these methods are simple and easy to apply for large numbers of species. However, with these methods usually no direct link is made between identified defragmentation locations and population viability.

Using the rule-based model LARCH, locations for defragmentation are directly related to the persistance of wildlife populations. The method ensures efforts at improving habitat connectivity across roads will be most rewarding on the population level. Using LARCH is relatively quick and simple if compared to the use of dynamic metapopulation models, especially if a large number of species has to be considered. Furthermore, using habitat maps instead of actual species distribution makes it possible to detect both actual and potential bottlenecks. However, high-priority road transects assessed with the LARCH-method often extend over many kilometers. To determine the exact locations for mitigation measures within these road transects, information of collision sites and animal trails may be a helpful tool.

4.6 Conclusion

Restoring habitat connectivity across roads should be given high priority by both policy makers and road managers. In many cases loss of network population viability is exclusively the result of the presence of roads. Therefore well designed, effective wildlife passages are required. At other locations mitigation measures to restore habitat connectivity across roads should be accompanied by additional measures, i.e. restoring wildlife corridors, to bridge the gap between habitat networks. Existing efforts to develop an NEN will only result in aimed population viability or biodiversity if defragmentation plans are carried out simultaneously. The assessment of defragmentation locations will be most effective if population viability analysis is included. LARCH turned out to be a relatively quick and simple model to identify such locations for large number of species.

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References

Apeldoorn, R. van, H. Houweling & G. Veenbaas (1995) Mitigerende maatregelen voor de das. Een methode voor probleemdetectie en evaluatie van voorzieningen, Landschap 12 (5) p. 5-12.

Bekker, H., B. van den Hengel, H. van Bohemen & H. van der Sluijs (1995) Nature across motorways, Delft, The Netherlands: Rijkswaterstaat Dienst Weg- en Waterbouwkunde.

Bekker, G.J., R. Cuperus, C.F. Jaarsma, D.A. Kamphorst & R.J.M. Kleijberg (2001) Dealing with fragmentation: prevention, mitigation and compensation, in: Piepers, A.A.G. [Ed] Infrastructure and nature; fragmentation and defragmentation. Dutch State of the Art Report for COST activity 341, Road and Hydraulic Engineering Division Defragmentation Series Part 39a, Delft, The Netherlands: Ministry of Transport, Public Works and Water Management, Road and Hydraulic Engineering Division, p. 77-97.

Bennett, A.F. (1991) Roads, roadsides and wildlife conservation: a review, in: Saunders, D.A. & R.J. Hobbs [Eds] Nature Conservation 2: The Role of Corridors, Chipping Norton, Australia, Surrey Beatty & Sons, p. 99-118.

Bennett, A.F. (1999) Linkages in the landscape: The role of corridors and connectivity in wildlife conservation, Gland, Switzerland and Cambridge, UK: IUCN.

Broekmeyer, M. (2001) Robuust beleid robuust ontsloten, Landschap 18 (4) p. 291-295.

Carr, M.H., P.D. Zwick, T. Hoctor, W. Harrell, A. Goethals & M. Benedict (1998) Using GIS for identifying the interface between ecological greenways and roadway systems at the State and sub-State scales, in: Evink, G.L., P. Garrett, D. Zeigler & J. Berry [Eds] Proceedings of the International Conference on Wildlife Ecology and Transportation, Tallahassee: Florida Department of Transportation, p. 68-77.

CBS (2000) StatLine Database, http://www.cbs.nl/en/statLine/index.htm [November 2000].

CBS (2001) Statistisch Jaarboek 2000, Voorburg/Heerlen, The Netherlands: Centraal Bureau voor de Statistiek.

Clarke, G.P., P.C.L. White & S. Harris (1998) Effects of roads on badger Meles meles populations in south-west England, Biological Conservation 86 p. 117-124.

Forman, R.T.T. & L.E. Alexander (1998) Roads and their major ecological effects, Annual Review of Ecology and Systematics 29 p. 207-231.

Foster, M.L. & S.R. Humphrey (1995) Use of highway underpasses by Florida panthers and other wildlife, Wildlife Society Bulletin 23 (1) p. 95-100.

Griffioen, A.J., H.A.M. Meeuwsen & S.A.M. van Rooij (2000) Afleiding inputbestand voor LARCH: Begroeiingstypenkaart 2000 (250x250m), Wageningen, The Netherlands: Alterra Green World Research.

Grift, E.A. van der & H.M.J. Kuijsters (1998) Mitigation measures to reduce habitat fragmentation by railway lines in The Netherlands, in: Evink, G.L., P. Garrett, D. Zeigler & J. Berry [Eds] Proceedings of the International Conference on Wildlife Ecology and Transportation, Tallahassee: Florida Department of Transportation, p. 166-170.

Grift, E.A. van der, Y.R. Hoogeveen, D.A. Kamphorst, C.F. Jaarsma, R.J.M. Kleijberg, A.A.G. Piepers, R.P.H. Snep, M. Soesbergen, G. Veenbaas & J.G. de Vries (2001) Fragmentation by existing infrastructure, in: Piepers, A.A.G. [Ed] Infrastructure and nature; fragmentation and defragmentation. Dutch State of the Art Report for COST activity 341, Delft, The Netherlands: Road and Hydraulic Engineering Division, p. 47-72.

Held, J.J. den & K.C. van Rij (1994) Van snippen en snippers. Ontsnipperingsmaatregelen voor de natuur langs rijkswegen in Gelderland, Arnhem, The Netherlands: Heidemij Advies.

Kalkhoven, J., R. van Apeldoorn, P. Opdam & J. Verboom (1996) Worden onze natuurgebieden groot genoeg? Schatting van benodigde oppervlakte leefgebied voor kernpopulaties van een aantal diersoorten, Landschap 13 (1) p. 5-15.

Kobler, A. & M. Adamic (1999) Brown bears in Slovenia: identifying locations for construction of wildlife bridges across highways, in: Evink, G.L., P. Garrett & D. Zeigler [Eds] Proceedings of the Third International Conference on Wildlife Ecology and Transportation, Tallahassee: Florida Department of Transportation, p. 29-38.

Langevelde, F. van & C.F. Jaarsma (1997) Habitat fragmentation, the role of minor rural roads and their traversability, in: Canters, K.J., A.A.G. Piepers & D. Hendriks-Heersma [Eds] Habitat fragmentation & infrastructure. Proceedings of the international conference on habitat fragmentation, infrastructure and the role of ecological engineering, Delft, The Netherlands: Road and Hydraulic Engineering Division, p. 171-182.

Lehnert, M.E., L.A. Romin & J.A. Bissonette (1996) Mule deer-highway mortality in northeastern Utah: causes, patterns, and a new mitigative technique, in: Evink, G.L., P. Garrett, D. Zeigler & J. Berry [Eds] Trends in addressing transportation related wildlife mortality. Proceedings of the Transportation Related Wildlife Mortality Seminar, Tallahassee: Florida Department of Transportation.

Levins, R. (1970) Extinction, in: Gerstenhaber, M. [Ed] Some mathematical problems in biology, Providence: American Mathematical Society, p. 77-107.

Ministerie LNV (1990) Natuurbeleidsplan, Den Haag, The Netherlands: SDU Uitgeverij.

Ministerie LNV (2000) Natuur voor mensen, mensen voor natuur. Nota natuur, bos en landschap in de 21e eeuw, Alkmaar, The Netherlands: Drukkerij Slinger.

Morel, G.A. & B.P.M. Specken (1992) Versnippering van de ecologische hoofdstructuur door de weginfrastructuur, DWW-Versnipperingsreeks deel 3, Delft, The Netherlands: Dienst Weg- en Waterbouwkunde.

Natuurplanbureau (2000) Natuurbalans 2000, Alphen aan den Rijn, The Netherlands: Samson BV.

Natuurplanbureau (2001) Natuurbalans 2001, Alphen aan den Rijn, The Netherlands: Kluwer.

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

Opdam, P., R. van Apeldoorn, A. Schotman & J. Kalkhoven (1993) Population responses to landscape fragmentation, in: Vos, C.C. & P. Opdam [Eds] Landscape Ecology of a stressed environment, London: Chapman and Hall, p. 147-171.

Opdam, P., C. Grashof & W. van Wingerden (2000) Groene dooradering. Een ruimtelijk concept voor functiecombinaties in het agrarisch landschap, Landschap 17 (1) p. 45-51.

Pelk, M., B. Heijkers, R. van Etteger, D. Bal, C. Vos, R. Reijnen, S. de Vries & P. Visschendijk (2000) Kwaliteit door verbinden; waarom, waar en hoe? Wageningen, The Netherlands: Alterra & IKC-Natuurbeheer.

Pouwels, R., M.J.S.M. Reijnen, J.T.R. Kalkhoven en J. Dirksen (2002). Ecoprofielen voor soortanalyses van ruimtelijke samenhang met LARCH. Alterra-rapport 493. Alterra, Research Instituut voor de Groene Ruimte, Wageningen.

Reijnen, R., E.A. van der Grift, M. van der Veen, M. Pelk, A. Lüchtenborg & D. Bal (2000) De weg mét de minste weerstand: Opgave ontsnippering, Wageningen, Alterra Green World Research & Experstisecentrum LNV.

Reijnen, R., R. Jochem, M. de Jong, M. de Heer & H. Sierdsema (2001) LARCH Vogels Nationaal. Een expertsysteem voor het beoordelen van de ruimtelijke samenhang en de duurzaamheid van broedvogelpopulaties in Nederland, Wageningen, The Netherlands: Alterra Green World Research.

RIVM (2001) Natuurcompendium 2001. De natuur in cijfers, http://www.rivm.nl/natuurcompendium [November 2001].

Ruediger, B., J.J. Claar & J.F. Gore (1999) Restoration of carnivore habitat connectivity in the northern Rocky Mountains, in: Evink, G.L., P. Garrett & D. Zeigler [Eds] Proceedings of the Third International Conference on Wildlife Ecology and Transportation, Tallahassee: Florida Department of Transportation, p. 5-20.

Scheick, B.K. & M.D. Jones (1999) Locating wildlife underpasses prior to expansion of Highway 64 in North Carolina, in: Evink, G.L., P. Garrett & D. Zeigler [Eds] Proceedings of the Third International Conference on Wildlife Ecology and Transportation, Tallahassee: Florida Department of Transportation, p. 75-83.

Singer, F.J. & J.L. Doherty (1985) Managing mountain goats at a highway crossing, Wildlife Society Bulletin 13 p. 469-477.

Singleton, P. & J.F. Lehmkuhl (1999) Assessing wildlife habitat connectivity in the Interstate 90 Snoqualmie Pass corridor, Washington, in: Evink, G.L., P. Garrett & D. Zeigler [Eds] Proceedings of the Third International Conference on Wildlife Ecology and Transportation, Tallahassee: Florida Department of Transportation, p. 75-83.

Smith, D.J. (1999) Identification and prioritization of ecological interface zones on state highways in Florida, in: Evink, G.L., P. Garrett & D. Zeigler [Eds] Proceedings of the Third International Conference on Wildlife Ecology and Transportation, Tallahassee: Florida Department of Transportation, p. 209-229.

Trombulak, S.C. & C.A. Frissell (2000) Review of ecological effects of roads on terrestrial and aquatic communities, Conservation Biology 14 p. 18-30.

Van der Zee, F.F., J. Wiertz, C.J.F. ter Braak & R.C. van Apeldoorn (1992) Landscape change as a possible cause of the badger Meles meles L. decline in the Netherlands, Biological Conservation 61 p. 17-22.

Verboom, J., P. Opdam & A. Schotman (1991) Kerngebieden en kleinschalig landschap: een benadering met een metapopulatiemodel, Landschap 8 (1) p. 3-14.

Verboom, J., J.A.J. Metz & E. Meelis (1993) Metapopulation models for impact assessment of fragmentation, in: Vos, C.C. & P. Opdam [Eds] Landscape ecology of a stressed environment, London: Chapman and Hall, p. 172-196.

Verboom, J., R. Foppen, P. Chardon, P. Opdam & P. Luttikhuizen (2001) Introducing the key patch approach for habitat networks with persistent populations: an example for marshland birds, Biological Conservation 100 p. 89-101.

Verboom, J. & R. Pouwels (in press) Ecological functioning of ecological networks: a species perspective, in: Jongman, R.H.G. & G. Pungetti [Eds] Ecological Networks and Greenways. Concept, design, implementation, Cambridge: Cambridge University Press.