Designing a Coherent Ecological Network for Large Mammals in Northwestern Europe

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Abstract: *In densely populated northwestern Europe, native large mammals are confronted with a very fragmented landscape, and most of the areas they inhabit are island-like reserves threatened with total isolation from other reserves. The only way to counteract the threat of further decline in the numbers of large-mammal species is to restore their habitats. The appropriate size of future reserves could be estimated from the habitat requirements of wild ungulates that are considered key species for ecosystem functioning. The species selected to guide the design of large nature reserves in northwestern Europe is the red deer* (Cervus elaphus) *because of its widespread distribution, key role in ecosystem functioning, and home-range size. We describe a network analysis of the Netherlands, Belgium, and adjacent parts of France and Germany, performed with the LARCH landscape ecology model, that was conducted in order to identify the structure of the ecological network for red deer and the spatial connectivity of the landscape. The resulting maps show areas that could support viable populations and indicate habitat areas that will support persistent populations only if they are in a network of linked habitats. The gaps and barriers that prevent connectivity in such networks guide the design of effective corridors to increase spatial connectivity. The results of our analysis can be used for policy decisions on nature conservation and spatial planning, and the method is applicable to other regions and species.*

Diseño de una Red Ecológica Coherente para Mamíferos en el Noroeste de Europa

Resumen: *En la región densamente poblada del noroeste de Europa, los mamíferos nativos grandes enfrentan un paisaje muy fragmentado y la mayoría de las áreas que habitan son reservas que funcionan como islas, amenazadas de ser totalmente aisladas una de la otra. La única forma de contrarrestar la amenaza de una mayor declinación en el número de especies de mamíferos grandes es mediante la restauración de sus hábitats. El tamaño apropiado para las reservas futuras podría estimarse en base a los requerimientos de hábitat de ungulados silvestres que son considerados especies clave para el funcionamiento de los ecosistemas. La especie seleccionada para guiar el diseño de reservas naturales grandes en el noroeste de Europa es el venado rojo* (Cervus elaphus) *debido a su amplia distribución, su papel clave en el funcionamiento de ecosistemas y el tamaño de su rango de hogar. Describimos una red de análisis de los Países Bajos, Bélgica y partes adyacentes de Francia y Alemania, llevado a cabo con el modelo de ecología de paisaje LARCH, empleado para identificar la estructura de la red ecológica del venado rojo y la conectividad espacial del paisaje. Los mapas resultantes muestran áreas que podrían sostener poblaciones viables e indican áreas que sostendrían solo poblaciones persistentes si se encuentran en una red de hábitats interconectados. Las aberturas y barreras que previenen la conectividad en éstas redes guían el diseño de corredores eficientes para incrementar la conectividad espacial. Los resultados de nuestros análisis pueden ser usados para la toma de decisiones políticas en la conservación de la naturaleza y la planificación espacial, y el método es aplicable a otras regiones y especies.*

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Introduction

In recent centuries, the loss and fragmentation of natural landscapes as a result of the extension and intensification of infrastructure, cities, cropland, and pasture in northwestern Europe has resulted in fragmented landscapes. As the amount of a given habitat declines, the chances of successful dispersal and colonization decrease stepwise (Andrén 1996; Fahrig 2001); and in many cases these chances are species-specific (Vos et al. 2001*a*). Small populations in isolated reserves are susceptible to the effects of stochastic, demographic, environmental, and genetic processes that may result in high extinction rates (Shaffer 1981; Roelke et al. 1993). If a subspecies goes extinct, genetic variation within the species is reduced (Harrison 1993).

So far, most conservation efforts to counteract this process in northwestern Europe have been relatively local. However, the reserves may not be large enough and the intervening land may not sustain the full range of ecological processes needed to ensure that populations persist (Soulé & Terborgh 1999*a*). We now know that the number of species of many taxa and also their within-species heterozygosity decrease with decreasing patch size (Wilcox 1980). If ecological core areas (containing natural or seminatural ecosystems or populations of European importance) become more isolated, the numbers of mammalian species in northwestern Europe will continue to decline unless appropriate management is implemented. Yet, given current economic trends in the landscape, the remaining natural habitat will become increasingly isolated, restricting natural colonization still further (Newmark 1987, 1995). This implies that it will be possible to conserve fragmentation-prone species only by repeated reintroduction. A better strategy, because it allows natural processes to take place, is to develop habitat networks by restoring the spatial connectivity of very fragmented habitat areas (Opdam 2002).

Red Deer as a Focal Species in the Design of Reserves in Northwestern Europe

Over the past 20 years, the scientific basis for selecting and designing reserves has developed rapidly, and more evidence has accumulated in support of larger spatial scales of conservation (Frankel & Soulé 1981; Opdam et al. 1995; WallisDeVries 1995; Soulé & Terborgh 1999*a*). Ungulates have been assigned keystone species status in the ecosystems of the temperate zone because of their effect on the structure and composition of vegetation by grazing, trampling, and rooting (Menge et al. 1994; McShea & Rappole 1999; Soulé & Terborgh 1999*a*). Their habitat requirements can be used to design viable regional conservation networks (WallisDeVries 1995; Soulé & Terborgh 1999*a*). The year-round habitat demands of herds of large ungulates require extensive areas that are linked by corridor zones and that provide sufficient cover, food, and shelter (Table 1; Soulé & Terborgh 1999*a*).

Northwestern Europe still harbors four widely distributed ungulate species: roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), wild boar (*Sus scrofa*), and red deer (*Cervus elaphus*). Because this region is under great pressure from economic development, large habitat areas are difficult to retain. Therefore, an additional and vital conservation strategy is to design and restore habitat networks on the basis of the metapopulation concept (Verboom et al. 1993; Fahrig & Merriam 1994; Opdam et al. 1995; Mills & Allendorf 1996; Opdam 2002; Verboom et al. 2001). Because of its range size, the red deer seems the obvious normative species (Soulé & Terborgh 1999*b*) for use in establishing the size, distribution, and habitat features of future natural areas in northwestern Europe. Therefore, we analyzed the potential habitat network(s) for red deer in northwestern Europe, based on available natural land, and identified discontinuities in the spatial distribution of habitat that preclude sustainable networks. We devised maps of ways in which the remaining natural areas could be linked into an ecological network that enables local populations to form a metapopulation. Our aim in presenting a tentative ecological network for red deer in northwestern Europe is to contribute to the conservation of large, wild mammals in this region.

Methods

The LARCH landscape ecology model (Landscape Ecological Rules for the Configuration of Habitat), developed at Alterra (Wageningen, The Netherlands), is a tool for visualizing the viability of metapopulations in a fragmented environment. LARCH is an example of habitat network assessment (Opdam 2002), a method based on the assumption that the potential persistence of a metapopulation can be assessed with ecologically scaled landscape indices (Vos et al. 2001*a*). It uses landscape characteristics that are ecologically scaled in relation to the spatial requirements of a species. LARCH can be used for scenario analysis and policy evaluation and has been described in detail elsewhere (Verboom et al. 2001). We briefly outline major aspects of the model and use the following definitions (cf. Verboom et al. 2001).

DEFINITION OF TERMS USED IN THE MODEL

Reproductive unit: for red deer, three individuals, a reproductive male and female and one other animal, which is the proportional part of the nonbreeding population.

Persistent or viable population: a population with at least a 95% probability of surviving for 100 years.

Minimum viable population: a population with exactly a 95% probability of surviving 100 years under the assumption of zero immigration.

Table 1. Home range, maximum reported movements, and range in body mass of adult male large-mammal species.

Species	Home range (ha)[a] +	Home range (ha)[a] −	Maximum movements (km)	Adult male body mass (kg)	References[b]
Roe deer	5	100	60	20–30	1, 2, 3
Fallow deer	50	750	90	45–60	1, 4
Wild boar	100	15,000	300	70–100	5
Red deer	500	20,000	120	85–150	6, 7, 8, 9

[a] *Symbols: +, high-quality habitat/high population density; −, low-quality habitat/low population density.*
[b] *Code: 1, Putman 1988; 2, Vincent et al. 1995; 3, Wahlström & Liberg 1995; 4, Niethammer & Krapp 1986; 5, Janeau & Spitz 1984; 6, Darling 1937; 7, Ruhle & Looser 1991; 8, Staines 1974; 9, Georgii & Schröder 1983.*

Metapopulation: a set of populations in a habitat network connected by interpatch dispersal.

Key population: a relatively large, local population in a network that is persistent, assuming one immigrant per generation.

Minimum key population size: a population size with exactly a 95% probability of surviving 100 years, assuming one immigrant per generation.

Minimum viable metapopulation: a metapopulation size with exactly a 95% probability of surviving 100 years, assuming zero immigration.

Habitat network: a set of habitat patches in a landscape matrix between which exchange of individuals is possible.

Key patch: a patch with a carrying capacity large enough to sustain a key population and close enough to other patches to receive, on average, one immigrant per generation.

Sustainable habitat network: a habitat network large and coherent enough to support a minimum viable metapopulation.

DEGREE OF FRAGMENTATION

LARCH distinguishes between three different levels of fragmentation, corresponding to three possible situations in which a network is expected to be viable (Verboom et al. 2001). (1) At a *low degree of fragmentation*, at least one patch in the network is large enough to support a minimum viable population. (2) At a *medium degree of fragmentation*, the network contains at least one key patch. This network is *sustainable* if the total network carrying capacity is high enough and the other patches are so close that enough dispersers will immigrate per generation. (3) At a *high degree of fragmentation*, no key patches occur in the network. This network is sustainable only if its total carrying capacity and its spatial connectivity allow a viable metapopulation.

ANALYSIS BY LARCH

Following is a step-by-step application of LARCH.

Step 1. We used the CORINE land-cover database (European Commission 1994), with a grid of cells of 250 × 250 m covering approximately 560,000 km^2 of northwestern Europe, as input for LARCH. The cells were grouped to define patches of habitat. If these patches were within home-range distance, we considered them functional for the red deer.

Step 2. We calculated the available digestible organic matter for an actual population of 60 red deer of known age and sex structure, living on natural foods in a 1400-ha reserve and sympatric with roe deer and wild boar. We used detailed knowledge of the main forage types (dry-matter percentage of diet), their availability in the area (percent coverage), and their digestibility by red deer (percent) to calculate total available digestible organic matter (in kilogram dry weight; Groot Bruinderink & Hazebroek 1995). We did this for February because this is the season in which red deer have most difficulty finding enough natural food. Because this population of red deer proved to be sustainable over the years, we defined this area's carrying capacity for red deer as 60 animals per 1400 ha. From these data we calculated the digestible organic matter requirements of one reproductive unit of red deer in late winter (Groot Bruinderink et al. 2000*a*, 2000*b*). For each patch of habitat, we calculated the standing crop (kilogram dry weight) of the main natural foods for red deer in February and converted this into available digestible organic matter (kilogram dry weight). Each patch was thus assigned a carrying capacity expressed as the number of reproductive units in late winter.

Step 3. We accounted for the barrier effect of roads. We derived data on roads from the Digital Chart of the World (Environmental Systems Research Institute 1993). Main roads, dual-lane roads, and major primary and secondary roads (classified in the Digital Chart of the World as 1, 2, and 8, respectively) are considered a barrier to local populations because they fragment home ranges and restrict day-to-day movements. If not separated by these major roads or urban areas, habitat patches <5 km apart (roughly the radius of a red deer home range; Staines 1974; Georgii & Schröder 1983; Carranza et al. 1991; Ruhle & Looser 1991) are fused by LARCH into a local population of a size that equals the sum of the reproductive units. For large vertebrates, the standard number of reproductive units for a key patch is 20 (Verboom et al. 2001).

Habitat patches within mean dispersal distance of each other (Schreiber et al. 1994) together form a habitat network that may support a metapopulation. The potential size of that metapopulation equals the sum of the maximum number of reproductive units of each patch.

Step 4. We calculated the spatial connectivity of the network derived in step 3. LARCH assesses the spatial connectivity of the network on the basis of the connectivity index developed by Verboom et al. (1991), Hanski (1994), and Ter Braak et al. (1998). The basic principle is that for each unit in the network, connectivity is a function of the potential immigration from surrounding patches within the dispersal range. In this calculation it is assumed that the smaller a patch is and the further away it is in the landscape the less it contributes to the inflow of dispersing individuals. It is also assumed that potential key populations in poorly connected landscapes are not part of a sustainable habitat network. The barrier effect of major roads and urban zones is also taken into account.

LARCH uses a grid base and therefore calculates the connectivity per grid cell. For each grid cell j, the area of the dominant type of land use is converted into a potential carrying capacity for red deer, expressed in the number of reproductive units RU_j. Therefore, each grid cell is surrounded by other grid cells, each of which has an RU related to the potential contribution to the stream of immigrants reaching cell i. To determine which cells could potentially contribute, it is necessary to know the dispersal range of red deer and the effect of the landscape on the dispersal distance. The number of migrants, S_i, reaching a patch of habitat from other patches at a distance d_{ij} away is estimated as

$$S_i = \sum_{j=1}^{n} Y_j A_j^b B_{ij} \cdot e^{-\alpha \cdot d_{ij}} \ (j \neq 1)$$

(Vos et al. 2001b), where $Y_j = 1$ for occupied patches and 0 for unoccupied ones, A_j is the area of patch j, and B_{ij} is an indicator of the presence of a barrier between i and j.

In this equation, α is a constant, setting the survival rate of migrants over the distance between the contributing patch j and the receiving patch i. We transformed the product of Y_j and A_j to an ecologically scaled measure, the carrying capacity of a grid cell j. On the basis of expert knowledge, we assumed that average major roads in our research area reduced the contribution of a grid cell j to the connectivity of cell i by 10%, but we took no account of the variation in traffic frequency between the regions. Vos et al. (2001*b*) explain how they transferred empirical data on dispersal distance to an estimate of α, and we used the same approach for the red deer. A conservative estimate of dispersal distances for red deer in northwestern Europe is 50 km (Darling 1937; Carranza et al. 1991). This coincides with α values of 0.05, assuming a landscape with no barriers. As yet, we have been unable to validate this assumption.

LARCH determines the connectivity, SC_i, of a habitat grid cell i by weighting the carrying capacity of all grid cells within the potential dispersal distance according to the distance and barrier effect of intervening major roads:

$$SC_i = \sum RU_j \cdot e^{-\alpha \cdot d_{ij}} \cdot p_n \, ,$$

where d_{ij} is the distance between the contributing grid cell j and cell i, measured as the shortest distance between j and i, avoiding built-up areas; RU_j is the maximum number of reproductive units in cell j (taking into account differences in carrying capacity between habitat types and the effect of barriers); and p_n is the coefficient of the "permeability," or ease of crossing, of all roads that are crossed ($p_1 * p_2 * p_3$). If no roads are present, $p_n = 1$.

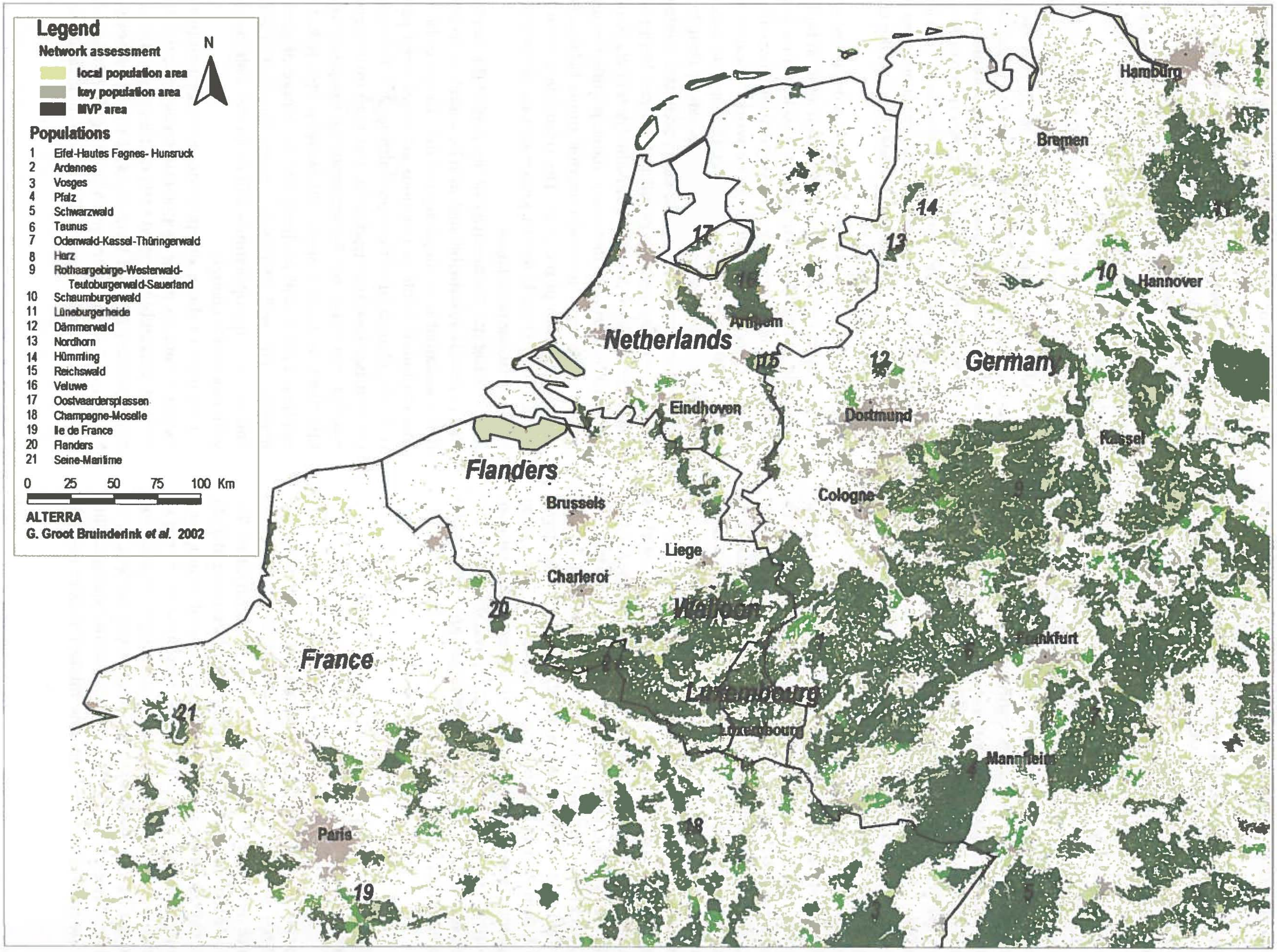
If no barriers are encountered, the Euclidian distance (as the crow flies) is calculated. If a barrier is encountered (built-up area, major road), the permeability of the barrier is accounted for in the algorithm by the parameter p, or the barrier is avoided by a detour. This detour increases the distance (d_{ij}) in the algorithm. The choice is based on the least costs.

Results

The result of steps 1-3 was a habitat-analysis map showing the spatial configuration of potential red deer habitat in northwestern Europe, which, in total, covered 80,143 km^2 (Fig.1). The map shows the distribution of three types of habitat areas: those large enough for local populations, those large enough for key populations, and those potentially containing minimum viable populations. The local populations can persist only if the patch is part of a sustainable habitat network. Many areas may still contain key populations. In some cases these key population areas are adjacent to but still physically separated from minimum viable population areas by barriers such as major roads. This is the case south of Cologne, north of Mannheim, or for a number of key populations near Paris. By definition, key populations are only viable as part of a population network.

Fragmentation of habitat in northwestern Europe has reached its highest level in western France, Flanders, The Netherlands, and adjacent Germany. Most of the habitat areas east of the Hamburg-Paris line are large enough to contain a minimum viable population. They are usually situated near each other, so one might pre-

Figure 1. Network analysis for red deer in northwestern Europe as calculated by the landscape ecology model LARCH. Numbers refer to existing populations, and MVP is minimum viable population.


Legend
Network assessment
local population area
key population area
MVP area
N
Populations
1 Eifel-Hautes Fagnes- Hunsruck
2 Ardennes
3 Vosges
4 Pfalz
5 Schwarzwald
6 Taunus
7 Odenwald-Kassel-Thüringerwald
8 Harz
9 Rothaargebirge-Westerwald-Teutoburgerwald-Sauerland
10 Schaumburgerwald
11 Lüneburgerheide
12 Dämmerwald
13 Nordhorn
14 Hümmling
15 Reichswald
16 Veluwe
17 Oostvaardersplassen
18 Champagne-Moselle
19 Ile de France
20 Flanders
21 Seine-Maritime
0 25 50 75 100 Km
ALTERRA
G. Groot Bruinderink et al. 2002
Hamburg
Bremen
Hannover
Netherlands
Germany
Eindhoven
Dortmund
Kassel
Flanders
Brussels
Cologne
Liege
Charleroi
France
Luxembourg
Paris

sume that deer disperse between them if areas are not fenced. These areas fall in the low-fragmentation category. The numbers on the map indicate present populations of red deer, which confirms the modeling results. Indeed, almost all minimum viable population areas contain a population of deer. Only around Paris, Kassel, and Eindhoven are there any minimum viable population areas not presently inhabited by red deer.

The result of step 4 was a map showing the spatial connectivity of red deer habitat in northwestern Europe. To determine which potential key population areas are located in highly or poorly connected landscapes, we projected the potential key populations from Fig. 1 into this spatial connectivity map (Fig. 2). Many key population areas situated in poorly connected landscapes in The Netherlands, western France, and northwestern Germany are not part of a sustainable habitat network. These cases indicate where the main conservation problems for this species are located.

Northwestern Europe still harbors large areas of well-connected red deer habitat, roughly indicating highly sustainable habitat networks that can support viable metapopulations. Good examples are the populations of the Eiffel-Hautes Fagnes-Hunsrück (area 1 in Figs. 1 & 2), the Ardennes (2), and the Pfalz (4). On the other hand, many existing red deer populations inhabit areas that are embedded in a poorly connected landscape, such as the populations of the Dämmerwald (12), Nordhorn (13), Hümmling (14), Flanders (20), and the Seine-Maritime (21) regions. Here migration is still possible, but, in case of the Dutch Veluwe population (16), poor connectivity with other areas results in zero migration. Some areas characterized by a relatively high degree of habitat connectivity are no longer inhabited by red deer, as is the case in the areas northeast of Paris and just south of the city of Eindhoven.

Discussion

Our study was based on the premise that to restore the habitat networks of large mammals it is necessary to preserve and restore large habitat areas and corridors. We have identified areas that, although they currently do not contain any red deer, have the potential to support a minimum viable population of this species. Some of these areas are well connected, and their colonization should be relatively easy, provided that no fences or other barriers are present. To increase the sustainability of the network as a whole, one might consider restocking these areas or—even better—improving their spatial connectivity to facilitate their colonization by red deer.

Analogously, different strategies are possible to improve the ecological network, including key population areas, whether they are actually inhabited by red deer or not: improve spatial connectivity, enlarge the number of occupied habitats, and increase the connectivity of sustainable parts of the network.

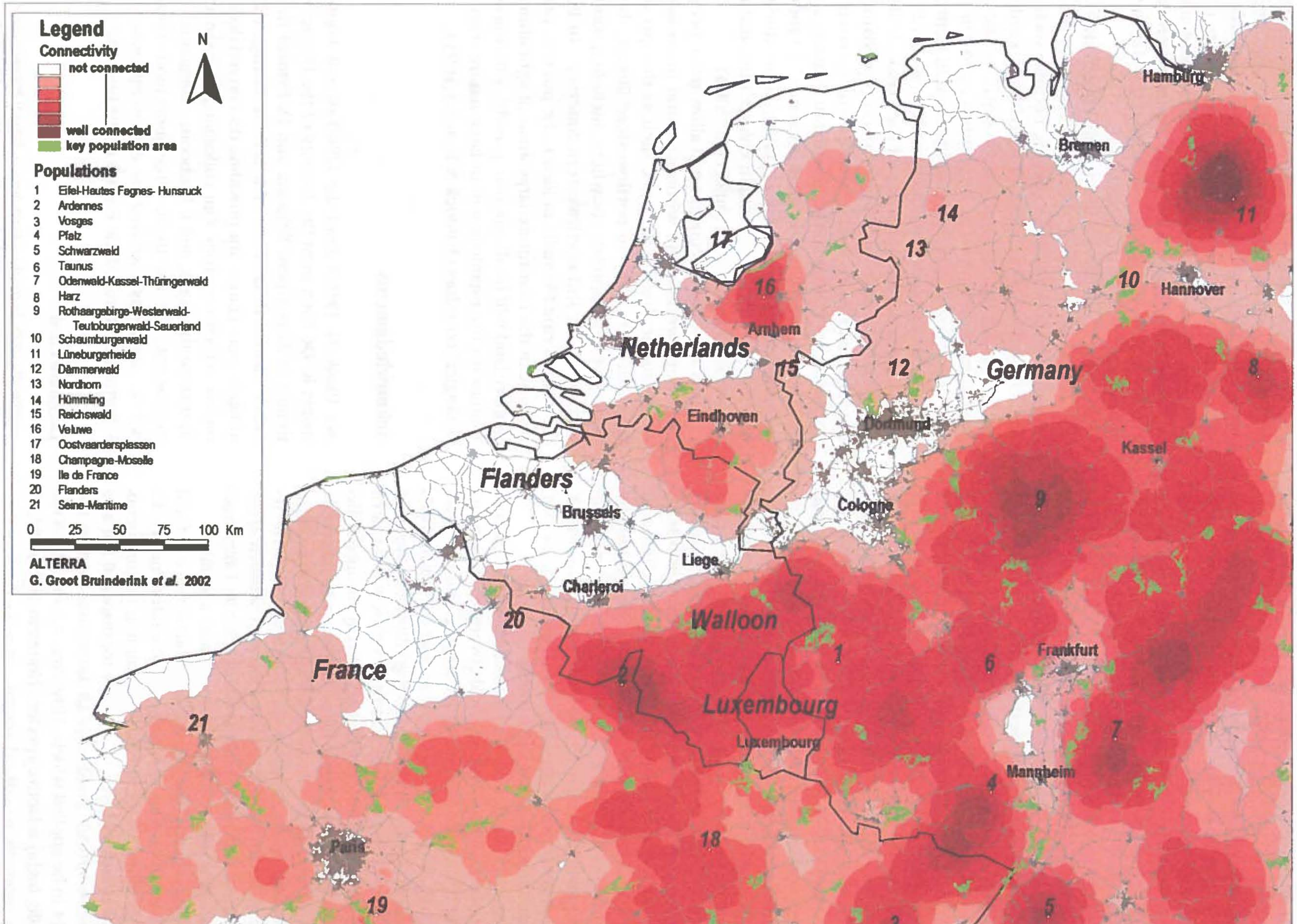
Improving spatial connectivity for populations occurring in unsustainable networks, effectively enlarging habitat, may result in a sustainable network. Realizing effective corridors between unpopulated key patches and other habitat patches may result in minimum viable populations. For example, it will be necessary to decrease cross roads or remove fences. This is the case with the key population areas adjoining the German-Belgian Eifel-Hautes Fagnes (area 1 in Fig. 2), the Veluwe in The Netherlands (16), and the Lüneburgerheide in Germany (11).

Enlarging the number of occupied habitat areas by connecting unpopulated key population areas in regions with little spatial connectivity may also lead to a populated sustainable network. Key population areas are effective ecological core areas in networks because networks with key population areas need less area to become sustainable (Verboom et al. 2001). This can be done by increasing the connectivity of the target area with minimum viable population areas or populated key patches in well-connected regions. An example is the (potential) population around Paris. All minimum viable population areas and key patches here would provide ample habitat for a large population of red deer. The population from Isle de France (19) could form a source area for development of the network population.

Increasing the connectivity of the part of the network that is already sustainable may also be a strategy to establish a sustainable ecological network. Despite the fact that minimum viable populations are considered persistent, the chance of extinction—although <5%—is still present because the models do not take into account risks of extinction by, for example, an epidemic virus. Effectively enlarging areas will decrease this risk. Connecting habitat will facilitate the exchange of genetic material. This will effectively enlarge the pool of genes, and as a result populations will be better able to cope with stochastic changes.

Examples of these stepping stones—key patches between minimum viable population areas—are the areas around Schaumbürgerwald (10) that may link the Lüneburgerheide (11) and Harz (8) and the areas between Vosges (3) and Champagne-Moselle (18). These stepping stones can be integrated in the ecological network

Figure 2. Spatial connectivity of red deer habitat in northwestern Europe as calculated by the landscape ecology model LARCH. Numbers refer to existing populations.


Legend
Connectivity
not connected
well connected
key population area
Populations
1 Eifel-Hautes Fagnes- Hunsruck
2 Ardennes
3 Vosges
4 Pfalz
5 Schwarzwald
6 Taunus
7 Odenwald-Kassel-Thüringerwald
8 Harz
9 Rothaargebirge-Westerwald-Teutoburgerwald-Sauerland
10 Schaumburgerwald
11 Lüneburgerheide
12 Dämmerwald
13 Nordhorn
14 Hümmling
15 Reichswald
16 Veluwe
17 Oostvaardersplassen
18 Champagne-Moselle
19 Ile de France
20 Flanders
21 Seine-Maritime
0 25 50 75 100 Km
ALTERRA
G. Groot Bruinderink et al. 2002
N
Hamburg
Bremen
Hannover
Netherlands
Arnhem
Eindhoven
Dortmund
Germany
Kassel
Flanders
Brussels
Cologne
Liege
Charleroi
Walloon
Frankfurt
France
Luxembourg
Mannheim
Paris

and will effectively form part of the habitat of red deer populations.

These intervention options all result in enlarged or new minimum viable population areas, with a decreased overall risk of extinction of the metapopulation. Which option is best depends on the situation, the possibilities for spatial planners, and political boundaries. Ultimately, our maps should be seen as a tool, providing information for planners and politicians on the possibilities for improvement of the landscape configuration.

Because species differ in the way they use a fragmented landscape, solutions for connectivity differ with the setting and species (Soulé & Terborgh 1999*a*, 1999*b*; Vos et al. 2001*a*). Frequently, corridors are being suggested for the improvement of spatial connectivity between minimum viable populations or key population areas. Although there is an urgent need for knowledge on how to construct the right type of ecological corridor, and although for many species scientific evidence on the value of corridors is still lacking (Beier & Noss 1998), areas in between minimum viable population areas and identified as crucial for migration should be safeguarded from further habitat loss.

LARCH enables the viability of a population or metapopulation to be assessed for any species in a fragmented landscape, providing that the species can be characterized by its habitat requirements, the carrying capacity of its habitat, its dispersal capacity, and its key population size (Verboom et al. 2001). The sensitivity of the model was assessed by Van der Lee et al. (2000), who showed that the most important parameter by far is carrying capacity. Because we accurately assessed this parameter with field data, we consider our modeling results to be robust.

The spatial cohesion has been assessed on the basis of available barrier maps with regional coverage. The permeability of 0.9 is estimated and might require more-accurate assessment. Moreover, the maps assume that main roads form barriers, but occasionally they go through tunnels or cross river valleys on bridges. In these cases, actual spatial cohesion will be better than that assessed by the model. Because this is likely to occur in hilly terrain with more suitable habitat, where spatial cohesion can be expected to be high, it has no large implications for our modeling results. The results generated by LARCH would be more immediately applicable if input data such as maps of vegetation and infrastructure, including deer-proof fences, were more accurate.

We have argued that the red deer can serve as a focal species in the design of large-scale ecosystem networks mainly because of the species' demanding requirements for habitat area and type of corridor for dispersal but also because its virtually pan-European distribution enables the concept to be applied widely. However, red deer are a nutritionally highly adaptive species (Hofmann 1989) and, although primarily woodland animals, they have adapted to widely differing environments (Staines 1974; Putman 1988; Caro & O'Doherty 1998). Having presented a concept, we are tempted to philosophize on its financial and ecological consequences, such as the thousands of hectares that would be needed for key areas, corridors, and stepping stones, or the risk of loosing habitat specialists when the area demands of a generalist like the red deer are used in designing an ecological net work. Application will therefore have consequences for conservation in general but also for land-use planning and spatial development in northwestern Europe in particular.

Maintaining corridors will not only effectively enlarge the habitat of the focal species but will also benefit many other small and large species, because such corridors facilitate the exchange of individuals, seeds, and genes. Among the species benefited will be the larger predators such as wolf (*Canis lupus*) and European lynx (*Lynx lynx*), which are still present in Central Europe. We deliberately did not choose a large carnivore as a focal species, although many of the classic ecological arguments we have cited apply to a top predator. The last large carnivore species were exterminated from northwestern Europe in the nineteenth century; so people are not familiar with their presence. To focus on them now would be to risk engendering so much controversy that rural people might change their attitude to conservation in general (Linnel et al. 2000).

Application of our concept will allow more people to encounter wildlife and witness natural processes. An ambitious ecological network such as that presented here can be realized in northwestern Europe, but the concept can be applied elsewhere, including south and eastern Africa and northwestern America). In Europe the time is ripe for such an idea to be put into practice because in the near future large areas of agricultural and military land will be abandoned, possibly offering opportunities for the establishment of large nature reserves or ecological corridors (Baldock & Beaufoy 1993).

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