HUMAN IMPACT ON POPULATIONS OF HEDGEHOGS *ERINACEUS EUROPAEUS* THROUGH TRAFFIC AND CHANGES IN THE LANDSCAPE: A REVIEW

by

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ABSTRACT

This paper focuses on the response of hedgehogs populations to human impact on the landscape, and discusses whether traffic mortality is likely to be a dominant factor in a possible decline of the species. Hedgehogs have relatively high population densities in small scale agricultural landscapes and urban areas with gardens and parks, whereas forests, large scale agricultural lands and urban centres have lower densities. Edge habitat was found to be favoured by hedgehogs and since the initial stages of human impact on natural forests must have led to an increase of this habitat, hedgehogs are likely to have benefitted. However, the later removal of hedgerows and small woodland fragments in agricultural areas has caused hedgehog populations to decline locally or regionally.

Hedgehogs are not particularly vulnerable to habitat fragmentation, but road density and traffic intensity have shown a strong increase over recent decades and they may have caused hedgehog populations to disappear in areas that already had low density. The current policy that aims for more compact urban areas leads to the loss of urban green spaces. Combined with an increase in barriers this will cause a reduction of hedgehog population density in these areas. Although hedgehog populations may decline, it seems unlikely that hedgehogs will be threatened with extinction in the near future. Furthermore, traffic mortality is unlikely to be the primary cause of a possible decline of the species. The way humans manage the landscape has far greater effects on the survival probability of hedgehog populations.

The primary habitat of hedgehogs, urban areas account for only 8% of the land area of the Netherlands and because of the relative scarceness of these areas, the long term survival of hedgehogs may also depend on how well hedgehog populations do in other habitats. The current policy for a less intensive management of forests and other natural areas, combined with a greater tolerance for various dynamic processes, could be beneficial to hedgehogs since edge habitat will increase. Similar benefits could result from a transformation of selected agricultural lands into nature areas or into a network of set-aside lands and field margins. This may result in healthy hedgehog populations in addition to those in urban areas.

Key words: *Erinaceus europaeus*, hedgehog, traffic victims, population density, habitat selection, human impact, urban wildlife.

1. Introduction

The hedgehog *Erinaceus europaeus* (L., 1758) is one of the most common mammal species found in road-kill surveys throughout Europe (Davies, 1957; Göransson et al., 1976; Mannaert, 1978; Blümel & Blümel, 1980; Reichholf & Esser, 1981; Garnica & Robles, 1986; Korhonen & Nurminen, 1987; Rodts et al., 1998; Smit et al., 1998). Minimum estimates on the number of hedgehogs killed per kilometre road per year vary between 0.3 and 2.9 (table 1). In the Netherlands, a country characterized by relatively high road density and traffic volume, hedgehog traffic victims occur throughout the country and their total annual number is estimated to lie between 113,000 and 340,000 (Huijser & Bergers, 1998). A study during the 1960s also indicated that the number of hedgehog traffic victims may be high: Sponholz (1965) estimated their number at 720,000-1,000,000 per year in western Germany.

Table 1. Estimates on the minimum number of hedgehog traffic victims per kilometre road per year in various parts of western Europe.
Tabel 1. Minimum schattingen van het aantal doodgereden egels per kilometer weg per jaar in verschillende delen van west-Europa.

location	no. victims $km^{-1}yr^{-1}$	source
W Switzerland	0.3-0.8	Berthoud (1980)
SE Great-Britain	0.5-2.1	Keymer et al. (1991)
SE Germany	0.6-1.0	Reichholf and Esser (1981)
Central Netherlands	0.9	Jonkers and De Vries (1977)
SW Netherlands	1.1-2.1	Meijer and Smit (1995)
S Sweden	1.7	Göransson et al. (1976)
N Spain	1.7	Garnica and Robles (1986)
S Great-Britain	2.3	Hodson (1966)
NW Germany	2.9	Heinrich (1978)

The apparently high number of hedgehog traffic victims may pose a threat to the survival of the species. Most studies that address this issue focus on the effect of roads and traffic on various population parameters such as the total losses within a population, population density, and population survival probability (e.g., Huijser et al., 1998). Here a more integrated view of the influence of humans on hedgehog populations is presented. This paper focuses on hedgehog population density in various landscapes and discusses whether traffic mortality is likely to be a dominant factor in a possible decline of the species.

2. Population density and habitat selection

The hedgehog is a common species throughout most of its range in western Europe (Reeve, 1994; Thissen & Hollander, 1996). Hedgehogs seem to be able to adjust to a great variety of habitats; in the Netherlands they have been recorded in almost every 5x5 km block in a survey grid (Hoekstra, 1992). However, hedgehog population density may vary greatly (Reeve, 1994; Mulder, 1996a). A review of the literature indicates that forests have far lower densities than small scale agricultural areas with hedgerows and woodland fragments (table 2). Large scale agricultural lands with little or no trees and shrubs to provide cover also have low hedgehog density. The highest densities have been recorded in urban areas with parks and gardens. Urban areas with little vegetation (e.g., village centres or inner city areas, from now on referred to as 'urban centres') usually have low densities.

Some studies have revealed selective habitat use during the night, i.e., when hedgehogs are active (table 3). In general, hedgehogs spend less time in forests, arable land and heathland than one would expect based on the area of these habitats within their home range. Grasslands, including lawns in gardens, hedgerows and urban areas with gardens and parks are positively selected. Berthoud (1978), Reeve (1981), Morris (1986) and Zingg (1994) all reported that hedgehogs spend a great deal of their time in 'edge habitat': along the edge of lawns, grasslands or arable land, under a solitary tree, along walls, buildings, hedgerows, a forest's edge, water, roads and side walks and near shrubs.

Table 2. Hedgehog density in various habitats.
Tabel 2. Dichtheden van egels in verschillende habitat typen.

habitat type	density/100 ha	source
forest	2-3, 5	Berthoud (1982)
small scale agricultural landscape with hedgerows and woodland fragments	21, 70	Doncaster (1994)
	25	Doncaster (1992)
	28-34	Berthoud (1982)
	33	Morris (1988)
large scale agricultural landscape with little cover	0	Dowie (1987)
	5-7, 6	Berthoud (1982)
urban areas with vegetation	16-26, 22-25, 22-30, 23-25, 53-60, 143	Berthoud (1982)
	48	Kristiansson (1990)
	83	Reeve (1981)
	50-300	Esser (1984)
	52-104	Bontadina e.a (1993)
	70-270	Dietzen & Obermaier (1989)
	179	Doncaster (1994)
	210-280	Palm & Stöwer (1990)
urban centres with little vegetation	4-6	Berthoud (1982)

Edge habitat may be preferred by hedgehogs for several reasons: e.g., (1) presence of food, (2) nearby cover or (3) to facilitate orientation. As far as food is concerned, hedgehogs mainly eat a wide variety of invertebrates, but vertebrates (mainly carrion) and plant material (including fruit) have also been recorded (see review in Reeve, 1994). However, earthworms, beetles and caterpillars are the most important source of food (Yalden, 1976; Wroot, 1984). The importance of earthworms is further illustrated by the fact that the distribution of hedgehogs on grasslands was found to be correlated with the availability of earthworms (Micol et al., 1994; Cassini & Föger, 1995). Esser (1984) showed that the availability of earthworms (mainly *Lumbricus terrestris*) decreased in the following order: grasslands - hedgerows - forest's edge - forest - arable land. The order for the combined dry weight of arthropods and snails in these habitats was: hedgerows - grasslands - forest's edge - forest - arable land. Again the results showed the importance of edge habitat over forest.

Reeve (1981) found that hedgehogs that were released in the open usually went directly to the nearest cover. Brambles, other shrubs and dead wood may provide shelter from predators. Although hedgehogs also prefer to build their day nests in such places (Reeve & Morris, 1985), good nesting sites are unlikely to keep them from leaving edge habitat when they are active.

Reeve's observations indicate that cover may play a role, but they also showed that hedgehogs can detect trees and bushes at night over distances well in access of ten metres, and that they could be using them for orientation. Their detection range may ac-

Table 3. Habitat selection of hedgehogs during the night (i.e., when they are active).
Tabel 3. Habitat selectie van egels gedurende de nacht (d.w.z. wanneer ze actief zijn).

habitat	selection[1] positive	negative	source
forest		–	Eser (1982)[2]
		–	Esser (1984)
	+	–	Doncaster (1992)
		–[3]	Doncaster (1994)
		–	Zingg (1994)
hedgerows	+		Esser (1984)
	±[4]		Zingg (1994)
agricultural land	–		Zingg (1994)
grasslands (or lawns)	+		Eser (1982)[2]
	+		Esser (1984)
	+[3]		Doncaster (1992)
	+[3]		Doncaster (1994)
	+		Zingg (1994)
arable land		–	Eser (1982)[2]
		–[3]	Doncaster (1992)
		–[3]	Doncaster (1994)
		–	Zingg (1994)
heathland		–[5]	Esser (1984)
urban areas (with vegetation)	+		Zingg (1994)

Notes.
[1] most studies lack statistical analysis and were based on use-availability ratio's (percentage of time spend in a certain habitat / percentage of that habitat within home range).
[2] as cited in Esser (1984)
[3] in two different areas
[4] hedges were in gardens and not in an agricultural setting
[5] few data.

Noten.
[1] *bij de meeste studies ontbreekt een statistische analyse zodat de resultaten alleen werden weergegeven in de vorm van gebruik-aanbod ratio's (percentage tijd doorgebracht in een bepaald habitat / percentage van dat habitat binnen het leefgebied).*
[2] *zoals geciteerd in Esser (1984).*
[3] *in twee verschillende gebieden.*
[4] *de heggen stonden in tuinen en niet in een agrarische omgeving.*
[5] *weinig gegevens.*

tually be much greater than ten metres: mice have been shown to be able to detect forested habitat from at least 20 m distance (Zollner & Lima, 1997). Hedgehogs have relatively large home ranges (males 32-47 ha, females 10-20 ha (Reeve, 1982; Kristiansson, 1984)) and trees and bushes may be used for orientation as they move from one part of their home range to another (Reeve, 1994; Zingg, 1994). Zingg (1994) described several observations that indicate that hedgehogs may have long-term memory, and know where they are within their home range and how to get to another location.

The three factors discussed above (food, cover, orientation) may all explain why hedgehogs are attracted to edge habitat. It is only through an experimental approach that their relative importance can be determined.

3. Hedgehogs, humans and agriculture in an historical perspective

During the Pleistocene and possibly also during the Pliocene and late Miocene, a series of ice-ages occurred that covered much of Europe in ice (e.g., Eyles, 1993; Prins, 1998). Mammals associated with forests are thought to have retreated in Iberia, southern France, Italy and south-eastern Europe. Herter (1934) suggested that the ancestors of modern day hedgehogs may have become (repeatedly) isolated in these refuge areas. This theory is supported by the genetic differences found between and within the two European species we know today: the western (*E. europaeus*) and the eastern hedgehog (*E. concolor*) (Santucci et al., 1998). Subsequent warming during the last 10,000 years or so enabled forests and associated fauna, including hedgehogs, to spread northwards once more.

There is considerable debate on what the forests in north-western Europe looked like before humans started to have a major impact (Prins, 1998; van Beusekom, 1998; Vera, 1998; Verkaar, 1998; Zeiler & Kooistra, 1998). According to one theory the forest was very dense. Non-forest vegetation such as grasslands is thought to have occurred only on locations where abiotic parameters (primarily hydrology and soil) prevented trees from becoming dominant. Another theory states that these forests were not homogeneous, but rather a mosaic of forest, grasslands and shrubs with abundant edge habitat (Vera, 1997).

Whatever these forests looked like, humans are likely to have increased the heterogeneity of the landscape through fires, grazing of livestock and the clearance of areas for agriculture (Forman & Baudry, 1984; Merriam & Wegner, 1992). Species richness may have benefitted from such moderate 'disturbance' of the landscape, especially if disturbance was local and spread over time (Connell, 1978; Huston, 1979; Picket & White, 1985; Kolasa & Picket, 1991). Disturbance of the landscape by humans, at least during the initial stages, must also have led to an increase in edge habitat that in turn must have benefitted hedgehogs. The latter is confirmed by the relatively high density of hedgehogs found in present day small scale agricultural landscapes (see table 2).

As human use of the landscape intensified, more and more of the forests disappeared. Eventually many of the small woodland relicts and hedgerows were removed too (Mader, 1984; Burel & Baudry, 1990; Brown, 1992; Opdam et al., 1993; Bazin & Schmutz, 1994; Kotzageorgis & Mason, 1997; Verboom, 1998). In the Netherlands, the length of hedgerows and rows of trees decreased by ±50% between 1900 and 1990, and the average field size increased by ±80% (Dijkstra et al., 1997). Both parameters indicate a change from a small scale agricultural landscape to a large scale agricultural landscape with little edge habitat. One may expect the latter landscape to be of poor quality to hedgehogs. Again this is confirmed by the hedgehog densities found in this habitat (table 2).

The effect of human impact on hedgehog population density through agriculture is visualized in figure 1. Although natural forests may have had considerable edge habitat to begin with (Vera, 1997), small scale agriculture led to an increase of this habitat and

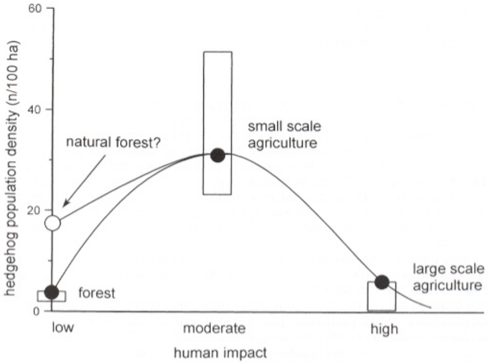

Fig. 1. The effect of agriculture on hedgehog population density. The landscape categories are the same as those in table 2. The points in the graph represent the median of the population densities listed in table 2. The boxes show the interquartile range.

Fig 1. Het effect van landbouw op de populatiedichtheid van egels. De landschapstypen zijn dezelfde als die in tabel 2. De punten in de grafiek staan voor de mediaan van de in tabel 2 genoemde populatiedichtheden. De rechthoeken geven de interkwartielafstand weer.

higher hedgehog population density. However, there is an optimum as increased human impact led to a strong decrease of edge habitat.

4. Hedgehogs and habitat fragmentation

Habitat loss and smaller and more isolated areas generally lead to reduced population survival probability for species that depend on the habitats concerned (e.g., Hanski, 1989; 1991). This process is referred to as 'habitat fragmentation' and may eventually lead to the extinction of local or regional populations or even a species (Vos & Opdam, 1993; Begon et al., 1996).

Certain species are more vulnerable to habitat fragmentation processes than others. Low population density, large home ranges (especially when also territorial), low dispersal rates or short dispersal distances, habitat or food specialization, stochastic population dynamics and low reproduction rate all increase the chance of (local) extinction (Van Apeldoorn & Kalkhoven, 1991; Bright, 1993; van Apeldoorn, 1994; Cuperus & Canters, 1997; Huijser et al., 1999). When habitat fragmentation results from infra-

Table 4. Characteristics of hedgehogs that may influence their vulnerability to habitat fragmentation.
Tabel 4. Karakteristieken van egels die mogelijk van invloed zijn op hun kwetsbaarheid voor habitat fragmentatie.

Population density
Variable, but usually high in landscapes that are dominated by humans (except for large scale agricultural lands and urban centres) (see table 2).

Home ranges
Relatively large: males 32-47 ha; females 10-20 ha (Reeve, 1982; Kristiansson, 1984). Males may travel 1.7-1.8 km on average per night during the mating period; females 0.8-1.0 km (Reeve, 1982; Kristiansson, 1984). On several occasions greater distances have been recorded: males 2.8 km (Reeve, 1982), 3.1 km (Morris, 1988) 6.3 km (Zingg, 1994); females 1.8 (Zingg, 1994), 2.1 km (Reeve, 1982).

Territoriality
No, there is complete overlap in home ranges of both females and males (see review in Reeve, 1994). But mutual avoidance (Morris, 1969) as well as an individual (feeding) space (Cassini & Föger, 1995) have been suggested.

Dispersal rates/distance
No detailed studies are available on dispersal rates, but dispersal seems to be rare (e.g., Kristiansson, 1990). Dispersal distances: 4 km (Esser, 1984), 5 km (Zingg, 1994) and 6 km (Kristiansson, 1990). Hedgehogs released back into the wild dispersed up to 2 km (Morris & Warwick, 1994), 3 km (Reeve, 1998), 4 km (Morris et al., 1993), and over 5 km (Morris, 1997) from the release site. Reeve (1994) cites Blewett (1979) who wrote about an eastern hedgehog that returned to a house where it had been cared for from 77 km away.

Habitat or food specialization
No, hedgehogs are considered habitat generalists (see table 1.1) and eat a wide variety of food, mainly invertebrates (see review in Reeve (1994)).

Stochastic population dynamics
Hedgehog populations may fluctuate considerably: density (n/100 ha) may double from one year to the next (30-66), but can also be drastically reduced (78-34) (Kristiansson, 1990). The total number of hedgehog traffic victims in 11 small villages surrounded by agricultural land also fluctuated strongly between successive seasons: 63-18 and 17-47 (Reichholf, 1983). However, these studies were conducted in relatively small non-natural habitats (villages) which were surrounded by non-natural barriers (agricultural lands and roads). Population fluctuations may have been greater than they would have been in larger areas in natural habitat.

Reproduction rate
Relatively high. Females may start reproducing in their second (Britain) or third summer (Sweden) (Reeve, 1994; Kristiansson, 1990). In the Netherlands it is unlikely for a female to have more than one litter per season (Huijser, 1997). There may be 4.1 (the Netherlands) or 4.4 (Britain) young on average (range 2-6) in litters less than two weeks old (Morris, 1977; Huijser, 1997). Kristiansson (1981) recorded 5.2 young per litter.

Speed of the animals
Average speed (m min^{-1}): males 3.7 (Reeve, 1982), 1.6-3.5 (Kristiansson 1984); females 2.2 (Reeve, 1982), 1.4-1.8 (Kristiansson, 1984). When running hedgehogs can reach speeds of up to 30-60 (Reeve, 1982) or even 120 m min^{-1} (Wroot, 1984). Note: their reaction to traffic varies from 'freezing' to running (Mulder 1996b).

Attraction to roads/road-side verges
No. Despite other reports (e.g., Poduschka, 1971) roads are generally avoided (Bontadina, 1991; Zingg, 1994; Mulder, 1996b). However, attraction to road-side verges is possible but has not been studied.

Table 5. Relative number of hedgehog traffic victims in forest and urban areas. Their numbers are standardized per road length unit and to the numbers found in an agricultural landscape (= 1.00).
Tabel 5. Het relatieve aantal egel verkeersslachtoffers in bossen en stedelijke gebieden. De aantallen zijn gestandaardiseerd per weglengte eenheid en ten opzichte van de aantallen die in een agrarisch landschap werden aangetroffen (= 1.00).

forest	urban areas	source
1.08	3.34	Reichholf & Esser (1981)
1.87	14.12	Göransson et al. (1976)
2.30	1.92	Palm & Stöwer (1990)
2.70	5.47	Berthoud (1980)

structure, slow animals or those that are attracted to roads or road-side verges (e.g., for food), are also considered to be at risk.

Hedgehogs have low population density in some habitats (e.g., forests, large scale agricultural landscapes and urban centres), their home range is relatively large and local population size or density may fluctuate considerably (table 4). As a result, local or regional populations could vanish. In certain areas the population size may be too small to cope with chance factors and (further) human induced changes in the landscape. Even if such changes are very local, hedgehogs may soon suffer because of their large home ranges. However, all other aspects lead to the conclusion that hedgehogs are not particularly vulnerable to habitat fragmentation (see also Bright, 1993). Non-territoriality and relatively great dispersal distances facilitate recolonization, and their ability to exploit a broad range of habitat and food types should enable hedgehogs to cope with considerable changes in the landscape and the availability of certain prey species. Finally, hedgehog reproduction is high enough to suggest that they should be able to withstand considerable mortality.

Habitat fragmentation through road infrastructure is a relatively new phenomenon. Fortunately, hedgehogs are fast enough to get out of the way of an approaching car if they decide to do so, and they tend to avoid asphalt with its apparent hazards (table 4). The highest number of hedgehog traffic victims is generally found in urban environ-

Table 6. Mean growth of traffic intensity (in %) during the day (6-21 hr) and night (21-6 hr) between 1989 and 1998. Based on data from 13 automatic registration devices located along major roads throughout the Netherlands. The relative growth between 1989 and 1998 was determined through linear regression analyses of the original data. These data were then analyzed for differences between day and night (Wilcoxon matched-pairs signed-ranks test, 2-tailed).
Table 6. Gemiddelde groei van verkeersintensiteit tussen 1989 en 1998 (in %) gedurende de dag (6-21 uur) en nacht (21-6 uur). Gebaseerd op gegevens van 13 geautomatiseerde telpunten langs rijkswegen verspreid over Nederland. De relatieve groei tussen 1989 en 1998 is bepaald op basis van lineaire regressieanalyses van de oorspronkelijke telgegevens. Deze gegevens werden vervolgens onderzocht op verschillen tussen dag en nacht (Wilcoxon matched-pairs signed-ranks toets, 2-zijdig).

	mean growth (%)	sd	N
day	40.56	13.89	13
night	50.91	18.07	13

sign.: p=0.006

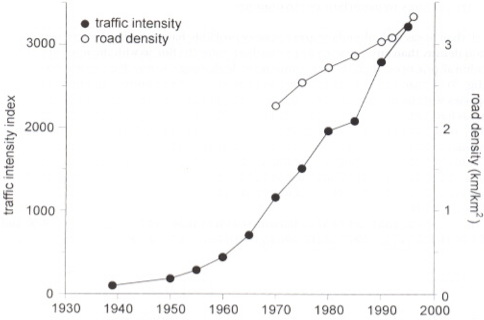

Fig. 2. Traffic intensity index (1939=100) and density of paved roads in the terrestrial part of the Netherlands (34,000 km^2) (based on data from the Central Bureau of Statistics (Anonymous, 1956-1998)). There were 6,757,000 motorized vehicles and 113,419 km of paved road in 1996.

Fig. 2. De verkeersintensiteitsindex (1939=100) en de wegendichtheid in het terrestrische deel van Nederland (34.000 km2) (gebaseerd op gegevens van het Centraal Bureau voor de Statistiek (Anonymous, 1956-1998)). In 1996 waren er 6.757.000 gemotoriseerde voertuigen en 113.419 km verharde weg.

ments and on roads through forests (usually small woodlots with abundant edge habitat) (table 5). Relatively few victims are found on roads through agricultural lands. Therefore some people argue that the number of hedgehog traffic victims simply reflects population density (see also table 2) and that traffic does not cause an immediate threat to the persistence of populations. Although hedgehog density and the number of traffic victims seem to be correlated, it does not necessarily imply that populations cannot go extinct. Furthermore, both road density and traffic intensity have shown a dramatic increase over recent decades and there is no indication that their growth rate is levelling off (fig. 2). Over the past ten years traffic volume has grown relatively more at night and nocturnal mammals may have been particularly affected (table 6). Because of the strong and continuous growth of traffic intensity and road density, a serious effect of traffic on the survival probability of hedgehog populations can not be ruled out. This is especially true in habitats in which hedgehog densities are low already (Bergers & Nieuwenhuizen, 1999). Even with a conservative average of 1 km paved road per km^2 and 2 hedgehog traffic victims per km road length per year, ±50% of the hedgehog population may be killed annually on the roads through forests, large scale agricultural landscapes and urban centres (see table 2).

5. Hedgehogs in an urban environment

Urban areas with abundant green spaces probably have a higher hedgehog population density than any natural habitat ever had (table 2). But, as with the intensity of agricultural practices, there is an optimum for hedgehogs in the degree of urbanisation (fig. 3). Urban centres usually have too few green spaces and too many barriers for species with large home ranges such as the hedgehog. Fortunately, most of the urban areas have sufficient green spaces. When an arbitrarily cut-off of 35 houses per ha is set, 93% of the urban areas in the Netherlands can be considered good quality hedgehog habitat (Farjon et al., 1997). However, hedgehogs in an urban environment are also confronted with new dangers. Wildlife hospitals report all kinds of injuries, poisoning (e.g., through slug pellets) and accidents that are related to humans, human made objects or constructions, garden machinery or pets (mainly dogs) (Reeve, 1994; Reeve & Huijser, 1999).

In the Netherlands urban areas have increased by more than 500% between 1900 and 1990 (Dijkstra et al., 1997) and further growth is foreseen (Farjon et al., 1997). Howev-

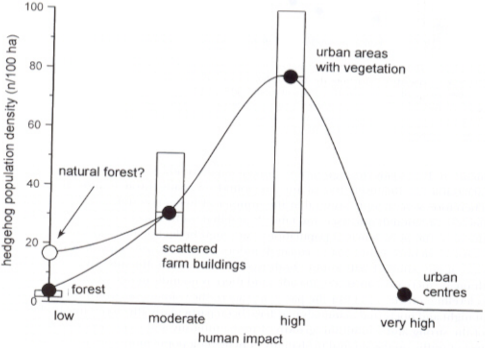

Fig. 3. The effect of urbanization on hedgehog population density. The landscape categories are the same as those in table 2, except for small scale agricultural landscape that was renamed to scattered farm buildings. The points in the graph represent the median of the population densities listed in table 2. The boxes show the interquartile range.

Fig 3. Het effect van urbanisatie op de populatiedichtheid van egels. De landschapstypen zijn dezelfde als die in tabel 2, met uitzondering van kleinschalig agrarisch landschap dat hier benoemd is als verspreid liggende boerderijen. De punten in de grafiek staan voor de mediaan van de in tabel 2 genoemde populatiedichtheden. De rechthoeken geven de interkwartielafstand weer.

er, the density of houses in these new urban areas may be much higher. The current Dutch policy is to focus on compact cities (Anonymous, 1990a), both on new locations and through infill development. Houses are generally built directly adjacent to one another and impermeable walls and fences are often erected around the remaining gardens. Although there may be less pressure on the countryside because of infill development, urban wildlife, especially those species that have large home ranges, will be negatively affected. Fewer and smaller gardens and public green spaces may also seriously reduce the availability of suitable nest sites for hedgehogs. Combined with a high human population density their nests are less likely to remain undisturbed during the day or winter.

However, there is some debate concerning the current policy that aims for compact cities (Farjon et al., 1997) and one may argue that the future is bright for hedgehogs after all. Although some have suggested an even higher concentration of houses and other buildings (e.g., Frieling, 1995), others have stated that houses with abundant green is what most people really want (e.g., Van Blerck, 1995; Anonymous, 1997a) and that a balance has to be found between all interests involved (Anonymous, 1997b). If 'green' urban expansion takes place on former agricultural lands with low hedgehog density, hedgehogs will certainly benefit. The high hedgehog densities that can be expected in such areas will then compensate for the loss of hedgehog habitat through infill development and more compact cities on other locations.

6. What does the future hold for hedgehogs?

Since hedgehogs show high densities in urban areas with vegetation, it is unlikely that hedgehogs will be threatened with extinction in the near future. Given the extent of the effect of intensive, large scale agriculture and extreme urbanisation (urban centres) on hedgehog population density, traffic mortality is unlikely to be the primary cause of a possible decline of the species. But care should be taken not to be too optimistic. Urban areas with vegetation account for only 3,059 km^2 in the Netherlands (93% of 3,289 km^2 which equals 8% of the total area of the Netherlands) (fig. 4). Furthermore, hedgehog population density in forests, large scale agricultural areas and urban centres is low enough to be at risk of extinction through traffic. Certain local or regional hedgehog populations may well be threatened or may have vanished already.

It is clear that the amount of urban green space is important to hedgehogs. The quality of this space can be greatly improved through less intensive management, careful gardening practices and improved access for hedgehogs to gardens and other green spaces. However, as far as traffic victims are concerned the possibilities for mitigation are limited in urban areas. Houses, other structures and the need for all sorts of vehicles to get on and off the road at almost every location, seem to exclude the option of the construction of physical barriers which would keep the animals from getting onto the road.

Although hedgehogs are not threatened with extinction, their optimal habitat, urban areas, is relatively rare (fig. 4). Therefore the long term survival of hedgehogs may also depend on how well hedgehog populations do in other habitats. Many Dutch forests and other nature areas have become less intensively managed since the 1970s and 1980s (e.g., Broekmeyer, 1999). This change in management involves the absence or selective

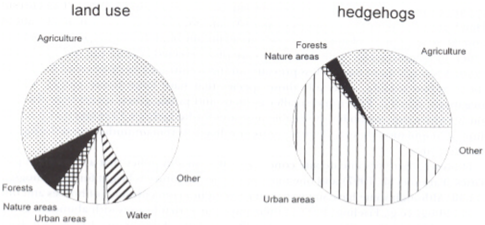

Fig. 4. Main categories of land use in the Netherlands, including large bodies of water (in 1997 the total area was 41,026 km² (Anonymous, 1956-1998)) and the estimated number of hedgehogs in these land use categories (total no. of hedgehogs is 434,364). The estimates on the number of hedgehogs were based on the median of the population densities listed in table 2. For this rough estimate all agricultural lands were classified as 'large scale', density in nature areas was set equal to that in forests, 93% of the urban areas were classified as having abundant green spaces, 7% as urban centres (see text) and density in 'other' was set at 5 hedgehogs per 100 ha.

Fig. 4. De belangrijkste categorieën van landgebruik in Nederland, met inbegrip van grote wateren (in 1997 was de totale oppervlakte 41.026 km2 (Anonymous, 1997)) en het geschatte aantal egels in deze landgebruikcategorieën (totaal aantal egels is 434.364). De schattingen van het aantal egels zijn gebaseerd op de mediaan van de in tabel 2 genoemde populatiedichtheden. Voor deze ruwe schatting werden alle agrarische gebieden geclassificeerd als 'grootschalig', de dichtheid in natuurgebieden werd gelijk gesteld aan die in bossen, 93% van de urbane gebieden werd geclassificeerd als 'met veel tuinen en parken', 7% als binnensteden (zie tekst) en de dichtheid in 'overig' werd gesteld op 5 egels per 100 ha.

small scale harvesting of trees, natural rejuvenation of forests, the presence of large ungulates, and a greater tolerance for the impact of storms, fire and, along the rivers, water level dynamics. These factors lead to more diverse and varied forests with a greater availability of edge habitat. Therefore the current policy (Anonymous, 1990b) of less intensive management is likely to be beneficial to hedgehogs. However, forests and other nature areas only amount to 4,513 km² which equals 11% of the total area of the Netherlands. Therefore a less intensive management of these areas alone may not lead to a substantial increase in the absolute number of hedgehogs, not even if their population density in these habitats would be, for example, doubled (see fig. 4 for reference). Therefore an additional strategy is needed.

Agriculture is the dominant category of land use in the Netherlands (23,700 km², 58%). Therefore, an increase of hedgehog population density on agricultural lands will make a considerable difference (see fig 4. for reference). One could either transform selected agricultural lands to natural areas, or one could increase the population density of large scale agricultural lands through a network of set-aside land and field margins (e.g., de Snoo, 1995; Remmelzwaal & Voslamber, 1996; Anonymous, 1997c; Ellenbroek et al., 1998, Opdam, 1998). Trees and shrubs would then have to be allowed to grow on at least some locations. This requires a certain consistency in management practices: not all set-aside lands and field margins can be brought back into cultivation once every two or three years if woody vegetation is to develop.

Hedgehogs reach relatively hugh population density in small scale agricultural landscapes with abundant edge habitat along hedgerows and small woodlands. Photograph: Marcel Huijser.
Egels bereiken een relatief hoge populatiedichtheid in kleinschalige agrarische landschappen met veel randzones langs houtsingels en kleine stukjes bos. Foto: Marcel Huijser.

If hedgehog population density can be significantly increased, infrastructure would probably no longer threaten the survival of local or regional populations in agricultural landscapes. Since buildings and other permanent structures are usually scattered, there is also a realistic option of putting mitigation and compensation measures for infrastructure into place. Corridors could then lead hedgehogs (and other wildlife) to wildlife passages. On other locations barriers could be installed or developed in order to keep the animals from getting on the road.

It is clear that the option of a network of set-aside lands and field margins would imply a compromise between agricultural and conservation interests and that the resulting edge habitat is subject to strong human influence. Nevertheless, to have substantial hedgehog populations in agricultural areas means that the survival of this species would no longer primarily depend on how well they do in urban areas.

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SAMENVATTING

Het effect van wegverkeer en veranderingen in het landschap op egelpopulaties: een overzicht

In Nederland worden veel egels *Erinaceus europaeus* doodgereden. Men kan zich afvragen of dat een bedreiging is voor het voortbestaan van de egel. Dit artikel gaat in op het effect van menselijke invloeden in het landschap op egelpopulaties, en op de vraag of verkeerssterfte een belangrijke factor is met betrekking tot een mogelijke achteruitgang van de soort. Egels hebben een relatief hoge populatiedichtheid in kleinschalig agrarisch landschap en urbane gebieden met tuinen en parken, maar bossen, grootschalige agrarische landschappen en dichtbebouwde urbane kernen hebben lagere dichtheden. Egels verblijven 's nachts, wanneer ze actief zijn, voor een belangrijk deel van hun tijd in overgangszones van bossen en struweel naar bijvoorbeeld grasland. De tijd die zij in deze overgangszones doorbrengen is meer dan men op basis van het oppervlak van dit habitattype in hun leefgebied zou mogen verwachten. Omdat de eerste menselijke invloeden in natuurlijke bossen moeten hebben geleid tot een toename van dit type overgangen hebben egels hier waarschijnlijk van geprofiteerd. In agrarische landschappen zijn lokale of regionale egelpopulaties echter naar verwachting sterk afgenomen als gevolg van de latere verwijdering van heggen, houtwallen en kleine stukjes bos.

Egels zijn niet bijzonder kwetsbaar voor habitat versnippering, maar de sterke toename van de wegendichtheid en de verkeersintensiteit gedurende de laatste decennia heeft mogelijk reeds geleid tot het verdwijnen van egelpopulaties in gebieden waar de populatiedichtheid al laag was. Het huidige beleid dat de bouw van compacte urbane gebieden voorstaat, leidt tot een achteruitgang van stedelijk groen in de bestaande dorpen en steden. Samen met de toename van het aantal barrières zal dit leiden tot een verminderde populatiedichtheid van egels. Hoewel egelpopulaties kunnen afnemen, lijkt het onwaarschijnlijk dat egels ook met uitsterven bedreigd worden. Bovendien lijkt het niet erg waarschijnlijk dat verkeerssterfte de hoofdoorzaak is van een mogelijke achteruitgang van het aantal egels. De wijze waarop mensen het landschap inrichten heeft een veel groter effect op de overlevingskans van egelpopulaties. Het belangrijkste leefgebied van de egel, urbane gebieden met veel groen, vormt slechts minder dan 8% van het oppervlak van Nederland en is dus relatief zeldzaam. Op langere termijn zou de overlevingskans voor de egel in Nederland dus weleens mede afhankelijk kunnen zijn van hoe het de egelpopulaties vergaat in andere habitats.

Het huidige beleid dat zich richt op een minder intensief beheer van bossen en andere natuurgebieden leidt waarschijnlijk tot meer overgangszones van bossen en struweel naar opener gebieden, en is dus gunstig voor egels. Hetzelfde gaat op voor een gedeeltelijke omzetting van agrarische gebieden in natuurgebieden of een netwerk van minder intensief beheerde of niet gebruikte percelen en perceelsranden. Dit zou tot omvangrijke egelpopulaties kunnen leiden naast die in de urbane gebieden. Daarmee worden de egelpopulaties in agrarische gebieden ook minder kwetsbaar voor verkeerssterfte.

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