LIFE ON THE EDGE

Hedgehog traffic victims and mitigation strategies in an anthropogenic landscape

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Proefschrift

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ABSTRACT

Life on the edge
Hedgehog traffic victims and mitigation strategies in an anthropogenic landscape

This study focused on the most frequently recorded mammal species in road-kill surveys in western Europe: the hedgehog (*Erinaceus europaeus*). Investigations were conducted in an anthropogenic landscape and had two major aims: 1. to quantify the effects of traffic mortality at individual, population, and species levels, and 2. to explore how the number of traffic victims could be reduced through changes in the landscape in areas adjacent to roads. The negative effects of roads and traffic were particularly clear at the individual level, and one could consider this reason enough to take mitigating actions. In addition, hedgehogs are likely to be affected at the population level. However, at the species level, the hedgehog has mostly benefited from many of the human-induced changes in the landscape. The way people manage the landscape seems to be the key factor in determining the long term future of the species. Manipulation of certain landscape features can be used to make wildlife passages more effective and also to keep hedgehogs away from road sections between passages.

Key words - agricultural lands, anthropogenic landscape, barriers, behaviour, body weight, compensation, corridor, disease, edge habitat, *Erinaceus europaeus*, footprints, habitat fragmentation, habitat selection, hedgehog, hedgerow, human impact, injury, landscape changes, mating strategy, mitigation, mortality, nest sites, The Netherlands, population density, relative population density, road density, road-kills, roads, traffic intensity, traffic victims, urban wildlife, vegetation, vehicle clearance, wildlife passages.

REFERAAT

Leven op het randje
Egel-verkeersslachtoffers en strategieën voor mitigerende maatregelen in een door mensen beïnvloed landschap

Dit onderzoek richtte zich op de egel (*Erinaceus europaeus*), het meest voorkomende zoogdier in verkeersslachtoffertellingen in west-Europa. De studie vond plaats in een door mensen beïnvloed landschap en kende twee hoofddoelen: 1. het kwantificeren van de effecten van verkeerssterfte op het niveau van individuen, populaties, en de soort, en 2. het verkennen van de mogelijkheden om het aantal verkeersslachtoffers terug te dringen door landschappelijke aanpassingen in direct naast wegen gelegen zones. De effecten van wegen en verkeer kwamen vooral naar voren op het niveau van individuen, en dit kan voldoende reden vormen om mitigerende maatregelen te treffen. Daarnaast ondervinden egels waarschijnlijk ook op populatieniveau negatieve effecten. Echter, op soortniveau heeft de egel vooral geprofiteerd van veel van de menselijke invloeden in het landschap. De wijze waarop mensen het landschap inrichten lijkt de belangrijkste factor te zijn voor het voortbestaan van de soort op de lange termijn. Bepaalde aanpassingen in het landschap kunnen niet alleen worden gebruikt om fauna passages effectiever te maken, maar ook om egels bij wegen vandaan te houden op weggedeelten die tussen de passages in liggen.

Kernwoorden - agrarische gebieden, barrières, compensatie, corridor, doodgereden dieren, egel, *Erinaceus europaeus*, faunapassage, gedrag, habitat fragmentatie, habitat selectie, habitat versnippering, houtwal, lichaamsgewicht, menselijke invloed, door mensen beïnvloedde landschappen, mitigatie, mortaliteit, Nederland, nestplekken, populatie dichtheid, randzones, relatieve populatie dichtheid, stads-ecologie, vegetatie, veranderingen in het landschap, verbindingszone, verkeersintensiteit, verkeersslachtoffers, verwonding, voetsporen, voortplantingsstrategie, wegen, wegendichtheid, wielhoogte van auto's, ziekten.

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LIFE ON THE EDGE

HEDGEHOG TRAFFIC VICTIMS AND MITIGATION STRATEGIES IN AN ANTHROPOGENIC LANDSCAPE

The Netherlands is one of the most densely populated countries in the world and agriculture, urbanisation and infrastructure cause severe habitat fragmentation problems for many plant and animal species. This study addressed the effects of roads and traffic in particular. Both road density and traffic intensity have shown a strong and consistent increase over the past decades in The Netherlands. Paved roads occupied a minimum of 3.5% of the land surface in 1985 and road density averaged 3.38 km road length per km^2 in 1998. Traffic intensity in The Netherlands is high too, with an estimated 7,319,000 motor vehicles using a total of 116,093 km of paved roads. Depending on the variable concerned, the negative effects of roads and traffic may extend from several metres up to several kilometres from the road surface, which leaves very few to no unaffected areas.

The research for this thesis focused on the most frequently recorded mammal species in road-kill surveys in western Europe: the hedgehog (*Erinaceus europaeus*). The study took place in an anthropogenic landscape and had two major goals: 1. to quantify the effects of traffic mortality at the level of individuals, populations, and the species, and 2. to explore how the number of traffic victims could be reduced through changes in the landscape in areas adjacent to roads. The effects of roads and traffic were particularly clear at the level of individuals. In The Netherlands an estimated 113,000-340,000 hedgehogs end up as a road-kill each year. Most of the animals are killed in the summer months (June - August) which coincides with the peak of the mating season. Adult males were more abundant among the traffic victims than young or females. The vulnerability of males to traffic is based on their relatively large home ranges and great distances travelled per night. As a consequence, males encounter many roads, cross them frequently, and therefore run a relatively great risk of being hit by traffic. Hedgehogs may not only be hit by the tyres of a vehicle, but may also collide with the underside of a car. About 26% of all the passenger cars on the Dutch roads may hit a walking (or running) subadult or adult of average size due to insufficient clearance. Hedgehogs that sit still and crouch run much less risk of being hit by the underside of a car, but since these animals remain on the road they can also be hit by the tyres. Thus the behaviour of an individual hedgehog is likely to influence its survival probability on a road, but the trade off between crouching and running away is unknown. Nevertheless, it is likely

that if many vehicles travel close together, a crouched hedgehog may never get off the road, and that it will eventually be run over. Thus, with the continuing growth in traffic intensity it may become more and more 'advisable' for a hedgehog to run away.

Traffic mortality is high enough to suggest that it also affects hedgehogs at the population level. About 9% of all deaths recorded in three wildlife rescue centres was caused by traffic. In total, 41% of all deaths in the centres were related to humans, their activities or man-made objects which indicates that humans are an important death factor for hedgehogs. Besides traffic mortality, these deaths resulted from drowning in water with steep banks, disturbance of nests with young, wounds inflicted by dogs and cats, poison, and other unnatural injuries. Other estimates on the relative importance of traffic mortality followed from a capture-mark-recapture study in a small scale agricultural landscape combined with an intensive search for traffic victims in the same area. Traffic mortality was 12% of the total losses (deaths and dispersal) of the hedgehog population, excluding the young of the year. Over two successive seasons 6% and 9% of the animals in the study population fell victim to traffic. A third way to estimate the importance of traffic mortality was through a combination of an estimate on the total population size of hedgehogs in The Netherlands, and the estimated number of traffic victims per year. According to this calculation, traffic deaths amounted to 9-26% of the total population size. Although the percentages given above provide insight into the relative importance of traffic mortality, they do not tell whether hedgehog populations really suffer from it through, for example, low population density or survival probability. Therefore a pairwise comparison was made of relative hedgehog densities in areas close to roads with those in areas that were at least 400 m away from roads. The results suggest that roads and traffic may reduce population density by about 30%, which may affect the survival probability of local populations. Finally, the predominance of adult males among traffic victims is likely to have an effect on the population structure, and reduced competition between males could eventually lead to negative effects on population viability.

At the species level, the hedgehog has mostly benefited from human induced changes in the landscape as people increased the amount of edge habitat. Hedgehogs have relatively high population densities in areas with abundant edge habitat and the importance of this habitat was further illustrated through a habitat use study. During the night, hedgerows received greater relative use than other habitats. The animals spent about 30% of their time here whereas hedgerows only comprised some 10% of the area. Although another 53% was spent on grasslands, more than half of these locations were within 5 m distance from a hedgerow or a forest's edge. This indicates that hedgerows can be used to identify hot spots for traffic victims and that wildlife passages can be made more effective by hedgerows oriented perpendicular to the road. This was confirmed by a detailed study on the road and landscape characteristics of traffic victim sites. Hedgehog traffic victims were widely dispersed along roads, but they were not-randomly distributed with respect to landscape characteristics. Wide roads and street lights led to fewer victims, probably because of an increased barrier effect. Forests and urban areas had more victims than agricultural areas, salt marshes or open sand dunes. When hedgerows, a forest's edge, a row of trees or urban green were present adjacent to a road, 36-47% more victims occurred compared to when these elements were at least 100 m away from the road. Grass verges also led to an increase in traffic victims. When linear elements such as hedgerows, a forest's edge, or grass verges were oriented perpendicular to a road, 20-27% more victims occurred compared to a situation where these elements were oriented in a more parallel way. Arable land and moorland resulted in fewer victims. This study indicated that existing and new wildlife passages can be made more effective for hedgehogs when their location in the landscape is considered and that their use could further be increased through changes in the landscape that guide animals towards a passage and keep them away from the road at sections between passages.

Massive traffic mortality among hedgehogs and possible effects on the population level are already reason enough to take mitigation and compensation measures. Nevertheless, it is argued that infrastructure is unlikely to be the sole cause for hedgehogs to disappear completely. The long term future of the species primarily depends on how people manage the landscape, and agricultural areas in particular. Over the last decades the habitat quality of agricultural lands has much decreased through the removal of small woodlots, hedgerows and other edge habitat. This has led to low population densities in these areas and since agricultural lands cover nearly 70% of the terrestrial part of The Netherlands, it makes the hedgehog relatively vulnerable to widespread regional extinction. The future of many other plant and animal species now also depends on the availability of suitable habitat and corridors in agricultural areas. Therefore mitigation and compensation efforts for infrastructure should be integrated in regional plans that address all major habitat fragmentation problems including those resulting from agriculture and urbanization.

LEVEN OP HET RANDJE

EGEL-VERKEERSSLACHTOFFERS EN STRATEGIEËN VOOR MITIGERENDE MAATREGELEN IN EEN DOOR MENSEN BEÏNVLOED LANDSCHAP

Nederland behoort tot de meest dicht bevolkte landen in de wereld, en landbouw, de uitbreiding van woongebieden en infrastructuur veroorzaken ernstige habitat versnipperingsproblemen voor veel planten- en diersoorten. Dit onderzoek gaat vooral in op de effecten van wegen en verkeer. Zowel de wegendichtheid als de verkeersintensiteit zijn de laatste decennia sterk toegenomen in Nederland. In 1985 besloegen verharde wegen ten minste 3,5% van het landoppervlak en de gemiddelde wegendichtheid in 1998 bedroeg 3,38 km weglengte per km^2. Met naar schatting 7.319.000 motorvoertuigen die de in totaal 116.093 km aan verharde wegen gebruiken is hier ook de verkeersintensiteit erg hoog. Afhankelijk van de factor waar men op let kunnen de negatieve effecten van wegen en verkeer zich uitstrekken over een afstand van enkele meters tot enkele kilometers van de wegverharding. Dit laat weinig tot geen ruimte over voor gebieden die niet op de één of andere wijze worden beïnvloed.

Dit proefschrift is toegespitst op de meest voorkomende zoogdiersoort in verkeersslachtoffertellingen in west-Europa: de egel (*Erinaceus europaeus*). Het onderzoek vond plaats in een door mensen beïnvloed landschap en kende twee hoofddoelen: 1. het kwantificeren van de effecten van het doodrijden van egels op het niveau van individuen, populaties, en de soort, en 2. het verkennen van de mogelijkheden om het aantal verkeersslachtoffers te verminderen door veranderingen aan te brengen in het naast de weg gelegen landschap. Vooral de effecten op het individu niveau waren zeer duidelijk. Naar schatting worden elk jaar 113.000-340.000 egels doodgereden op de Nederlandse wegen. De meeste dieren worden gedood gedurende de zomermaanden (juni - augustus), hetgeen samenvalt met de piek van de paartijd. De aangereden dieren betroffen vooral adulte mannelijke dieren. De kwetsbaarheid van volwassen mannelijke dieren voor verkeer houdt verband met hun relatief grote leefgebieden en de lange afstanden die ze op een nacht afleggen. Hierdoor komen mannelijke egels veel wegen tegen, en steken ze deze ook vaak over. Dit leidt ertoe dat ze een relatief grote kans hebben om te worden doodgereden. Egels kunnen niet alleen geraakt worden door de autobanden, maar ook door de onderkant van een auto. Ongeveer 26% van alle personenauto's in Nederland kan een lopende (of rennende) egel van gemiddelde grootte raken doordat de auto niet hoog genoeg op de wielen staat. Egels die stil blijven zitten en hun buik en snuit tegen de wegverharding aandrukken hebben een veel kleinere kans om te worden geraakt door de onderkant van een auto. Omdat deze dieren op de weg blijven kunnen ze echter ook alsnog door de autobanden worden geraakt. Hoewel het gedrag van een individuele egel van invloed is op zijn overlevingskans op de weg, is het onbekend waar de balans ligt tussen wegrennen en stil blijven zitten. Niettemin is het zo dat een egel die stil blijft zitten misschien nooit meer van de weg af kan komen als er veel auto's vlak achter elkaar rijden, en dat hij uiteindelijk wordt doodgereden. Gezien de toenemende verkeersintensiteit zou er steeds meer voor te zeggen zijn dat een egel weg moet rennen bij naderend verkeer.

De verkeerssterfte is zodanig hoog dat het zeer aannemelijk is dat egels hier ook op populatieniveau nadelige gevolgen van ondervinden. Ongeveer 9% van alle dieren die doodgingen in drie verschillende egelopvangcentra stierf als gevolg van verkeer. In totaal was 41% van alle doodsoorzaken in de egelopvangcentra gerelateerd aan mensen, hun activiteiten of door mensen gemaakte voorwerpen of structuren. Behalve door verkeer stierven deze dieren door verdrinking in wateren met een steile oever, het verstoren van nesten met jongen, wonden toegebracht door honden en katten, vergif, en overige onnatuurlijke verwondingen. Andere schattingen van de relatieve omvang van verkeerssterfte volgden uit een merk-terugvangproef in een kleinschalig agrarisch landschap die werd gecombineerd met een intensief zoeken naar verkeersslachtoffers in hetzelfde gebied. De verkeerssterfte bedroeg 12% van de totale verliezen (sterfte en emigratie) in de egelpopulatie, exclusief de jongen die in het betreffende jaar geboren werden. Gedurende twee opeenvolgende seizoenen eindigden respectievelijk 6% en 9% van de dieren in de onderzochte populatie als verkeersslachtoffer. Een derde methode op basis waarvan de relatieve omvang van verkeerssterfte werd geschat bestond uit een combinatie van een schatting van de totale Nederlandse egelpopulatie en het geschatte aantal doodgereden egels per jaar. Volgens de bewuste berekening bedroeg het aantal verkeersslachtoffers 9-26% van de totale populatiegrootte. Hoewel bovengenoemde percentages ons inzicht verschaffen in de relatieve omvang van verkeerssterfte geven ze niet aan of egelpopulaties hier ook hinder van ondervinden door bijvoorbeeld een negatief effect op de populatiedichtheid of op de overlevingskans van een populatie. Daarom werd de relatieve egeldichtheid in gebieden vlak langs wegen paarsgewijs vergeleken met die in gebieden die tenminste 400 m bij van een weg vandaan gelegen waren. De resultaten gaven aan dat wegen en verkeer de populatiedichtheid met ongeveer 30% kunnen verlagen, en dit leidt mogelijk tot een verlaagde overlevingskans van lokale populaties. Tot slot heeft het grote aandeel van adulte mannelijke dieren in de verkeersslachtoffers mogelijk een effect op de populatiestructuur, en kan verminderde concurrentie tussen mannelijke dieren uiteindelijk leiden tot een negatief effect op de overlevingskans van een populatie.

Op het niveau van de soort als zodanig heeft de egel vooral geprofiteerd van menselijke invloeden in het landschap. Menselijke activiteiten hebben geleid tot een toename van randzones, die gekarakteriseerd worden door een overgang van bomen en struiken naar een lage vegetatie zoals grasland. Egels hebben een relatief hoge populatiedichtheid in gebieden met veel randzones en het belang van dit habitat werd bovendien geïllustreerd door een studie naar het habitat gebruik. s' Nachts werden houtwallen veel vaker gebruikt dan andere habitattypen. De dieren brachten hier ongeveer 30% van hun tijd door terwijl houtwallen slechts ongeveer 10% van het gebied uitmaakten. Hoewel nog eens 53% werd doorgebracht op grasland, bevond meer dan de helft van deze lokaties zich binnen 5 m afstand van een houtwal of bosrand. Dit geeft aan dat houtwallen een rol kunnen vervullen bij het lokaliseren van risico-plekken met veel doodgereden egels, en dat faunapassages effectiever zouden kunnen worden benut indien ze aansluiten op houtwallen die loodrecht op de weg georiënteerd zijn. Dit laatste werd bevestigd door een gedetailleerde studie naar de weg- en landschapskarakteristieken van plekken waar doodgereden egels werden aangetroffen. De egels lagen weliswaar sterk verspreid langs de wegen, maar hun locatie hield duidelijk verband met bepaalde landschapskarakteristieken. Brede wegen en straatverlichting leidden beide tot minder slachtoffers, waarschijnlijk door een toename van het barrière effect van de infrastructuur. In bossen en binnen de bebouwde kom werden meer slachtoffers aangetroffen dan in agrarische gebieden, kwelders, en open duingebieden. Bij de aanwezigheid van een houtwal, een bosrand, een bomenrij, of stedelijk groen naast een weg, werden 36-47% meer slachtoffers gevonden dan wanneer deze elementen tenminste 100 m van de weg aflagen. Grasbermen leidden ook tot een toename in slachtoffers. Indien lineaire elementen zoals een houtwal, een bosrand, of grasbermen loodrecht op een weg georiënteerd waren, werden 20-27% meer slachtoffers gevonden dan bij een meer parallelle oriëntatie van de betreffende elementen. Langs akkers en heide kwamen relatief weinig slachtoffers voor. Dit onderzoek gaf aan dat zowel bestaande als nieuw aan te leggen faunapassages beter zouden kunnen worden benut wanneer rekening gehouden wordt met hun locatie in het landschap, en dat het gebruik verder kan worden gestimuleerd door veranderingen in het landschap die de egels naar een passage toeleiden en weghouden van de weg in gebieden tussen passages.

Massale verkeerssterfte onder egels en de mogelijke effecten op populatieniveau zijn al reden genoeg tot het treffen van mitigerende en compenserende maatregelen. Het is echter onwaarschijnlijk dat de egel compleet verdwijnt als gevolg van infrastructuur alleen. De toekomst van de egel op de lange termijn is vooral afhankelijk van hoe mensen omgaan met het landschap, en agrarische gebieden in het bijzonder. De laatste paar decennia is de kwaliteit van de leefgebieden in agrarische landschappen sterk achteruit gegaan door het verwijderen van houtwallen, kleine stukjes bos en overige randzones. Dit heeft geleid tot relatief lage populatiedichtheden in deze gebieden en doordat agrarische gebieden bijna 70% van het landoppervlak in Nederland beslaan, is de egel relatief kwetsbaar voor wijdverbreid regionaal uitsterven. Ook de toekomst van veel andere planten- en diersoorten hangt nu sterk af van de aanwezigheid van goede leefgebieden en verbindingszones in landbouwgebieden. Daarom zou het goed zijn als de mitigerende en compenserende maatregelen voor infrastructuur geïntegreerd worden in regionale plannen. Deze plannen richten zich op de aanpak van de belangrijkste habitat versnipperingsproblemen in een gebied, met inbegrip van die als gevolg van landbouw en de uitbreiding van woongebieden.

CHAPTER 1

GENERAL INTRODUCTION

Based on: Human impact on populations of hedgehogs *Erinaceus europaeus* through traffic and changes in the landscape: a review.

Marcel P. Huijser
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GENERAL INTRODUCTION

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.

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

Table 1. Estimates on the minimum number of hedgehog traffic victims per kilometre road per year in various parts of western Europe.

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)

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 are able to exist in 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.

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

Table 2. Hedgehog density in various habitats.

Habitat type	Density (*N*/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 (1988a)
Large scale agricultural landscape with little cover	0	Dowie (1987)
	5-7, 6	Berthoud (1982)
Urban areas with 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 et al. (1993)
	70-270	Dietzen & Obermaier (1989)
	179	Doncaster (1994)
	210-280	Palm & Stöwer (1990)
Urban centres with little vegetation	4-6	Berthoud (1982)

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 excess of ten metres, and that they could be using them for orientation. Their detection range may actually 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

Table 3. Habitat selection of hedgehogs during the night (i.e., when they are active).

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)

[1] Most studies lack statistical analysis and were based on use-availability ratio's (% of time spend in a certain habitat / % 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.

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, 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 benefited from such moderate disturbance of the landscape, especially when it was local and spread over time (Connell, 1978; Huston, 1979; Picket & White, 1985; Kolasa & Picket, 1991). Disturbance in 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 benefited 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 about 50% between 1900 and 1990, and the average field size increased by roughly 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 higher hedgehog population density. However, there is an optimum as increased human impact leads to a strong decrease of edge habitat.

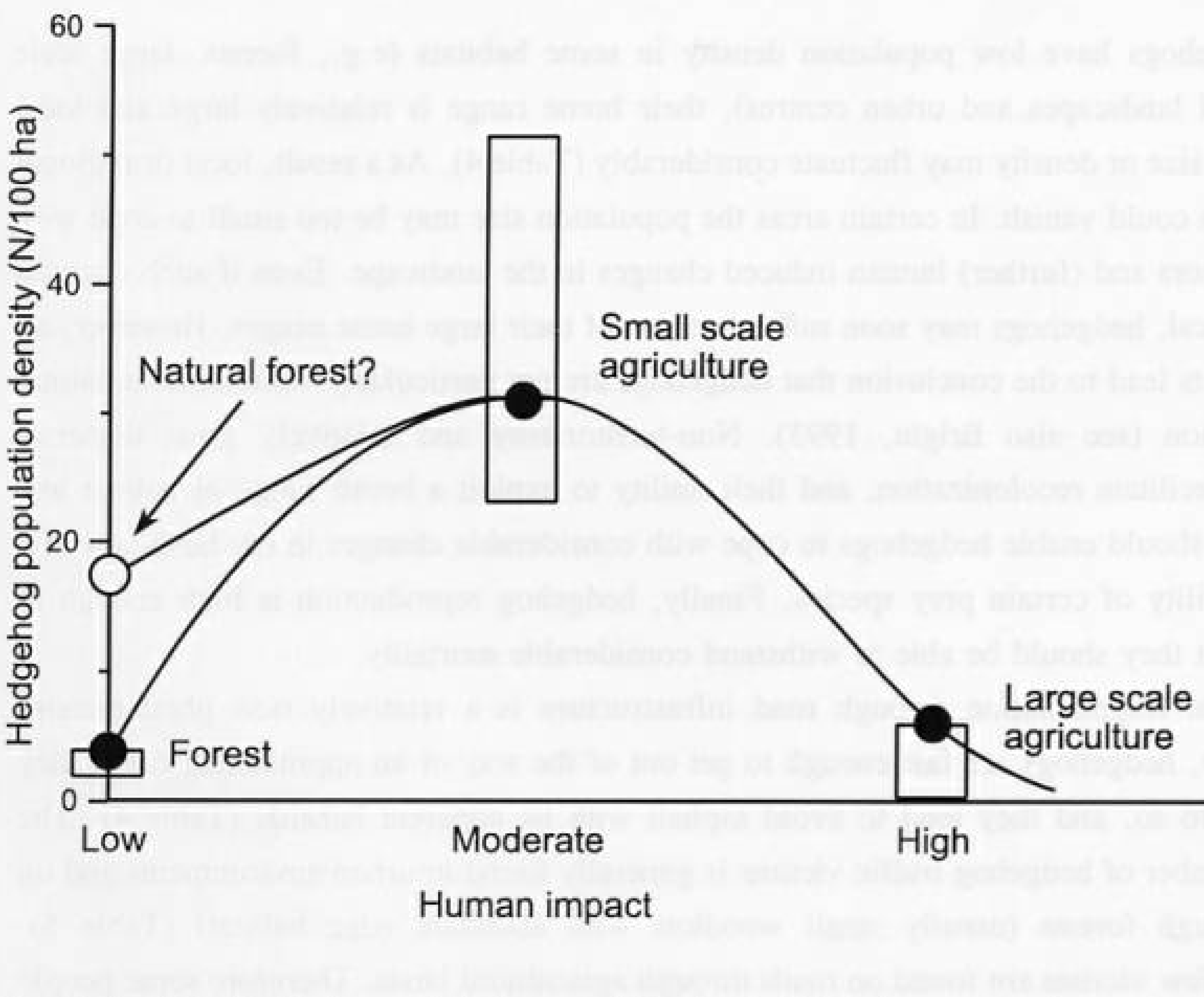

Fig. 1. The effect of agriculture on hedgehog population density. The landscape categories are the same as those in table 2. The points in the graph represent the median of the population densities listed in table 2. The boxes show the interquartile range.

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 infrastructure, 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 environments 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 4. Characteristics of hedgehogs that may influence their vulnerability to habitat fragmentation.

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, 1988a) 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) cited 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 2) 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 a non-natural barriers (agricultural lands and roads). Population fluctuations may have been greater than they would have been in larger areas with 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 50-60 m min^{-1} (Reeve, 1982; 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).

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)

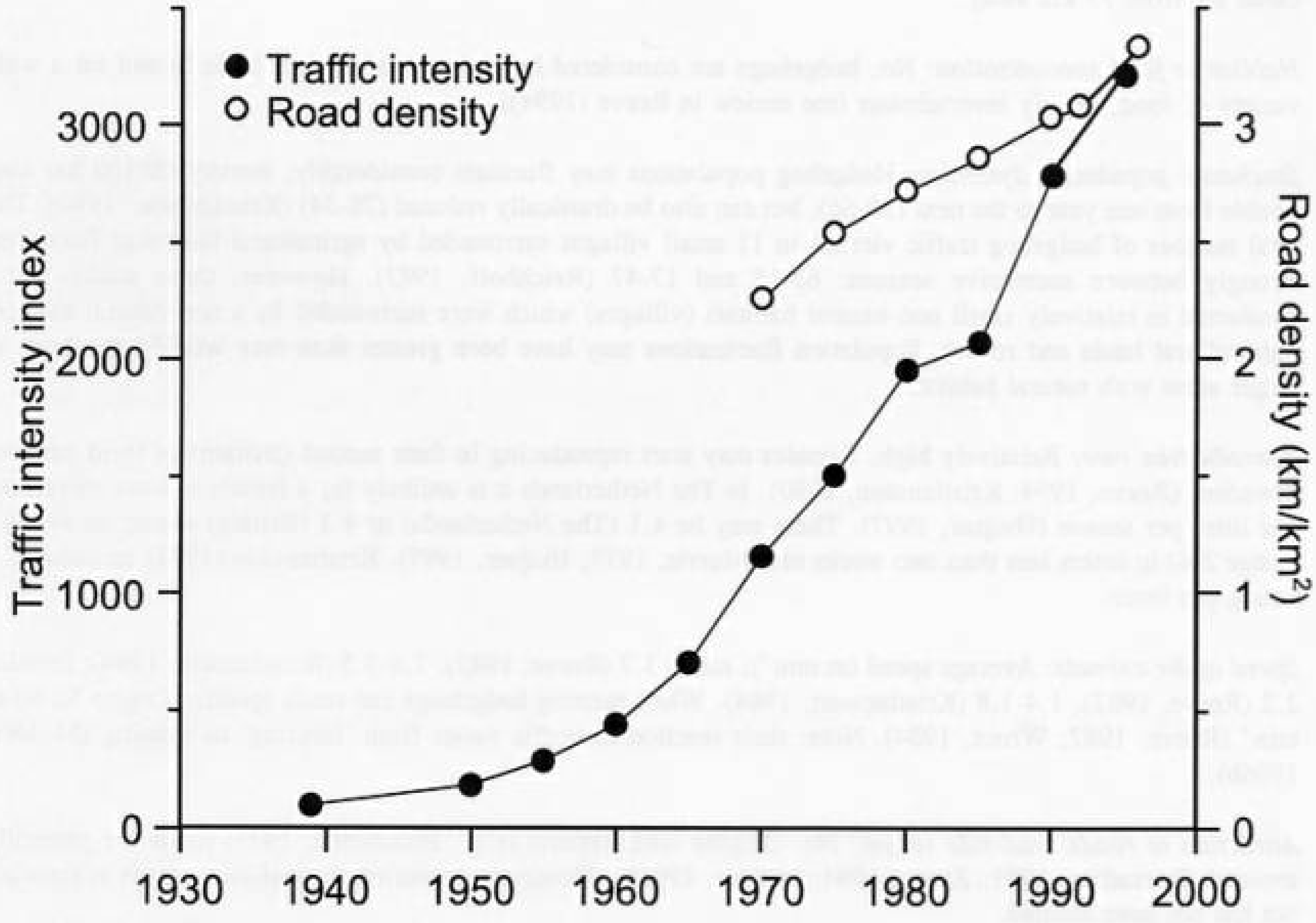

Fig. 2. Traffic intensity index (1939 = 100) and density of paved roads in the terrestrial part of The Netherlands (34,000 km^2) (based on data from the Central Bureau of Statistics (Anonymous, 1956-1998)). There were 6,757,000 motorized vehicles and 113,419 km of paved road in 1996.

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 (Sign.: $P=0.006$, Wilcoxon matched-pairs signed-ranks test, 2-tailed).

	Mean growth (%)	SD	*N*
Day	40.56	13.89	13
Night	50.91	18.07	13

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, roughly 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 areas 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 areas and too many barriers for species with large home ranges such as the hedgehog. Fortunately, most of the urban areas have sufficient green

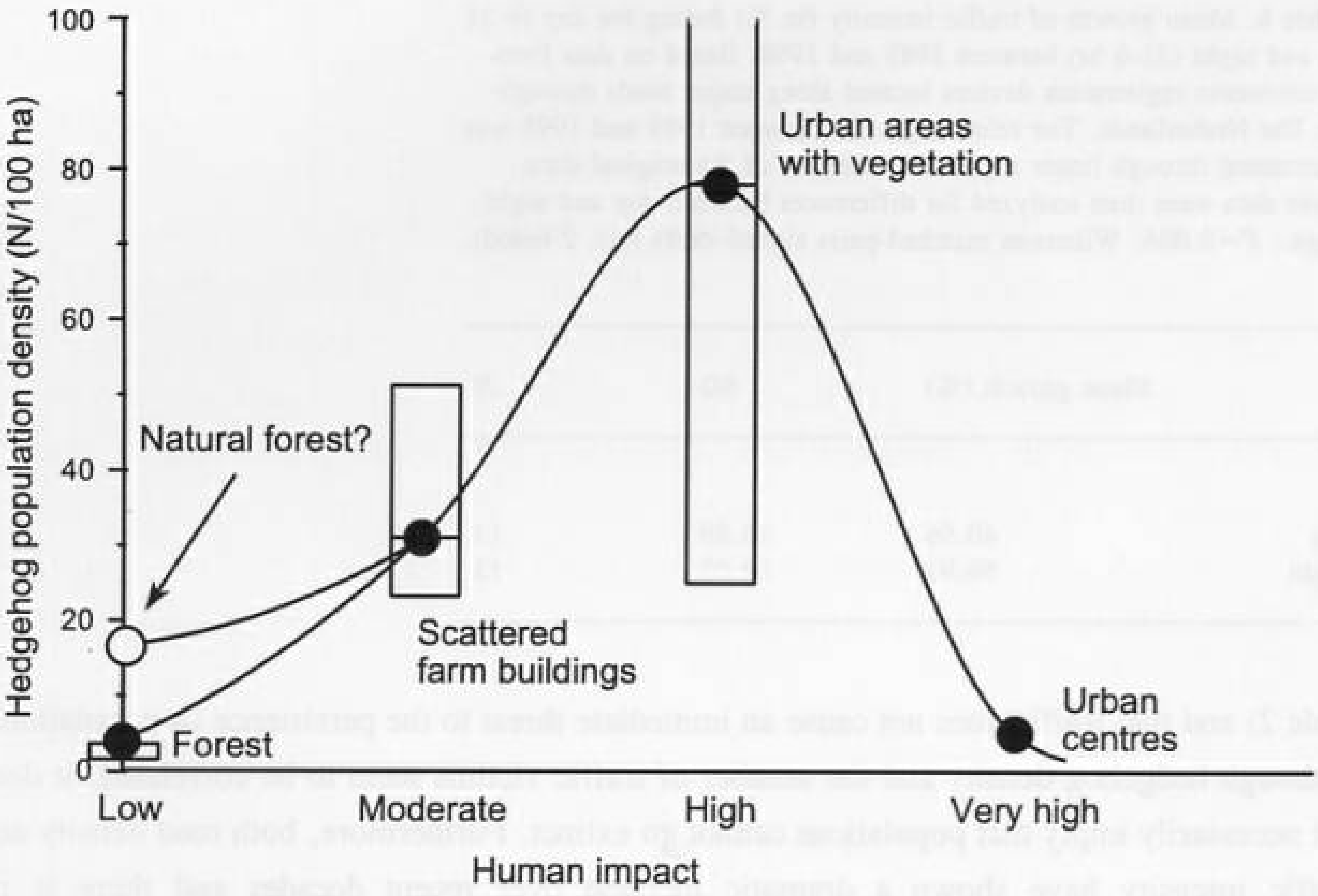

Fig. 3. The effect of urbanization on hedgehog population density. The landscape categories are the same as those in table 2, except for small scale agricultural landscape that was renamed to scattered farm buildings. The points in the graph represent the median of the population densities listed in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

areas. When an arbitrary 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). However, 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 areas 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 areas is important to hedgehogs. The quality of these areas can be greatly improved through less intensive management, careful gardening practices and improved access for hedgehogs to gardens and other green areas. 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.

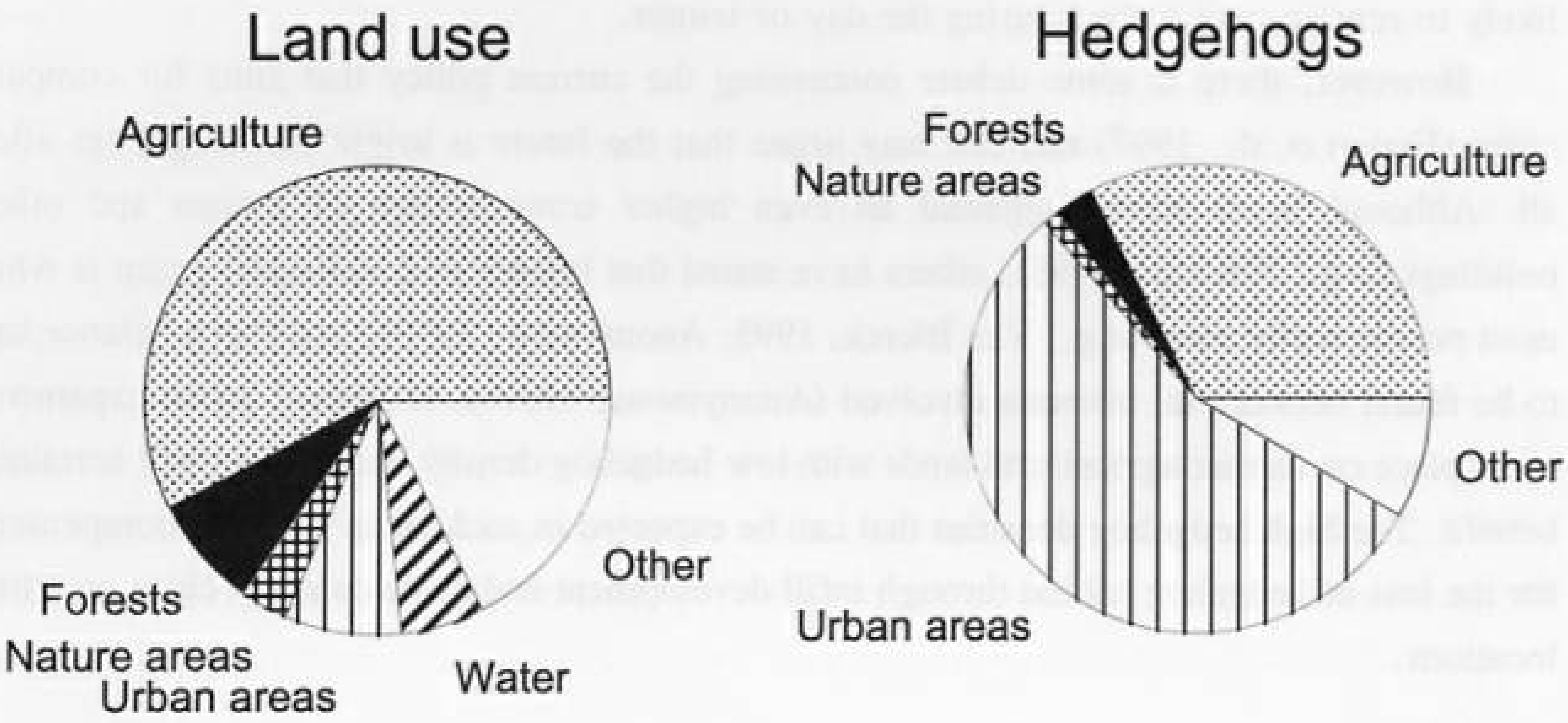

Fig. 4. Main categories of land use in The Netherlands, including large bodies of water (in 1997 the total area was 41,026 km² (Anonymous, 1956-1998)) and the estimated number of hedgehogs in these land use categories (total no. of hedgehogs is 434,364). The estimates on the number of hedgehogs were 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 areas, 7% as urban centres (see text) and density in 'other' was set at 5 hedgehogs per 100 ha.

Although hedgehogs are not threatened with extinction, urban areas, the habitat they reach highest population density in, are 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 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 km^2, 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 brought back into cultivation once every two or three years if woody vegetation is to develop.

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.

7. Outline of the thesis

The Netherlands is one of the most densely populated countries in the world (465 people per km^2 on average; Anonymous, 2000) and agriculture, urbanisation and infrastructure cause severe habitat fragmentation problems for many plant and animal species. This study focuses on infrastructure in particular. Although roads are a linear landscape feature, they still occupied 3.5% of the land surface in The Netherlands in 1985 (Anonymous, 1993a). This figure does not include roads in urban areas, nor the verges and cycling paths, which makes this a very conservative estimate of the area that is lost for wildlife. Apart from habitat loss, the construction, presence and use of roads also causes traffic mortality, modification of animal behaviour, reduction of habitat quality, disruptions in the physical environment, pollution, the spread of exotic species, and increased human access to places that used to be hard to reach (see overviews by Forman & Alexander, 1998; Trombulak & Frisell, 2000).

It is clear that there are many negative aspects of roads and traffic and that this study can only address a fraction of these problems and possible solutions. This thesis focuses on the most frequently recorded mammal species in road-kill surveys in western Europe: the hedgehog. The study takes place in an anthropogenic landscape and has two major goals: 1. to quantify the effects of traffic mortality on the level of individuals, populations, and the species as a whole, and 2. to explore how the number of traffic victims could be reduced through changes in the landscape in areas adjacent to roads. Here, in chapter 1, a broad view has been given of how hedgehogs have responded to human induced changes in the landscape, and how vulnerable the species is to habitat fragmentation in general, and traffic mortality in particular. Chapter 2 identifies other mortality causes in anthropogenic landscapes and gives insight into how important traffic mortality is compared to these other causes. Similar estimates were derived from a field study that also addressed sex differences in the hedgehogs' vulnerability to traffic (chapter 3). Whether traffic mortality leads to reduced population density was investigated in chapter 4. Chapter 5 deals with the question whether hedgehogs could not only be killed through a collision with the tyres of a car, but also through low vehicle clearance and airflow underneath a car. The second part of the thesis addresses the habitat use of hedgehogs, and how their movements through the landscape can be influenced through the arrangement of certain landscape features such as hedgerows (chapter 6). Chapter 7 expands on this issue and also takes many other road, traffic and landscape features into account. In chapter 6 and 7, and in the general discussion (chapter 8) suggestions are given on how to mitigate or compensate for hedgehog traffic victims and other negative aspects of infrastructure. In addition, chapter 8 summarizes the results with respect to the effects on the level of individuals, populations, and the species, and how the mitigation and compensation strategies could be integrated in plans that address all major habitat fragmentation in a region.

CHAPTER 2

MORTALITY FACTORS AFFECTING WILD HEDGEHOGS: A STUDY OF RECORDS FROM WILDLIFE RESCUE CENTRES

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MORTALITY FACTORS AFFECTING WILD HEDGEHOGS: A STUDY OF RECORDS FROM WILDLIFE RESCUE CENTRES

Abstract - This paper reviews the known principal causes of mortality in hedgehogs and uses a large data set (collected 1992-1998) from wildlife rescue centres to characterise the threats posed to the hedgehogs admitted. Data were obtained from the records of a total of 856 hedgehog fatalities from two hedgehog rescue centres in the United Kingdom (Jersey and Yorkshire) and one in The Netherlands (Den Haag). Summary data for a further 11,541 hedgehogs were obtained from the British Wildlife Rehabilitation Council (BWRC) quarterly statistics of wildlife casualties for the United Kingdom (1993-1997).

Hedgehogs accounted for a mean of 54% of the mammal casualties (16% of casualties of all taxa) received by rescue centres in the BWRC scheme. Combined data from all sources showed a significantly male-biased sex ratio of 1.2 (m:f) in the total admissions. Stronger male-biased ratios occurred early in the season.

Records from the three hedgehog rescue centres revealed 59% of deaths to be from causes that were probably natural such as parasitic diseases and infections; 41% of deaths resulted from factors that were clearly anthropogenic (unnatural), e.g., injuries from garden tools, road accidents, disturbance of nests (causing abandonment of young), drowning in waters with unnaturally steep banks, bite wounds from pets and poisoning. The BWRC data (including hedgehogs that recovered) showed a similar pattern, but a large non-specific category for 'other causes' (13% of cases) limited comparison.

Adult males outnumbered the females in the 'unnatural injuries' and 'traffic victim' categories. This is in accordance with the expectation that males would suffer significantly more from accidents because of their wider ranging behaviour. Seasonal variation in the incidence of cause of death showed that most of the animals that died of natural causes did so in the second half of the year and that subadults were more common than the other age groups in this death category. The peak in deaths due to traffic and other unnatural causes was several months earlier in the year. Endoparasite infestations were found in 64% of 498 animals tested; the incidence varied significantly with age but not with sex. Subadult hedgehogs had a remarkably high infestation rate.

Despite the inherent biases in samples from wildlife rescue centres, anthropogenic factors seemed to make a significant contribution, additional to natural mortality. This appears to substantiate current concerns about their possible effect on hedgehog populations.

1. Introduction

Admissions of mammals to wildlife rescue centres in western Europe typically include a large proportion of hedgehogs *Erinaceus europaeus* which are admitted with a very wide variety of illness and injuries. Natural mortality factors include the many parasites and diseases recorded from European hedgehogs (Table 1). The literature is too extensive to review here, but see Reeve (1994) and more recent works e.g., Poduschka et al. (1995), Lambert (1995), Schicht-Tinbergen (1995), Zaltenbach-Hanßler et al. (1998) and Biewald et al. (1999). However, despite numerous surveys, the relative importance of parasitic diseases and other illnesses as causes of death remains poorly studied. In Germany, Timme (1980) used autopsy data to establish the cause of death of 410 hedgehogs from wildlife hospitals. Overall, parasitic diseases caused 39% of deaths, general bacterial infections (mainly *Salmonella* spp. and *Escherichia coli*) killed 19%. Diseases of organs, principally lung and gut infections, also killed 19%.

Direct anthropogenic (unnatural) causes of death were infrequently recorded by Timme (1980), only 7 (1.7%) of deaths were attributed to road traffic accidents and other injuries. Nevertheless, anecdotal evidence from numerous wildlife rescue centres, such as those in the present study, indicates that unnatural deaths may have a significant effect on hedgehog populations. This is hard to verify from many published studies because of sample biases. For example Dickman (1988), in a study of hedgehog diet based on 109 hedgehog corpses, noted that 78% were road kills, 2.8% had apparently died from eating slug pellets, 1.8% were the result of accidental burning and 17.4% had died from unknown causes. However, 64% of the corpses had actually been collected from roads. In contrast, a study of 30 translocated wild hedgehogs (Doncaster, 1992) found road kills to account for 4 (33%) of the 12 known deaths. Also, in a 15 week follow-up study of 12 hedgehogs released from a wildlife hospital (Reeve, 1998) two died of natural causes (pneumonia and badger predation), one drowned in a garden pond and four were killed by road traffic. In both these studies the behaviour of the animals may have been affected by their release into an unfamiliar area which may have affected their vulnerability to certain mortality factors. However, these studies add to a general weight of circumstantial evidence that anthropogenic mortality factors may be important (see table 2 for a summary).

The demographic effect of deaths from road traffic accidents has received more attention than other anthropogenic mortality factors. The hedgehog is one of the mostly commonly recorded mammal species in road-kill surveys throughout Europe: for reviews of studies see

Table 1. The principal parasites and pathogens of hedgehogs (*Erinaceus europaeus*) in Europe and their typical effects. A large number of less commonly found species are excluded. Adapted from Reeve (1994) and Zaltenbach-Hanßler et al. (1998).

Group	Organism	Effects
Ectoparasites		
Fleas Ticks Mites	*Archaeopsylla erinacei*, *Ixodes hexagonus*, *I.ricinus* *Caparinia tripilis*, *Demodex erinacei*, *Sarcoptes* spp.	Arthropod ectoparasites. Rarely cause death, but severe infestations may be complicated by bacterial infections (e.g., staphylococci).
Fungi	*Trichophyton erinacei*	Skin infection, typically non-lethal.
Maggots	blowfly larvae (Fam. Calliphoridae)	Infest wounds, ears, anus etc. Can kill, but animal often already weak.
Endoparasites		
Nematodes	*Crenosoma striatum*	Often lethal. Worms infest the lumen of trachea, bronchi, bronchioles and alveolar ducts.
	Capillaria aerophila	Often lethal. Worms infest the epithelium of the trachea, bronchi and bronchioles.
	Capillaria erinacei, *C. ovoreticulata* and at least one other *Capillaria* spp.	Infest intestine. All may kill if infestation is severe causing diarrhoea/enteritis and lesions of the intestinal wall.
Trematodes	*Brachylaemus erinacei*	
Cestodes:	*Rodentolepis* (=*Hymenolepis*) *erinacei*	
Acanthocephala:	*Moniliformis erinacei* & oth.	
pathogenic micro-organisms		
Coccidia	*Isospora rastegaivae* & others	Intestinal. Rarely lethal but haemorrhagic diarrhoea can kill.
	Toxoplasma gondii	Severity unknown. Affects blood and other tissues.
Fungi	*Candida albicans*	Affects gastrointestinal tract, mouth genito-urinary tract. Rarely lethal.
Bacteria	*Leptospira interrogans*	Several serotypes. Rarely lethal. Affects blood and urinary systems.
	Salmonella enteriditis and other *Salmonella* spp., *Escherichia coli*,	Common enteric bacteria often present subclinically but infections often lethal.
	Bordetella bronchiseptica, *Pasteurella* spp.	Respiratory tract; often lethal in association with lungworm infections.
Viruses		Many viruses isolated but importance not known. In Britain, paramyxoviruses of the morbilli group are common in wild hedgehogs (Visozo & Thomas, 1981). Symptoms: circle-running, poor coordination, lesions (eyes, feet and mouth, internal organs) and death.

Table 2. The principal anthropogenic hazards causing the death or injury of hedgehogs (*Erinaceus europaeus*). Sources: Stocker (1987), Reeve (1994), Sykes & Durrant (1995) Zaltenbach-Hanßler et al. (1998).

Hazard	Notes
Traffic	Studies throughout Europe have shown that hedgehogs are one of the commonest mammals to be found dead on the roads.
Disturbance	Nests of dependent young are frequently disturbed by people or domestic dogs and cats. This may cause, directly or indirectly, abandonment and the death of the young. Hedgehogs are easy to catch and some, especially newly independent youngsters, may be unnecessarily 'rescued' from the wild.
Injury (accidental)	Agricultural and garden tools, forks, spades, strimmers, mowers etc. commonly injure hedgehogs of all ages. Injuries may also be caused by broken glass, barbed wire and similar hazards.
Injury (by pets)	Mainly attacks by domestic dogs. Domestic cats probably only affect youngsters which may be taken from nests.
Fire	Hedgehogs may build day-nests, breeding nests and hibernacula in piles of leaves or wood and so may be burned in bonfires if these are not checked first.
Poison	Direct consumption of slug pellets has been shown - indirect poisoning via consumption of poisoned slugs is less likely. Even if not ingested, contact with many other hazardous substances that are used in farms, parks, gardens, golf courses etc. may cause skin damage and subsequent disability and infection.
Becoming trapped	Entanglement in netting or litter e.g., plastic binders for drink cans, becoming stuck in large-mesh fencing or becoming trapped after falling into steep-sided holes, drains, cattle grids etc. Hedgehogs may also be accidentally locked inside buildings which have been left open at night.
Drowning	Any water-body with unnaturally steep sides e.g., garden ponds, swimming pools, canals, steep-sided ditches etc. may cause drowning.
Animal traps	Hedgehogs are usually caught accidentally while trapping for other species. May be a problem in areas subject to ground predator control programmes e.g., game-keepered estates.

Reeve (1994) and Huijser et al. (1998). Road accidents killed about 17-22% per year of a population of 23-27 hedgehogs in a three year study in southern Sweden (Göransson et al., 1976). In the same study area, Kristiansson (1990) used eight years of population data to estimate that road-kills accounted for most summer losses, averaging around 12% (range 3-22%) of the subadults/adults and between 0-6% of juveniles each year. This should be compared to estimates of total annual losses (deaths + emigration) which averaged 34% in juveniles and 47% in adults and subadults. In a rural area of The Netherlands, Huijser et al. (1997) found that road-kills accounted for 12% of the total losses (deaths + emigration) of the local population and that in two successive seasons 6% and 9% of the population were killed on the roads. Typically, studies have shown that the deaths are mainly males early in the season and during the rut (when males are more active than females) and most of the female deaths occur late in the season - probably after they have reproduced. This suggests that the demographic effects of road kills might be less than one might guess from the sheer numbers involved, because pre-reproductive females and juveniles are relatively unaffected (Kristiansson, 1990; Huijser et al., 1997a).

Although studies of road mortality contribute valuable data, road deaths are only part of the overall problem. The impact of other anthropogenic mortality factors (Table 2) should also be evaluated. Without expensive long-term demographic studies, records from hedgehogs admitted to wildlife rescue centres are the only practical source of substantial data. Some inherent biases of such data can be anticipated. The casualties admitted to wildlife rescue centres represent only animals that have not been killed outright and so must underestimate the effects of, for example, road traffic accidents or agricultural and garden machinery. Casualties from built-up areas will be over-represented because these will be more commonly found by the public and, because people commonly disturb breeding nests, dependent young and their mothers may also be over-represented. Also, the data in rescue centre records are principally concerned with issues of treatment and so may not always distinguish between different causes of injury and may only selectively contain detailed information on parasites, diseases and other potential causes of death that would only be apparent from faecal assays and/or autopsy examinations.

Nevertheless, with such biases kept in mind, an analysis of data from wildlife rescue centre records should allow some insight into which mortality factors most affect wild hedgehogs. This study is a first attempt at using a large data set collected from a number of wildlife rescue centres in order to characterise the nature of the problems affecting the hedgehogs admitted.

2. Material and methods

2.1. Sources of data

The records of a total of 856 hedgehog fatalities were obtained from three hedgehog rescue centres: 286 records (October 1992 - December 1997) Jersey, Channel Islands; 194 records (September 1997 - December 1998), Yorkshire, England; 376 records (January 1992 - December 1997) Den Haag, The Netherlands. Only records of deaths were included mainly because many hedgehogs successfully treated for injuries, illnesses or simply brought in by the public, might not have died if left in the wild. It is also true that another bias may have been introduced because of this, since hedgehogs that would have died in the wild, but survived because of the help they were given in a rescue centre, were excluded. The percentages of all hedgehogs admitted that were later released, and hence excluded from the present study, were 66.8% (Jersey), 40.0% (Yorkshire) and 75.4% (Den Haag).

In addition, pooled data on a total of 11,541 hedgehog casualties (January 1993 - December 1997) were provided by the British Wildlife Rehabilitation Council (BWRC) who collate wildlife casualty records nationally from 20-30 rescue centres. The BWRC data included 35% of animals that recovered and were later released, but these could not be identified and removed *post-hoc* because the data were in the form of quarterly and yearly totals.

2.2. Coding cause of death

The casualties were coded into eight categories of illness or injury which encompassed the existing six categories into which the BWRC data were already classified; as indicated in brackets below:

1. Natural causes - all injuries and disease not associated with human activity (= BWRC category 4) interpreted by us to include congenital abnormalities and malformations, failure to thrive etc. Not all animals within this category may have died from natural causes alone. Anthropogenic factors may make hedgehogs more susceptible to parasites and diseases. However, all animals for which apparent natural injuries, disease or infections were clearly secondary to anthropogenic factors were classified into the appropriate non-natural death category.

2. Injured - from 'unnatural or wilful agents' (BWRC category 1) other than road traffic accidents, injuries judged to be natural were recorded in category 1.
3. Road traffic accidents (included in BWRC category 1).
4. Orphaned - abandonment of dependent young (<6 weeks old, BWRC category 3).
5. Drowned in garden ponds and steep sided ditches etc. - an unnatural cause of death because hedgehogs (which swim well) should be able to escape from most natural ponds and rivers which have sloping banks that allow escape.
6. Injury caused by domestic cat or dog (similar to 'cat kill' BWRC category 6).
7. Poisoned/polluted - can be hard to determine, only confirmed or highly suspicious cases were included (BWRC category 2).
8. Other - any casualties not fitting into other categories (BWRC category 5).

Thus category 1 represents death from natural causes, whereas categories 2-7 cover anthropogenic causes of death.

2.3. Other variables

The BWRC data also contained records (for each quarter of the year) of totals of animals of each sex (male, female, unknown) and age class (immature, adult, unknown), plus the numbers surviving 48 hours and the numbers released.

The more detailed records from the three hedgehog rescue centres did not all contain the same information, but all were coded as individuals for which each of the following were recorded: sex (male, female, unknown), the month of admission (quarter only for the Yorkshire data), and presence or absence of endoparasite infestations. Also three age categories were distinguished: juvenile (dependent young), subadult (independent young) and adult. However, because the young of the previous year (older subadults) grade into adults, such animals were classed as adults (>1 year) if admitted in July or later. Further data from the Jersey and Den Haag samples were available for body weight on admission, the exact number of days survived after admission, the presence or absence of maggots. The Den Haag sample alone contained presence or absence records of ectoparasites. Both the Yorkshire and Jersey samples contained records of endoparasite species from faecal samples.

3. Results

3.1. Seasonal variation

The BWRC data revealed that, over the five years, hedgehogs accounted for a mean of 54% of all mammal casualties received by participating rescue centres (16% of casualties of all taxa). Hedgehogs were 35% of all mammal casualties in the first quarter of the year, 52% in the second and 68% in each of the third and fourth quarters. All sources showed seasonal variation in the numbers of hedgehogs admitted with relatively few admissions in the first quarter and peak numbers in the third or fourth quarters. Of all admissions 73.5% took place in the second half of the year (Table 3). The joined data from all sources showed that the sex ratio of the admitted animals depended on the quarter of year (G-test statistic (with William's correction) = 11.31, df=3, $P<0.025$). There was a progressive reduction in male-bias from 1.5:1 (m:f) in the first quarter to 1.1:1 in the final quarter of the year. Overall, there remained a significant male-biased sex ratio of 1.2:1 (N=5592 of known sex, G-test statistic = 47.31, df=1, $P<0.0001$).

Table 3. Number of hedgehog casualties and the sex ratio (N=5592 animals of known sex) for each quarter of the year. Total BWRC data plus fatalities from the Jersey, Yorkshire and Den Haag rescue centres for all years.

	Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec	Total
Total	655	2,627	5,395	3,720	12,397
Males	180	652	1,411	810	3,053
Females	119	486	1,188	746	2,539
Sex ratio (m:f)	1.5:1	1.3:1	1.2:1	1.1:1	1.2:1

3.2. Age structure

The proportion of juveniles, subadults and adults varied between the three hedgehog rescue centres. The Jersey sample contained relatively more subadults (41%), the Yorkshire sample contained relatively few juveniles (12%), whereas the Den Haag group had relatively few subadults (26%). However, when the data from the three hedgehog rescue centres are totalled, the three age classes are equally abundant (N=850 of known age, G-test statistic = 4.05, df=2, P=0.15) with approximately one third of casualties in each age group: juveniles 30%, subadults 35%, adults 35%. The BWRC data showed a similar pattern although only two age categories were used, 58% immature (juveniles and subadults) and 33% adult, plus 9% of unknown age.

The age structure of fatalities from the three hedgehog rescue centres varied seasonally (Fig. 1). The combined data showed that from January to June, almost all casualties were subadults and adults (in roughly equal numbers) with only 4.6% of casualties being juveniles in the April-June period. The proportion of juveniles increased to about 33% and again to 40% in the third and fourth quarters respectively. The BWRC data set is less useful here

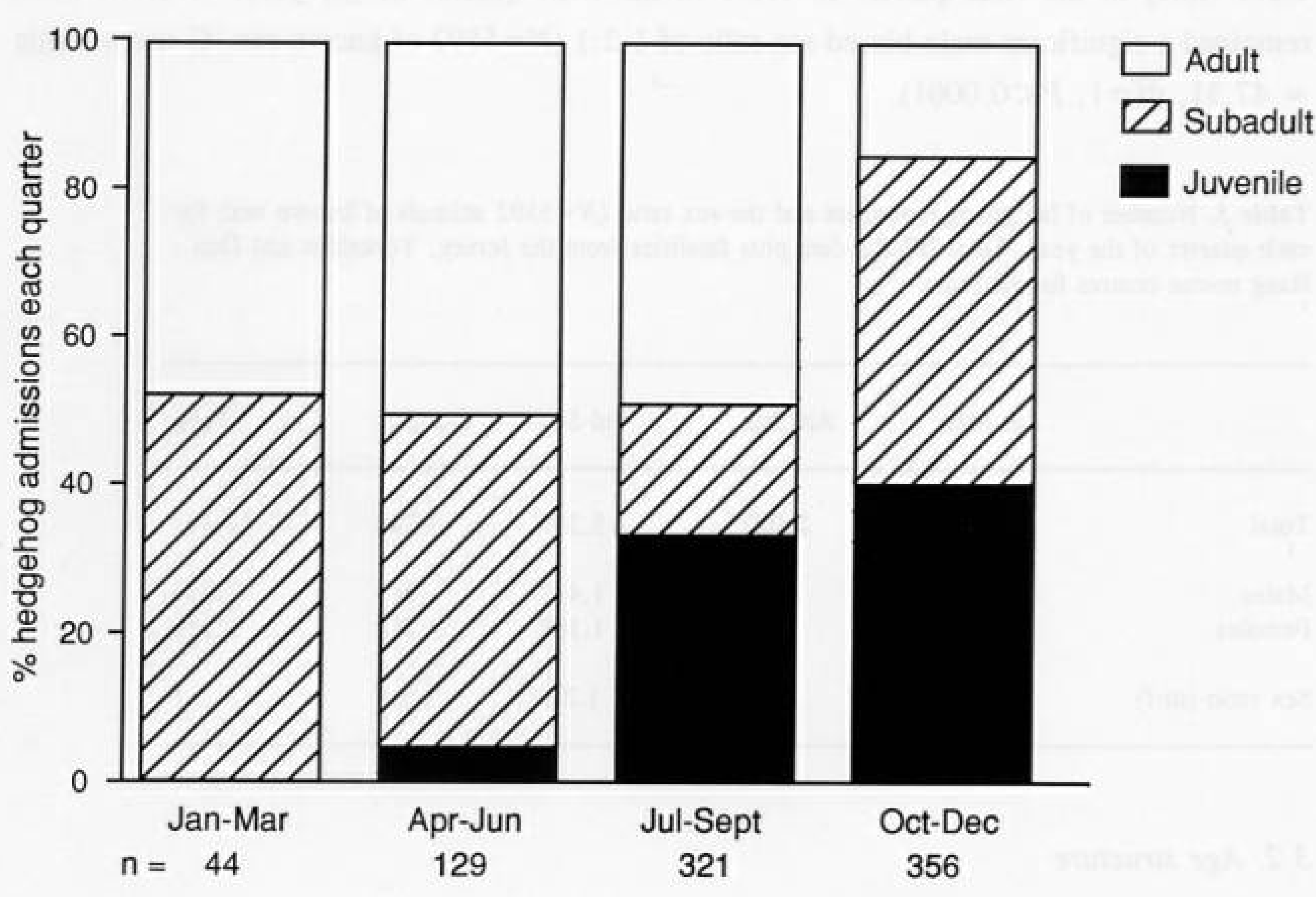

Fig. 1. The proportion (%) of fatalities for each age group in each quarter of the year. Data from the three hedgehog rescue centres only. N = number of animals in each quarter for which age estimates were recorded.

because it did not distinguish between dependent and independent young. Nevertheless, for those of known age the same trend is shown with 57% adults and 43% immatures (N=2,740) in the first half of the year, and with 29% adults and 71% immatures (N=7,691) in the second half of the year.

3.3. *Mortality factors*

Fatality data from the three hedgehog rescue centres are presented in table 4 and in figure 2 which also provides a comparison with the BWRC casualty data. The data from the three hedgehog rescue centres show that 58.5% of deaths can be attributed to 'natural causes'. In contrast, categories 2 to 7 are all, in one way or another, the result of human activity. Overall, anthropogenic mortality factors may therefore account for up to 40.9% of deaths in this sample with 'other causes' accounting for an additional 0.5%

The BWRC data, which included hedgehogs that recovered, showed a somewhat similar pattern (Fig. 2) with 22.1% of animals suffering unnatural injuries, 1.8% poisoned and 0.7% taken by cats. This latter figure compares well to 0.2% cat kills, and 2.1% dog kills (total 2.3%) in the hedgehog rescue centre data. There was a relatively high proportion (27.9%) of abandoned young - over twice the total from the hedgehog rescue centres although these varied from 5.2% to 20.7%. Those admitted with problems of a natural origin were 27.5%

Table 4. The number of fatalities from the three hedgehog rescue centres (total = 856) classified into death categories. 1 = natural causes, 2 = unnatural injury, 3 = road traffic accident, 4 = orphaned, 5 = drowned, 6 = injury from dog or cat, 7 = poisoned/polluted, 8 = other.

	Death category							
Hospital	1	2	3	4	5	6	7	8
Jersey	200	40	12	15	3	9	4	3
%	*69.9*	*14.0*	*4.2*	*5.2*	*1.0*	*3.1*	*1.4*	*1.0*
Yorkshire	131	7	33	17	0	4	2	0
%	*67.5*	*3.6*	*17.0*	*8.8*	*0*	*2.0*	*1.0*	*0*
Den Haag	170	54	30	78	5	7	31	1
%	*45.2*	*14.4*	*8.0*	*20.7*	*1.3*	*1.8*	*8.2*	*0.3*
Total	501	101	75	110	8	20	37	4
%	*58.5*	*11.8*	*8.8*	*12.8*	*0.9*	*2.3*	*4.3*	*0.5*

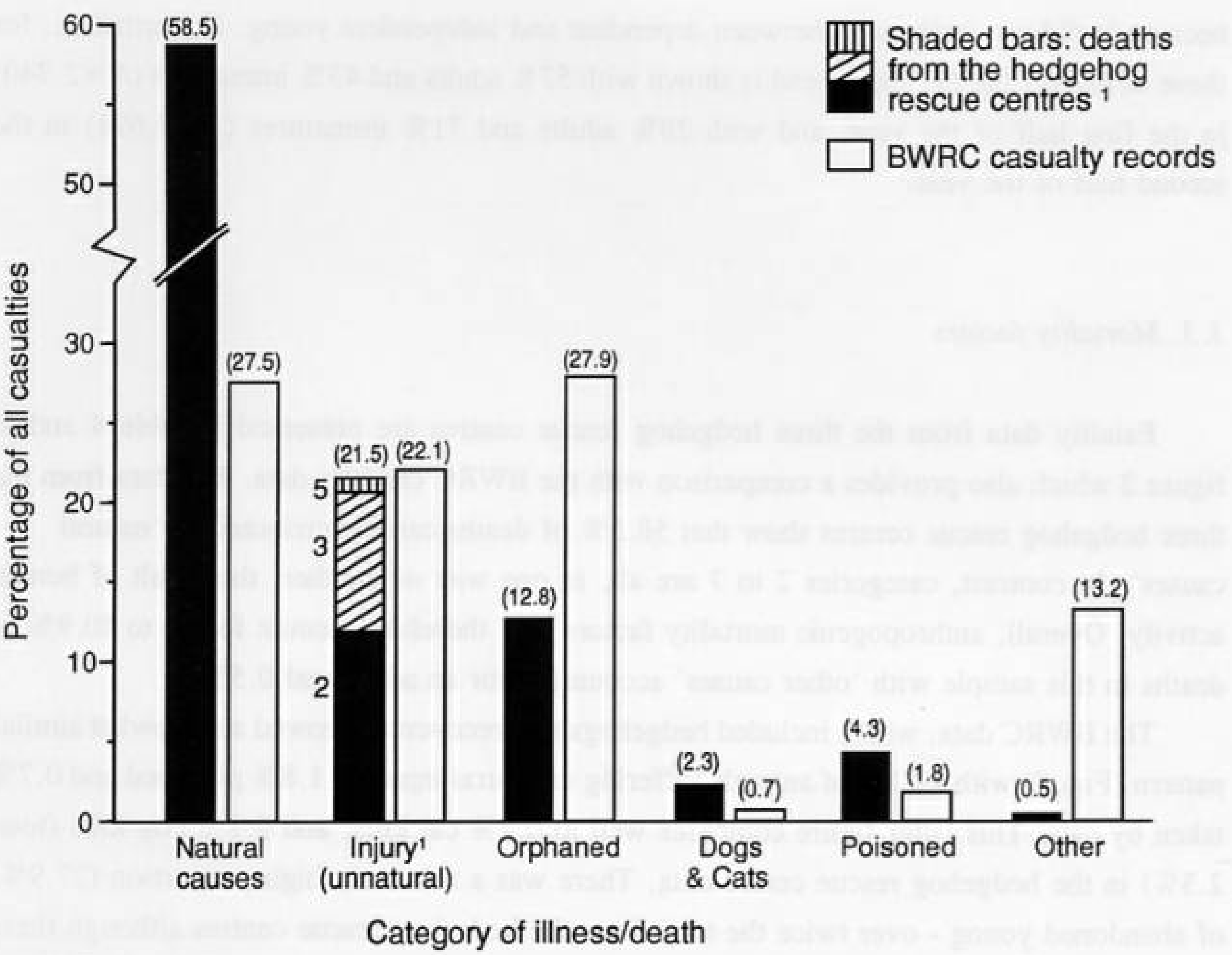

Fig. 2. The percentage of hedgehog casualties in each cause of death category from the three hedgehog rescue centres (shaded bars) and the BWRC records (unshaded bars) which recorded all casualties, not just deaths. [1] The hedgehog rescue centre data for unnatural injury (cat. 2), road accidents (cat. 3) and drowning (cat. 5) is here taken to be equivalent to the BWRC category 1 (unnatural injury).

of cases, just under half the hedgehog rescue centre sample total. Additionally, 13.2% of deaths were from 'other causes'.

Given the more or less equal abundance of the three age categories in our sample from the three hedgehog rescue centres, subadult hedgehogs are relatively vulnerable to dying of natural causes (Table 5). Adult males are most susceptible to 'unnatural injuries' and becoming a traffic victim. By definition juveniles were the only age group in the 'orphaned' category.

Seasonal variation in the incidence of cause of death shows that most animals that died of natural causes did so in the second half of the year (Table 6). The peak in deaths due to unnatural causes and traffic victims was several months earlier in the year whereas orphaned hedgehogs were first found in the third quarter.

Table 5. Fatalities from the three hedgehog rescue centres showing the incidences of causes of death of animals of known sex and age (N=753) across the four most common death categories. j = juvenile, s = subadult, a = adult.

Death category	Age	Male (N)	Female (N)
Natural causes	j	50	39
	s	111	106
	a	89	78
Unnatural injury	j	9	16
	s	8	11
	a	34	22
Road traffic accident	j	1	1
	s	13	10
	a	31	17
Orphaned	j	47	60
	s	0	0
	a	0	0
Total		393	360

Table 6. Fatalities from the three hedgehog rescue centres showing the incidences of causes of death for each quarter of the year across the four most common death categories.

	Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec
Natural causes	32	74	161	235
%	*6.4*	*14.7*	*32.1*	*46.8*
Unnatural injury	1	15	57	25
%	*1.0*	*14.9*	*56.4*	*24.8*
Road traffic accident	5	20	34	16
%	*6.7*	*26.7*	*45.3*	*21.3*
Orphaned	0	0	50	59
%	*0.0*	*0.0*	*45.9*	*54.1*

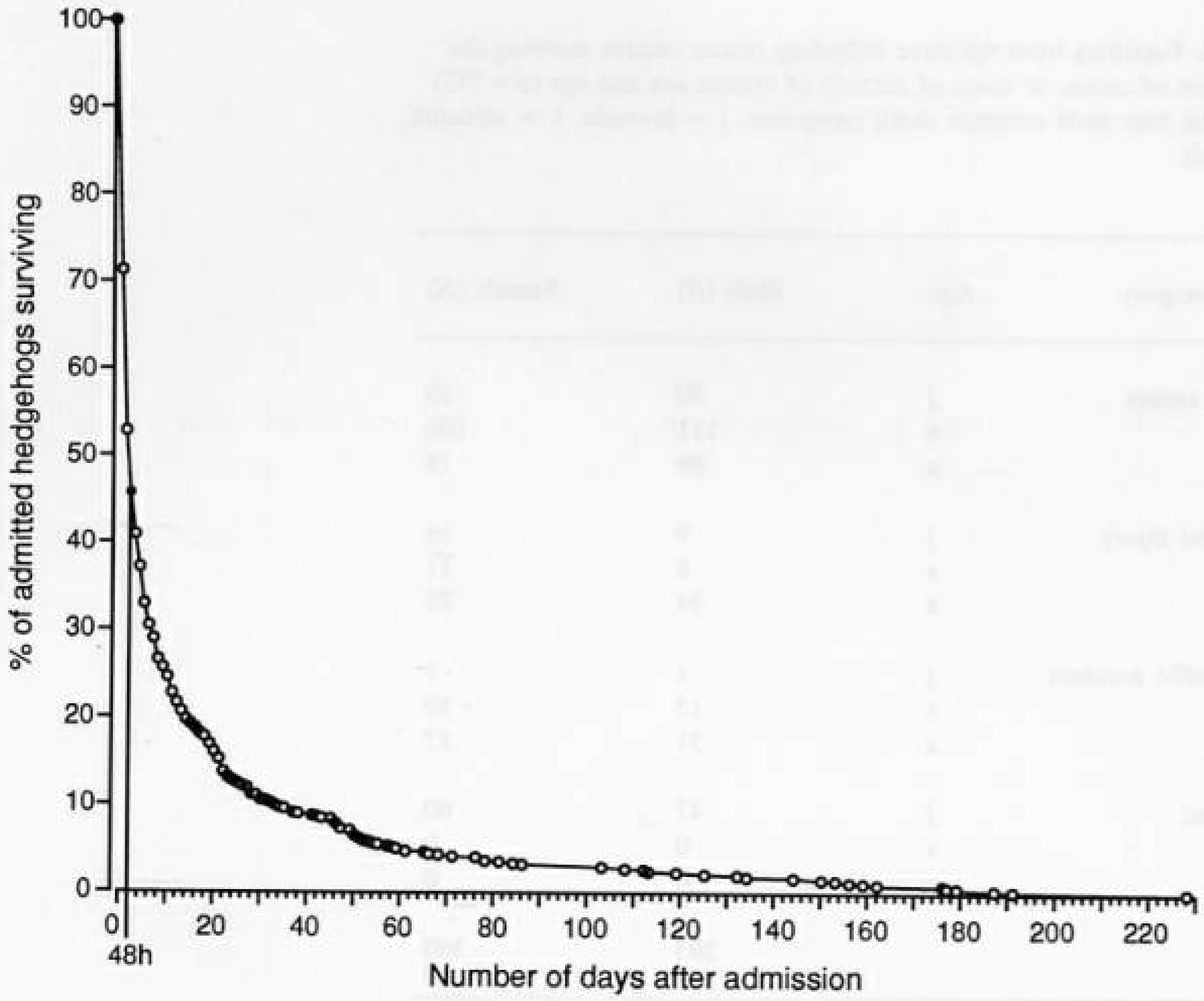

Fig. 3. The percentage of hedgehogs that survived a certain number of days after admission (N=658 hedgehog fatalities from the Jersey and Den Haag hedgehog rescue centres). Animals that died within the first day were recorded as having a survival of 0 days. Only 45.7% of admissions survived 48 hours.

The number of days from admission to death were obtained from two of the hedgehog rescue centres (Jersey and Den Haag) which showed no significant difference between the centres (Mann-Whitney U test, P=0.96, N_1=282, N_2=376). Non-parametric analysis was used because the data showed a very strong positive skew, with most animals having low survival rates but with some surviving for long periods, up to 228 days. The median survival period was two days, with only 25% surviving beyond 10 days (Fig. 3).

3.4. Parasites

Of the animals that died at hedgehog rescue centres 64% of 498 animals tested had endoparasite infestations confirmed by routine faecal analysis or autopsy. There was no interaction of sex and age (G-test statistic (with William's correction) = 0.74, df=2, $P>0.50$). The incidence of parasites was equally distributed over the sexes (G-test statistic = 0.19, df=1, $P>0.90$), but not over the age categories (G-test statistic = 21.83, df=2, $P<0.001$). Only 49% of dependent juveniles were infected but the incidence was 67% in adults and 85% in subadults. The records of endoparasite species are summarised in table 7. Ectoparasites were only recorded (presence or absence) consistently by the Den Haag rescue centre. Of the 315 animals examined, 87.6% had ectoparasites. Myiasis (maggot infestation) was more reliably reported by all three centres, of 664 animals examined, 7.5% had maggots or fly eggs.

Table 7. The incidence of endoparasite species recorded from the Jersey and Yorkshire hedgehog rescue centres (combined data). Results were obtained from faecal analysis (usually simple faecal smears) and/or autopsy examination. Not all animals were examined in each case (sample sizes are as shown).

Endoparasite	Hedgehogs examined (*N*)	Positive (*N*)	Positive (%)
Capillaria spp.	256	128	49.6
Crenosoma striatum	265	103	38.9
Capillaria aerophila	263	55	20.9
Brachylaemus erinacei	256	42	16.4
Coccidia	269	41	15.2
Cestodes	258	3	1.2
Acanthocephala	256	4	1.6

4. Discussion

4.1. Sample composition

Both sexes and all age groups were well-represented in the sample and the seasonal changes in the sample composition conformed to expectations based on field studies and a knowledge of the life-cycle of the species (Reeve, 1994). The seasonal variation in the number of casualties can be partly explained by the seasonal activity cycle of hedgehogs which typically hibernate from November to March or April in the areas studied. Hedgehogs were 35% of mammal casualties even in the first quarter but the absolute numbers were relatively very low. However, in the fourth quarter, hedgehogs still made up 68% of mammal casualties and the absolute numbers remained high. These late casualties were dominated by juveniles and newly independent subadults (almost 85% of admissions) which commonly remain active to boost their fat stores prior to hibernation while the majority of adults have begun hibernation by November (Reeve, 1994). The appearance of juveniles in small numbers in the second quarter, and then in larger numbers in the third and fourth quarters also corresponds to the known breeding season, the rut typically begins during May and few young are born before mid June (Reeve, 1994; Huijser, 1997).

The male bias in the sex ratio was most marked in the first quarter of the year and reduced to an approximately even sex ratio late in the year. This is in line with the results of field studies and studies of road casualties (e.g., Göransson et al., 1976; Reeve, 1982). Early in the season males become fully active earlier than the females (Zingg, 1994) and during the rut adult males typically travel longer distances and range more widely than females (Reeve, 1982), behaviour likely to result in a greater risk of accidents.

4.2. Mortality

That hedgehogs accounted for 54% of recorded wildlife casualties could be a result of a thriving population in association with areas of human habitation and the relative ease with which hedgehogs may be caught. However, the finding that 41% of recorded deaths are attributable to anthropogenic factors must be a cause for concern. Although some biases may have artificially inflated this estimate, it is also true that many deaths must have been unrecorded, such as those that are killed immediately or never found after injury e.g., after road accidents, or those affected by pesticides and pollution but with non-specific symptoms. Built-up areas are one of the most important refuge habitats for hedgehogs in the UK and The Netherlands (Morris, 1993; Huijser, 1999) yet these data suggest that hedgehogs are under considerable pressure from anthropogenic mortality factors which must be acting strongly in such areas. However, without corroborative population studies, the demographic effects of such mortality can only be guessed.

The three hedgehog rescue centres showed some variation in the numbers in each cause of death category. The Yorkshire centre recorded proportionately more road casualties but many fewer unnatural injuries of other types, this may represent a genuine difference but could also have been due to differences in the interpretation of injuries and their context, or stochastic effects on a relatively small sample. The comparatively few road casualties recorded from Jersey (4.2%) may be partly explained by the slow traffic on the island (speed limits from 24-64 km/h) a factor associated with a reduced number of road-kills (Gunther et al., 1998). Furthermore, in contrast to studies elsewhere (e.g., Doncaster, 1992; Reeve, 1998) none of 13 released hedgehogs in Jersey was killed on the roads (Morris, 1997).

Another disparity between the three hedgehog rescue centres was in the number of deaths of orphans - relatively high (20.7%) in the Den Haag sample, however this was closer to the 27.9% of orphans recorded in the BWRC data. In contrast the figure for death by natural causes was consistently much higher in the Jersey and Yorkshire samples (67.5 and 69.9%) than in the Den Haag and BWRC samples (45.2% and 27.5%). It should be remembered that the BWRC data also included animals that recovered and therefore the numbers would be boosted by successfully reared orphans, nevertheless, these differences suggest a systematic difference in coding where an underweight youngster could either have been recorded as an orphan (still dependent) or as a death by natural causes (failure to thrive of an independent subadult). More precise criteria for recorders could help to improve consistency in future.

In other respects the hedgehog rescue centres and the BWRC data showed reasonable consistency with a very similar proportion of animals suffering from human-related injuries (21.5% and 22.1% respectively) but the comparatively heavy use of the 'other causes' category in the BWRC data makes detailed comparison unsafe. Poisoning/pollution is clearly a minor cause (4.3% and 1.8%) but is likely to be under-reported because of the difficulty and expense of obtaining laboratory confirmation of suspected poisoning. Under-reporting is also likely when poison results in either the immediate death or the hiding and reduced activity of poisoned animals. The Den Haag sample reported 8.2% of deaths being due to poisoning or pollution, this is considerably more than the 1.0 - 1.8% range from the other three sources. This may be due to less conservative reporting or could be related to the more densely urban nature of Den Haag. Dog bites are a well-known cause of injury to hedgehogs (2.1% of hedgehog rescue centre deaths) although they were not separately recorded in the BWRC scheme. Cats are less important at 0.7% and 0.23% (BWRC and hedgehog rescue centre data respectively) and the reports are related to the taking of nestlings or the desertion of dependent young after nest disturbance.

Adult males outnumbered the females in the 'unnatural injuries' and 'traffic victim' categories. This is in accordance with the expectation that males would suffer significantly more from accidents because of their wider ranging behaviour.

The effect of age on the likelihood of death from certain causes was obvious in some cases. Only juveniles can be orphaned and dependent juveniles are unlikely to have been victims of road accidents (only three instances) unless they were out with their mother, hence these two categories showed strong age differences. However, the strong bias towards subadults (and away from juveniles) dying of natural causes is of interest. Subadults also have particularly high endoparasite infestation rates (see later). The majority of juveniles dying of natural causes would never have been discovered and taken to a rescue centre, hence the data may reflect the general vulnerability of the young; as shown in population studies of survivorship (Kristiansson, 1984). Why adults (with an even sex ratio) should have been more susceptible to unnatural injury than subadults is not fully clear. However, not all unnatural injuries may have occurred during the day and since adults travel greater distances than subadults they run a greater risk of injuries. That juveniles should also outnumber subadults in this category is also baffling, although it is certainly possible that juveniles may be accidentally injured (a whole litter at a time) in their nests by, for example, agricultural and garden tools.

Most of the seasonal differences in the causes of death can easily be accounted for. The 'orphaned' casualties can only be associated with the birth of youngsters, and hence are confined to the third and fourth quarters. Unnatural injury peaks in the second and third quarters when gardeners are most active. Road accidents also peak in the middle two quarters when males are most active and subadults may be dispersing (Reeve, 1982). Deaths from natural causes show a large increase, to 66.6% of all deaths, in the fourth quarter. This seems likely to be associated with the relatively large numbers of newly independent subadults which are very vulnerable late in the year.

The BWRC records included a count of the number of casualties surviving 48 hours, the assumption being that the 37% of all admissions that died within 48 hours were unlikely to have survived, whatever the treatment. Applying the 48 hour criterion to the median of 2 days from admission to death in both the Jersey and Den Haag centres, it might be suggested that half those animals that died had little chance of being saved. However, the fact that as many as 25% survived beyond 10 days before dying indicates that 48 hours is too short a period for an accurate prognosis.

4.3. Endoparasites

Endoparasite infections were common overall (positive in 64% of animals tested). Juveniles, who will have had only limited exposure to vectors, had predictably lower infection rates (49%); as was also found by Majeed et al. (1989) and Schicht-Tinbergen (1995). In the present study, the comparatively high 85% infection rate in subadults (67% in adults) may contribute to an explanation of why they had such a high rate of mortality from natural causes. The lack of a significant sex difference in the incidence of endoparasite infections found in the present study was also reported for lungworm infections by Majeed et al. (1989).

The recorded incidences of particular parasites are comparable with those from published studies - but these are highly variable. Lungworms, *Crenosoma striatum* and *Capillaria aerophila* infections are commonly fatal in hedgehogs (Reeve, 1994). *Crenosoma striatum* were found in 38.9% of animals, this is similar to the 35.9% incidence reported by Epe et al. (1993) but rather lower than typical; in order of incidence: 45.2% (Bauer & Stoye, 1984), 47.8% (Löwenstein et al., 1991), 52-72.3% (Barutzki et al., 1984), 74-79.9% (Laux, 1987), 76.9% (Giannetto, 1995), 79.2% (Schicht-Tinbergen, 1995), 79.4% (Schütze, 1980). *Capillaria aerophila* infections had an incidence of 20.9% of hedgehogs, within the range of other studies but slightly lower than typical: 23.4% (Schicht-Tinbergen, 1995), 15.1-40.7% (Barutzki et al., 1984), 41.7% (Schütze, 1980), 47% (Laux, 1987).

Intestinal *Capillaria* species (e.g., *C. erinacei, C. ovoreticulata*) were found in 49.6% of animals tested. Again, the figure is within the range of published studies; in order of incidence: 12% (Timme, 1980), 30.7% (Giannetto, 1995), 48.8% (Epe et al., 1993), 55.8% (Schicht-Tinbergen, 1995), 56.4% (Schütze, 1980), 61.8% (Bauer & Stoye, 1984), 72.3-74% (Barutzki et al., 1984), 74% (Laubmeier, 1985), 79% (Boag & Fowler, 1988), 74% from faeces and 89.6% from autopsy (Laux, 1987).

The 16.4% incidence of *Brachylaemus erinacei* in the present study represents a moderate value within the very variable published range. In order of incidence: 0.2% (Timme, 1980), 0.3% (Löwenstein et al., 1991), 1.6% (Bauer & Stoye, 1984), 2.3% (Epe et al., 1993), 2.7% (Keymer et al., 1991), up to 4.8% (Barutzki et al., 1984), 24.4% overall but 1-80% depending on region (Schütze, 1980), 34.2% (Schicht-Tinbergen, 1995), 41% (Giannetto, 1995), 14.5% from faecal samples, but 53.4% from autopsy (Laux, 1987).

Other endoparasites included a 1.2% incidence of tapeworms (Cestodes), a rate comparable to the range of other studies: 0.5% (Barutzki et al., 1984), 0.7% (Schütze, 1980), 1.4% (Keymer et al., 1991), 2.6% (Boag & Fowler, 1988), 3.7% (Laubmeier, 1985), 4.3% (Löwenstein et al., 1991), 7.6% (Giannetto, 1995). Acanthocephala were rare at 1.6%, not far from the 2.9% reported by Löwenstein et al. (1991) but far below the very high figure of 69.2% given by Giannetto (1995). Coccidia were found 15.2% of animals tested. This figure fits very well with published results (in order of incidence): 1.4-12.9% (Barutzki et al., 1984), 2.5% (Giannetto, 1995), 10.5% (Laux, 1987), 11.3% (Schütze, 1980), 13.3% (Bauer & Stoye, 1984), 13.5% (Schicht-Tinbergen, 1995), 15% (Laubmeier, 1985), 17% (Epe et al., 1993), 21.6% (Löwenstein et al., 1991).

Overall the incidences of these endoparasites were similar to those reported in the literature, indicating that the hedgehog rescue centre samples were not unusually heavily parasitised, but it should be noted that the majority of animals used in the published studies were also casualties from rescue centres. Thus these figures cannot safely be generalised to the wild hedgehog population as a whole.

4.4. Recommendations

Casualty records of hedgehogs from wildlife rescue centres provided a large sample representing both sexes and all age groups throughout the year. Hence, despite the likely biases of such data, hedgehog rescue centre records can provide useful insights into the mortality factors affecting wild hedgehogs. We recommend that researchers and carers work together to develop a more standardised and somewhat more detailed scheme of casualty records for hedgehogs, but that the system should use a coding compatible with the current BWRC scheme. As it stands, the BWRC scheme imposes severe limitations on the possible analysis because fatalities and survivors are combined and each case is not individually coded. This makes it impossible to attribute certain causes of death to particular age or sex classes. The added value of such analyses is considerable and the hedgehog scheme should therefore use a case by case coding (as was used by the three participating hedgehog rescue centres). However, the BWRC scheme is comparatively simple to operate and there is likely to be a trade-off between the complexity of the scheme, the level of participation and the ability of participating centres to comply.

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CHAPTER 3

SEX-DEPENDENT SEASONAL MORTALITY IN A HEDGEHOG *ERINACEUS EUROPAEUS* POPULATION

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Submitted

SEX-DEPENDENT SEASONAL MORTALITY IN A HEDGEHOG *ERINACEUS EUROPAEUS* POPULATION

Abstract - We conducted a capture-mark-recapture study in a hedgehog (*Erinaceus europaeus*) population to investigate the relative importance of traffic mortality and body condition related natural deaths. The study focused on a population of subadult and adult hedgehogs in a small scale agricultural landscape in The Netherlands. Traffic mortality of the study population was 12% of the total losses (deaths + dispersal). Over two successive seasons 6 and 9% of the animals in the study population fell victim to traffic. Most traffic victims were males (69%). We also found that far more males (N=11, N=8) than females (N=3, N=2) crossed one of the two paved roads in the study area, probably because the mobility of males increased when they searched for females in the summer months. Increased activity of males in summer caused considerable loss of body weight (17% on average). Weight loss coincided with reduced probability of male survival. Because of the nature of the analysis, the reduction may have been caused by either emigration or the depletion of their energy reserves or a combination of both. The same accounts for females which had low survival rates during, or immediately following, hibernation. They may have had little time to store sufficient fat reserves for hibernation as they suckled their young in late summer and autumn. Body weight data support this hypothesis. Sex-dependent seasonal survival has not been shown in previous studies on hedgehogs, but is in accordance with the present knowledge of the mating strategy of this species.

1. Introduction

The hedgehog (*Erinaceus europaeus*) is one of the most frequently occurring mammal species in European road kill studies (e.g., Davies, 1957; Göransson et al., 1976; Mannaert, 1978; Reichholf & Esser, 1981; Garnica & Robles, 1986; Korhonen & Nurminen, 1987; Meijer & Smit, 1995). Traffic mortality may limit hedgehog population size. In theory such limitation is most likely to occur in regions with high traffic intensity and road density such as The Netherlands (Vos & Zonneveld, 1993). The main objective of measures to reduce the number of traffic victims should be to mitigate negative effects on the population level (Huijser et al., 1998). However, little is known on how hedgehog traffic mortality relates to the total mortality in a population (Reeve, 1994; Mulder, 1996a).

Mortality during hibernation due to insufficient fat reserves is believed to be a major natural cause of death (Reeve, 1994). The hedgehog hibernates throughout most of its range in western Europe (Reeve, 1994). Triggered by low temperatures, its hibernation season in north-western Europe usually starts in October, November or December and may last until April or May (Reeve, 1994). In southern Sweden, Kristiansson (1990) showed that both juveniles (i.e., animals in their first summer) and subadults (i.e., animals having survived one hibernation) that died in winter, weighed significantly less than the animals that did survive the winter. He found the same trend for adults (i.e., ≥ 2 hibernations), but here the difference in body weights between the animals that survived and the animals that died was not significant. Morris (1984) also pointed out that a certain minimum body weight (450 g) seemed to be required to survive the British winter.

We studied the yearly survival in a hedgehog population in The Netherlands through a capture-mark-recapture method and determined the role of traffic mortality by an intensive check for hedgehog traffic victims in the same study area. We also monitored the body weight of hedgehogs in order to gain insight into condition related (winter) mortality.

2. Material and methods

2.1. Study site

The study was conducted on the estates of Schouwenburg and Zwaluwenburg near Elburg, The Netherlands (52°26'N, 5°52'E) (see Huijser & Bergers (1997) for a topographical map). A busy two-lane secondary road (N309) and a paved country-road (Laanzichtsweg) crossed the 150 ha study area (Fig. 1). The N309 had a mean traffic intensity of 9412 (SD=1044) vehicles per 24 hours (counted by the city of Elburg from 11 through 15 May 1995). The landscape was characterized by small scale pastures and hay meadows (59%) and arable land (5%), separated by hedgerows (mostly 10-20 m wide, with mature trees) (11%) and woodland fragments (8%). Premises, farm buildings, gardens, ponds, roads and road-side verges accounted for the remaining surface.

The hedgerows and woodland fragments were dominated by broad-leafed species as oak (*Quercus robur*), beech (*Fagus sylvatica*) and alder (*Alnus glutinosa*), with serviceberry

(*Amelanchier lamarckii*) and rowan (*Sorbus aucuparia*) in the shrub layer. Brambles (*Rubus* ssp.) were also abundant, especially along the edges.

The study area was divided into three 50 ha sections (each 1000 m x 500 m). Section I and II were separated by the busy two lane secondary road.

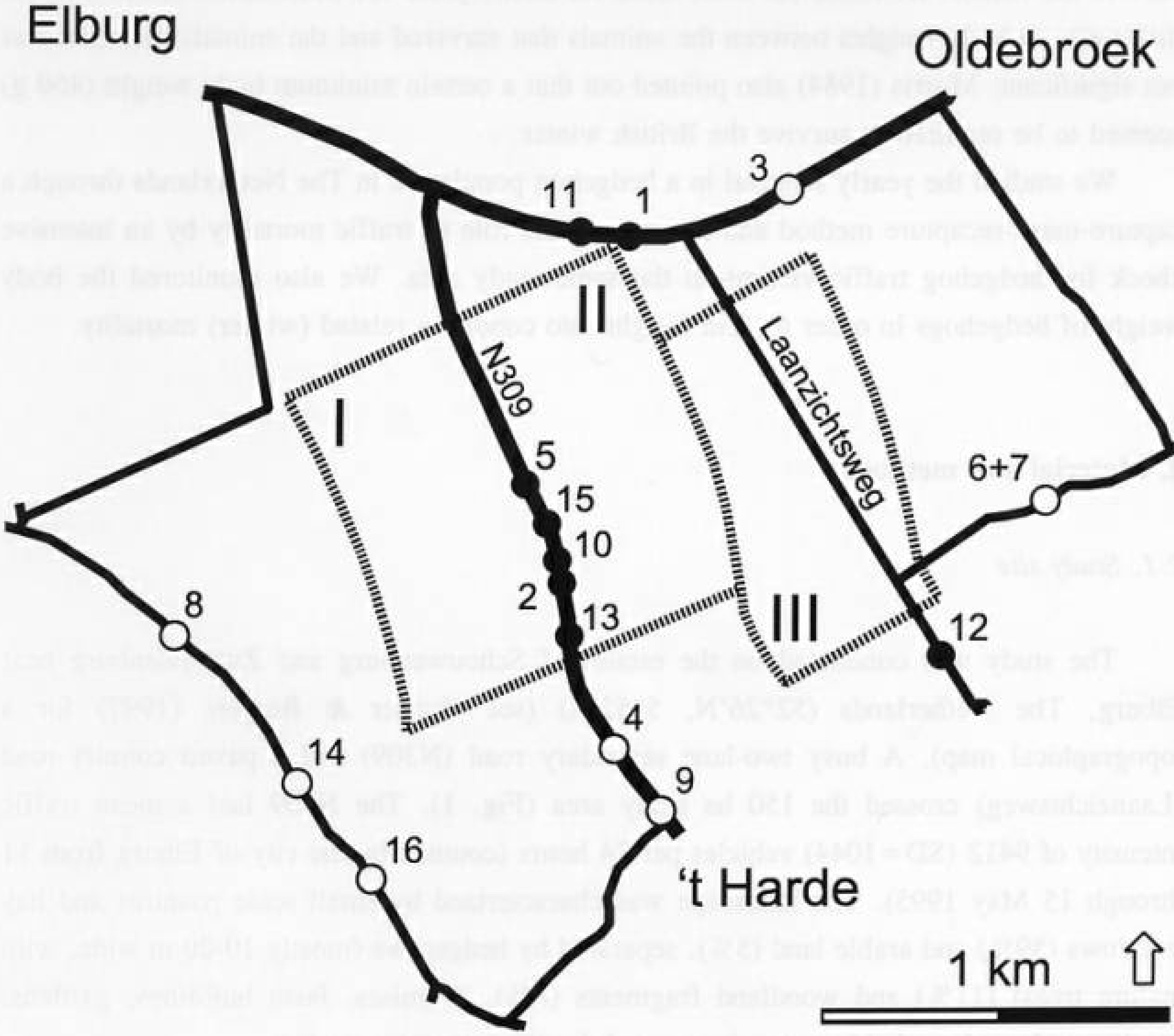

Fig. 1. The study area: the location of the three sections (I-III, each 1000 m x 500 m) and the roads in and around the study area, notably the secondary two-lane secondary road (N309) and the paved country-road (Laanzichtsweg). The numbered dots indicate the location of the traffic victims. The numbers correspond with the running numbers in table 4. The closed dots indicate traffic victims that were considered part of the study population. Open dots represent other hedgehog traffic victims.

2.2. Trapping

In 1994 and 1995, for a period that lasted well over a year in total, hedgehogs were captured in wooden traps with canned dog food as bait. The traps (N=90) were placed throughout the study area (i.e., 30 in each section). The traps were often located in the hedgerows or woodland fragments, on the edge of grasslands or arable land. On some occasions a trap was situated in the open field, along a ditch or under a solitary tree. The traps were prebaited during the week preceding a capture. A capture consisted of two consecutive trapping nights. The captures in the three sections occurred successively at intervals of one week (1994) or two days (1995): one capture (i.e., two trapping nights) in section I, followed by a capture in section II and III respectively, together forming one capture round.

The traps were redistributed throughout the study area before a new capture round was initiated. Between May and October 1994 six capture rounds, about one month apart (Table 1), were conducted in each section. In 1995 there were four capture rounds (about three weeks apart) between May and July. The traps were checked in the first few hours after sunrise after which the animals were released. Apart from the trapping, hedgehogs were also captured by hand when encountered in the field.

Table 1. Time schedule of the capture rounds.

Capture round	Median date of capture		Capture round	Median date of capture	
94_1	19 May	1994	94_6	20 October	1994
94_2	18 June	1994	95_1	5 May	1995
94_3	28 July	1994	95_2	26 May	1995
94_4	25 August	1994	95_3	16 June	1995
94_5	22 September	1994	95_4	7 July	1995

2.3. Marking

The captured hedgehogs were split into two age categories based on size and body weight: juveniles (relatively small, weight less than 600 g) and (sub)adults (relatively large, heavier than 600 g) (Kristiansson, 1984; Dietzen & Obermeier, 1989). Unmarked hedgehogs were anaesthesized using Halothane after which the animals were given uniquely numbered ear tags, a plastic tag (Dalton mini tag, UK) in one ear and a metal tag (customized Michel surgical wound clip, 2.5 x 8 mm (Le Boulenge-Nguyen & Le Boulenge, 1986)), in the other. An animal was also marked by attaching coloured plastic tubes on ten adjacent spines. Each of the ten tubes was a unique marking due to its combination of colour and location on the animal's back. This study was reviewed by an ethical commission on animal experiments and found to be in accordance with the Dutch law. The field workers were licensed to anaesthesize and tag the animals.

For our separate analysis for the juvenile population (see paragraph on capture-mark-recapture analysis), we had to recognize an additional age group in 1995: unmarked subadults. Subadults can be hard to tell apart from adults. This did not confront us with a serious problem since we conducted our 1995 captures in the first couple of months of the season: subadults and adults still have a clear weight difference at that time (Kristiansson, 1984; Dietzen & Obermeier, 1989).

2.4. Traffic victims

Between April 1994 and December 1995 all paved roads in and around the study area (Fig. 1) (total length 12.6 km) were checked for hedgehog traffic victims almost every day early in the morning. The roads were inspected from a car (driving at low speed) or from a bicycle. When high vegetation hindered a clear view, the road-side verges were also checked on foot.

All hedgehog traffic victims found within the study area were considered to be part of the study population. Obviously, the same applied to marked individuals killed on a road outside the study area. Most of the boundary of the study area coincided with a change from a small scale agricultural landscape to large-scale grasslands with little cover for hedgehogs. Because of their need for cover to nest in (Morris, 1973; Reeve & Morris, 1985) and their wide-ranging non-territorial habits (Reeve, 1982; Kristiansson, 1984; Reeve & Morris, 1986), the home range of individuals found just outside the boundaries of the study area was likely to lie partly within the study area. Of these individuals, juveniles and subadults have had very limited opportunity to have been caught and marked: their life span only partly overlapped the study period. Therefore unmarked traffic victims that were found within 100 m of the study area were also considered part of the population. This distance lies well within the radius of the average home range size of subadults (12 ha, r=195 m) (Reeve, 1982). The two traffic victims involved were subadults that probably died before we could catch and mark them.

In addition to the traffic victims found on the roads in the immediate vicinity of the study area, we also collected hedgehog traffic victims within a wider radius (about 20 km). Only the roads in and around the actual study area (Fig. 1) were surveyed frequent enough to ensure the finding of all or virtually all victims.

2.5. *Capture-mark-recapture analysis*

(Sub)adults

The capture-mark-recapture data of the (sub)adult hedgehogs were analyzed using the Jolly-Seber stochastic model (Jolly, 1965; Begon, 1979; Seber, 1982), which is designed for open populations. We determined population size (N_i), survival (Φ_i) and total losses (deaths + dispersal) ($L_i=(1-\Phi_i)N_i$) at the time of or between the capture rounds (i). Asymmetric 95% confidence intervals were calculated following Krebs (1989). The Jolly-Seber model has several assumptions (Krebs, 1989; Lancia et al., 1994). The assumptions regarding equal capture- and survival-probability were tested with TEST 1, 2 and 3 as described by Burnham et al. (1987) (program RELEASE).

Juveniles were excluded from the Jolly-Seber analysis beforehand since we suspected their capture probability to differ from (sub)adults. When juveniles leave the nest at the age of three to four weeks, they can be potentially captured, but these otherwise solitary animals are reported to continue to accompany their mother for another two to three weeks (Reeve, 1994). Since most of the young in our study area were not born until August, this dependence in capture probability is likely to have persisted until mid-October. The juveniles of 1994 turned into subadults after their first hibernation and were therefore included from the first capture round in 1995 onwards. Thus our Jolly-Seber analysis always applied to the (sub)adult population.

In order to ensure sufficient animals per test group, the capture records of two successive capture rounds were combined. RELEASE showed that males and females differed in survival rate and capture probability ($\chi^2=5.33$, d.f.= 1, $P=0.02$) and that (sub)adult males tended to have higher survival rates than females in winter ($\chi^2=3.11$, d.f.=1,

$P=0.08$). All further analyses for (sub)adult males and females were therefore conducted separately. The other RELEASE tests did not lead to the rejection of the assumptions ($P \geq 0.34$) or could not be run due to insufficient animals in the test groups, despite pooling of the capture records of two successive capture rounds.

It was highly unlikely for a marked individual to lose all of its markings and not to be recognized when recaptured. Under this assumption, the loss of the individual markings (plastic ear tag, metal ear tag, spine tubes) was recorded in 6.5, 0.8 and 0% of all recaptures respectively. Furthermore, the time needed for a capture within a section (two trapping nights) was relatively short compared to the intervals between the capture rounds (three to four weeks), satisfying the final assumption of the Jolly-Seber model.

Juveniles

The number of juveniles in 1994 was estimated using the modified Petersen estimate (Begon, 1979). The captures of the 1994 generation were divided into two groups: 1. the captures of juveniles in 1994, 2. the captures of subadults in 1995. The Petersen estimator assumes that birth and immigration do not occur, or can be neglected during the sampling period (Begon, 1979). Since all captures of 1994 were combined, it is likely that the influence of the variation of time of birth, and thus of capture probability, was strongly reduced. There was no evidence of significant immigration during the sampling period. If this should nevertheless have been the case, the juvenile population in 1994 is likely to have been overestimated.

2.6. Body weight

Until July 1995 all hedgehogs that were weighed (in 10 g units) were either caught in a trap or by hand. Starting from 10 July 1995 throughout 1996, radio-tagged hedgehogs (equal sex ratio) were also regularly weighed (see Huijser et al., 1997b). Since body weight is dependent on sex and age in many animal species (e.g., Harder & Kirkpatrick, 1994) we focused on two groups: adult males and adult females. Based on our capture data from 1994 and the individual marks of the animals, we were sure to have excluded subadults and juveniles.

The influence of sex, season (month) and year on body weight was analyzed using an ANOVA. When an animal was weighed more than once a month, only the first observation was included in the analysis. Despite the fact that it was not unusual for an individual to be weighed several months in a row, the data proved to be independent: serial correlation was virtually absent ($r=-0.038$) (program TRIM) (Pannekoek & Van Strien, 1996). In addition, the variances were equal for all variables (Bartlett's test for homogeneity of variances: sex $P=0.844$, month $P=0.105$, year $P=0.619$). Therefore we considered the use of an ANOVA appropriate.

2.7. Road crossings

Since our traps were located on both sides of the two roads that ran across the study area, we could tell when an individual had previously been seen on the other side of a road. In addition to these capture records, we used data from the telemetry study to determine the number of animals that were known to cross a road. An individual was either known to cross a road or not known to cross a road; we ignored the number of crossings per individual.

3. Results

3.1. Population size (sub)adults and juveniles

The Jolly-Seber analysis was carried out based on 37 male and 28 female marked (sub)adult hedgehogs. In October 1994 the capture probability for males was very low (Table 2). Females had low capture probabilities in June and October 1994 and in May and June 1995. The capture probability of males was higher than that of females during the summer months (June-September 1994 and May-June 1995).

The percentage of animals marked in the population increased gradually during the first four capture rounds, and then remained at least 73% for both males and females. The increase in estimated population size for both sexes during the summer months of 1994 coincided with an increasing percentage of marked individuals. In 1994 the maximum number of males and females was estimated at 21 and 28 respectively. In 1995 the maximum numbers were higher at 24 and 32.

In the summer of 1994 (from June to August) the survival (Table 3, see table 1 for dates) of males was lower than that of females. Male survival rates were lower than the

Table 2. Capture probability, percentage of marked individuals in the population and the population size estimate for (sub)adult male (N=37) and female (N=28) hedgehogs based on the Jolly-Seber analysis.

	Males				Females			
Capture round	Capture prob. (P)	% Marked indiv.	Population-size (N)	95% Conf. interval	Capture prob. (P)	% Marked indiv.	Population size (N)	95% Conf. interval
94_1	-	-	-	-	-	-	-	-
94_2	0.64	42.9	9.3	(6.0-24.1)	0.42	33.3	12.0	(5.9-30.7)
94_3	0.84	33.3	13.1	(11.0-24.1)	0.79	70.0	11.4	(9.6-13.6)
94_4	0.94	56.3	16.0	(15.1-19.3)	0.84	66.7	16.7	(14.6-19.7)
94_5	0.72	92.3	16.6	(14.0-17.4)	0.60	73.3	23.2	(16.8-28.7)
94_6	0.14	100.0	21.0	(10.4-29.6)	0.40	75.0	27.8	(16.3-40.3)
95_1	0.51	80.0	17.5	(12.7-19.0)	0.16	83.3	31.8	(12.9-65.3)
95_2	0.74	86.7	18.8	(15.9-20.0)	0.47	85.7	12.8	(9.11-13.8)
95_3	0.71	77.8	24.0	(18.5-31.2)	0.35	75.0	19.7	(11.3-28.0)
95_4	-	-	-	-	-	-	-	-

lower limit of the confidence intervals of the females. Females had a remarkably low survival probability at the end of the winter of 1994-1995 (from the beginning to the end of May 1995), although the confidence intervals of their survival rates were relatively large throughout the entire winter and early spring (from October 1994 through the end of May 1995). Their survival rate of 0.40 was lower than the lower limit of the confidence intervals for the males during that time period. Males also had reduced survival probability in winter, but they seemed to survive better than females.

In 1994 eight juveniles were captured and marked. One year later, in 1995, 16 subadults were captured. Four of these animals had already been captured and marked in 1994. Based on these numbers, the modified Petersen estimate indicated a juvenile population size of 27.2 (±9.3 SE) in 1994.

Table 3. Survival rates of (sub)adult male (N=37) and female (N=28) hedgehogs based on the Jolly-Seber analysis. The survival rate was also standardized to a 30 day period.

	Males			Females		
Capture round	Survival (Φ)	95% Conf. interval	Stand. 30 day surv.	Survival (Φ)	95% Conf. interval	Stand. 30 day surv.
94_1	-	-	-	-	-	-
94_2	0.55	(0.25-1.00)	0.69	1.00	(0.91-1.00)	1.00
94_3	0.73	(0.49-0.97)	0.71	1.00	(0.87-1.00)	1.00
94_4	1.00	(0.87-1.00)	1.00	1.00	(0.77-1.00)	1.00
94_5	1.00	(0.58-1.00)	1.00	0.99	(0.63-1.00)	0.99
94_6	0.67	(0.36-1.00)	0.94	1.00	(0.44-1.00)	1.00
95_1	1.00	(0.88-1.00)	1.00	0.40	(0.17-0.94)	0.27
95_2	1.00	(0.75-1.00)	1.00	1.00	(0.69-1.00)	1.00
95_3	-	-	-	-	-	-
95_4	-	-	-	-	-	-

3.2. *Traffic victims*

In 1994 and 1995 16 hedgehog traffic victims were found in and around the study area (Fig. 1). Since the bodies of these animals were often seriously damaged by traffic, the sex of the traffic victims could only be determined in seven cases (Table 4). Most of the traffic victims were male (N=5, 71%) and fell within the age category (sub)adults (N=14, 88%). Including the animals collected within a wider radius from the study area, we found far more male (N=41, 69%) than female (N=18, 31%) traffic victims (χ^2=8.97, d.f.=1, P=0.003).

Eight of the traffic victims were considered to be part of the (sub)adult population in the study area, five of which were found in the period that the total losses of the population were determined (Table 4 and 5). The sex of three of these victims was unknown.

According to the Jolly-Seber analysis, the total losses in the (sub)adult population amounted to 15 males and 19 females between June 1994 and June 1995; in the same period we found 1-4 male and 0-3 female traffic victims (Table 5). Traffic mortality accounted for 7-27% of total losses for male and 0-16% for female (sub)adult hedgehogs (12% for both sexes combined).

Table 4. The hedgehog traffic victims that were found in and around the study area. The individuals with a '*' following their running number were considered to be part of the study population (see text). The running numbers correspond with those in Fig. 1 indicating the location of the traffic victims.

Run. no.	Date of find	Ear tag	Sex	Age category	Run. no.	Date of find	Ear tag	Sex	Age category
1*	1-Jun-1994	-	♂	subadult	9	04-May-1995	-	?	(sub)adult
2*	23-Jul-1994	R51	♂	adult	10*	26-May-1995	-	?	subadult
3	23-Aug-1994	-	♂	adult	11*	26-May-1995	-	?	subadult
4	29-Aug-1994	-	♀	adult	12*	21-Jun-1995	R88	♀	adult
5*	30-Sep-1994	-	?	adult	13*	02-Aug-1995	R33	♂	adult
6	14-Oct-1994	-	?	juvenile	14	02-Oct-1995	-	?	(sub)adult
7	14-Oct-1994	-	?	juvenile	15*	13-Oct-1995	R61	♂	adult
8	08-Nov-1994	-	?	(sub)adult	16	14-Oct-1995	-	?	(sub)adult

The total number of traffic victims in 1994 and 1995 was 2-3 and 2-4 males and 0-1 and 1-3 females respectively. In 1994 and 1995 the highest population estimates were 21 and 24 for males and 28 and 32 for females. Hence traffic mortality accounted for a minimum of 10-14% and 8-17% of the (sub)adult male population and 0-4% and 3-9% of the (sub)adult female population in 1994 and 1995 respectively (6-9% (1994-1995) for both sexes combined).

Our capture records, data from a radio-telemetry study and encounters of hedgehogs in the field showed that many more males than females crossed one of the two paved roads in our study area (Fig. 2). The sex ratio (males:females) of the road crossing individuals was 79:21. This ratio is similar to that of the recorded traffic victims (69% male), again indicating that males ran a two to four times greater risk of becoming a traffic victim than females.

Neither of the recorded juvenile traffic victims was considered part of the population in the study area. Therefore juvenile traffic victims were not included in any calculation.

Table 5. The total losses (deaths + dispersal) based on the Jolly-Seber analysis, the traffic victims and the percentage of traffic victims in the (sub)adult male (*N*=37) (a) and female (*N*=28) (b) hedgehog population. The minimum and maximum values of the total losses and the percentage of traffic victims in the population were calculated based on the 95% confidence limits of the survival rate and estimated population size respectively (Table 2 and 3). The traffic victims placed between brackets did not occur within a period we could calculate the losses for. '?' indicates an unmarked individual with an unknown sex: these individuals are found in both the male and female panel.

a. Males

Capture round	Losses (*L*)	Min-max	Traffic victims[1]	% Traffic victims in population	Min-max
94_1	-	-	(1)	-	-
94_2	4.2	(0.0-7.0)	2	10.8	(4.1-16.7)
94_3	3.6	(0.4-6.7)	-	0.0	(0.0-0.0)
94_4	0.0	(0.0-2.1)	-	0.0	(0.0-0.0)
94_5	0.0	(0.0-7.0)	5?	6.0?	(5.7?-7.1?)
94_6	7.0	(0.0-13.4)	-	0.0	(0.0-0.0)
95_1	0.0	(0.0-2.1)	10?,11?	11.4?	(10.5?-15.7?)
95_2	0.0	(0.0-4.7)	-	0.0	(0.0-0.0)
95_3	-	-	(-)	0.0	(0.0-0.0)
95_4	-	-	(13,15)	-	
Sum	14.8	(0.4-43.0)	1-4 (excluding ())		

b. Females

Capture session	Losses (*L*)	Min-max	Traffic victims[1]	% Traffic victims in population	Min-max
94_1	-	-	(-)	-	-
94_2	0.0	(0.0-1.1)	-	0.0	(0.0-0.0)
94_3	0.0	(0.0-1.5)	-	0.0	(0.0-0.0)
94_4	0.0	(0.0-3.8)	-	0.0	(0.0-0.0)
94_5	0.2	(0.0-8.6)	5?	4.3?	(3.5?-6.0?)
94_6	0.0	(0.0-15.6)	-	0.0	(0.0-0.0)
95_1	19.1	(1.9-26.4)	10?,11?	6.3?	(3.1?-15.5?)
95_2	0.0	(0.0-4.0)	-	0	(0.0-0.0)
95_3	-	-	(12)	5.1	(3.6-8.8)
95_4	-	-	(-)	-	
Sum	19.3	(1.9-61.0)	0-3 (excluding ())		

[1] Running number according to table 4.

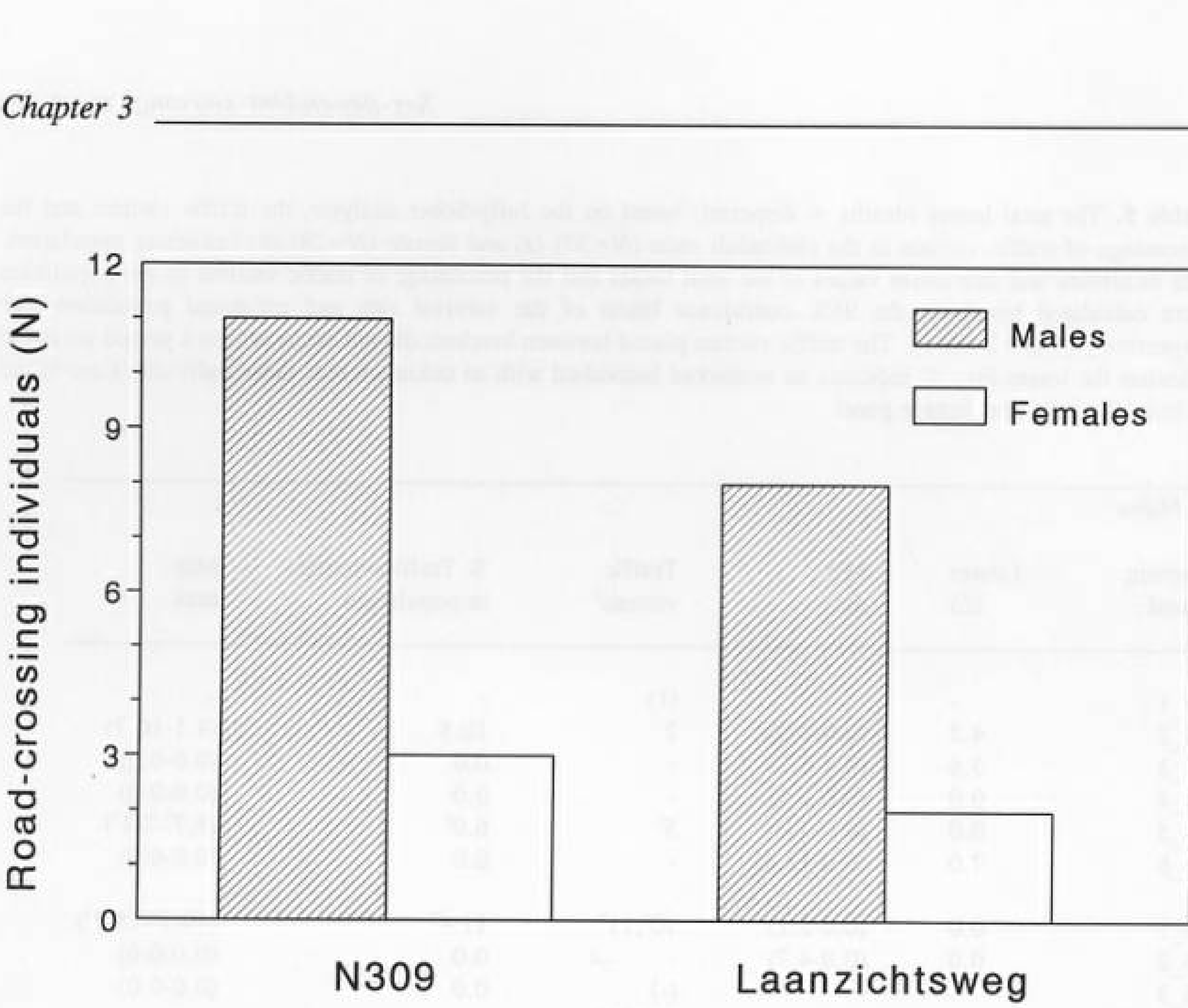

Fig. 2. The number of individual male and female (sub)adult hedgehogs that were known to cross the two paved roads within the study area.

3.3. Body weight

Male hedgehogs lost considerable weight (180 g on average, 17%) in July and August, whereas females gained some weight during the same period (Fig. 3). In August and September males and females had about equal body weights. From October to December 1995 we were not able to gather sufficient data from males. During these months females continued to gain weight until October after which a decrease followed. The animals carrying a radio-transmitter indicated that hibernation started in November-December and lasted until April-May. At the end of hibernation female hedgehogs weighed (on average) 150 g less than males

The weight measurements recorded between October and December 1995 were excluded from the ANOVA since we lacked data of males in that period (Fig. 3). A third order

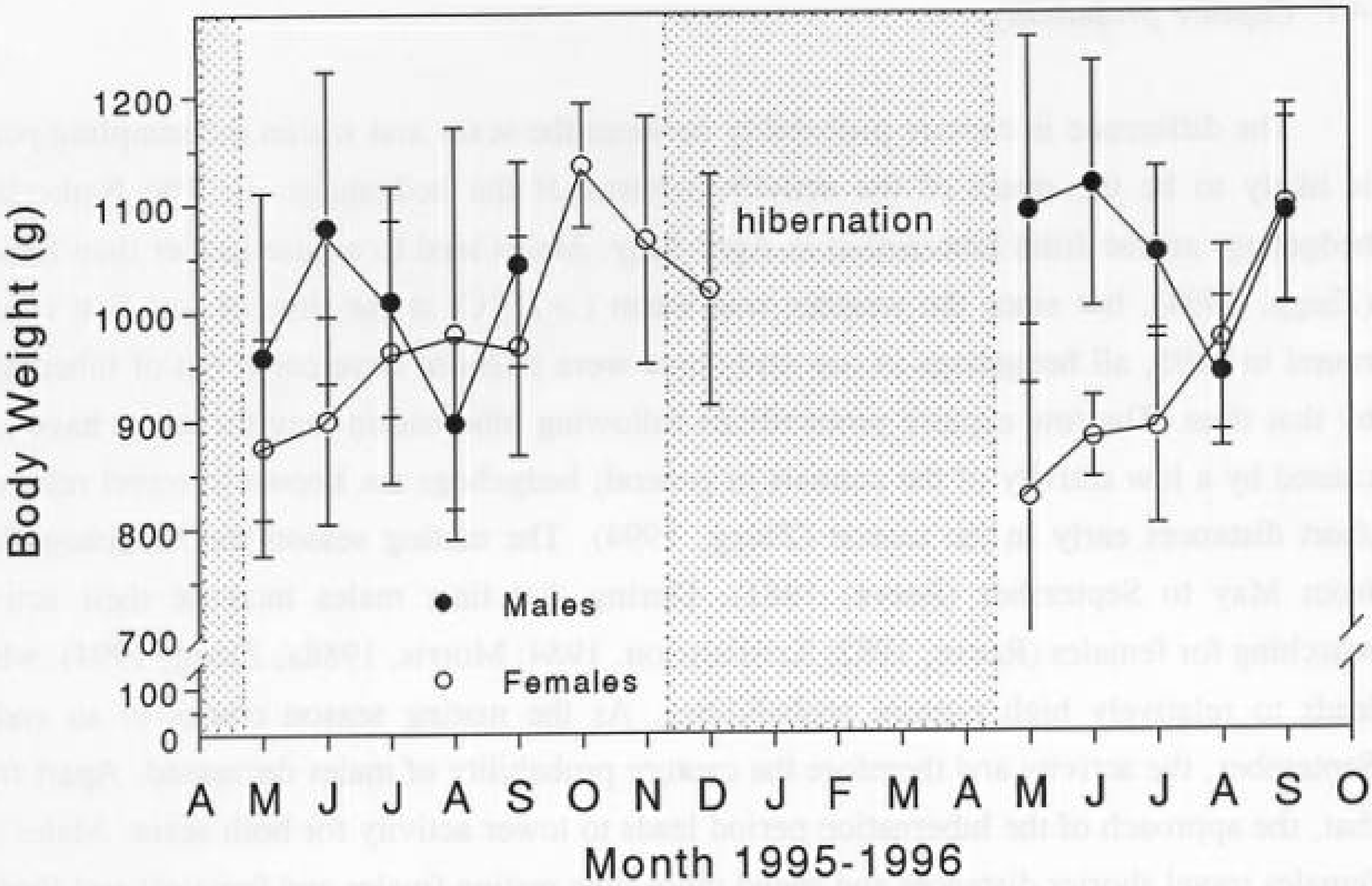

Fig. 3. Seasonal change in body weight (±SD) of adult male and adult female hedgehogs (the number of animals per dot lies between 4 and 16).

interaction (sex x month x year) proved to be absent (ANOVA: $F_{4,135}=0.972$, $P=0.425$). After suppression of this third order interaction, the interaction of sex x month (ANOVA: $F_{4,139}=5.278$, $P=0.001$) was significant whereas sex x year and month x year were not significant ($P>0.05$) (ANOVA: $F_{1,139}=3.807$, $P=0.053$ and $F_{4,139}=0.717$, $P=0.582$ respectively). A year effect could not be demonstrated (ANOVA: $F_{1,139}=1.012$, $P=0.316$). Thus hedgehog body weight is dependent on the interaction of sex and month, while a year effect seems to be absent. The explained variance was 33.2%.

4. Discussion

4.1. Capture probability

The difference in capture probability between the sexes and within the sampling period is likely to be the result of the activity patterns of the hedgehogs. In The Netherlands hedgehogs arouse from hibernation in April-May. Males tend to arouse earlier than females (Zingg, 1994), but since the weather was warm (>25°C) at the time of our first capture round in 1995, all hedgehogs in our study area were likely to have come out of hibernation by that time. The low capture probabilities following hibernation may therefore have been caused by a low activity of the animals in general; hedgehogs are known to travel relatively short distances early in the season (Zingg, 1994). The mating season for hedgehogs lasts from May to September (Reeve, 1981). During that time males increase their activity searching for females (Reeve, 1982; Kristiansson, 1984; Morris, 1988a; Zingg, 1994), which leads to relatively high capture probabilities. As the mating season comes to an end in September, the activity and therefore the capture probability of males decreased. Apart from that, the approach of the hibernation period leads to lower activity for both sexes. Males and females travel shorter distances and spend more time resting (males and females) and feeding (males) (Reeve, 1994; Zingg, 1994).

4.2. Population size and density

During the first capture rounds, population size estimates of both sexes varied, probably as a result of a low percentage of marked animals in the population, real changes in population size, and inaccuracy of the method in populations that are relatively small. The highest estimates were 24 male and 32 female (sub)adult hedgehogs (density = 37 (sub)adults 100 ha^{-1} in 1995). The highest estimate in 1994 leads to a density of 33 (sub)adult hedgehogs per 100 ha.

Since we are dealing with an open population, our population estimates do not only apply to the actual study area, but also to an adjacent zone of half the diameter of the average home range size. However, in our study area the boundary coincided with a transition from a small scale agricultural landscape into large-scale grasslands or closed pine forests in which hedgehog densities are likely to be much lower (Berthoud, 1980; 1982;

Dowie, 1987; Mulder, 1996a). It is therefore likely that a correction for a boundary effect would not significantly improve our population estimates.

The number of juveniles present in 1994 was estimated to be 27 (density = 18 juveniles 100 ha^{-1}). When this density is added to the 33 (sub)adults (1994), a total population density of 51 hedgehogs per 100 ha results for 1994. This density lies within the broad range given by other studies (which also combined juveniles and (sub)adults) in more or less similar landscapes: 25 (Doncaster, 1992), 21 and 70 in two different areas (Doncaster, 1994), 28-34 (Berthoud, 1982) and 33 (Morris, 1988a) per 100 ha.

4.3. Survival

(Sub)adult male hedgehogs had relatively low survival rates during the summer months. Unfortunately we can not distinguish between real mortality and dispersal out of the study area. However, body weight decreased with 17% on average for adult males between June and August, whereas we have no evidence for dispersal out of the study area into the less favoured habitat types of its surroundings. Furthermore, one of the radio-tagged adult males was found dead in the study area for no apparent reason other than the fact that the animal had lost 270 g (23%) of its body weight between the end of May and the end of July 1995. Traffic mortality is unlikely to be an important cause of the observed low survival probability; of the six (sub)adult males that were last seen at the time of capture round two or three in 1994, only one was reported as a traffic victim.

According to the results of the Jolly-Seber analysis, female hedgehogs had relatively low survival rates from the beginning to the end of May 1995. These animals may also have been lost during the preceding winter months since the confidence intervals of the survival rates are relatively great in both periods. Again, the losses could have been caused by either emigration or death. However, we think that females may have entered hibernation weighing less than males and may therefore have had insufficient reserves while hibernating. This hypothesis is supported by the fact that females weighed (on average) 150 g less than males by the end of winter, but this difference may also have resulted from males arousing earlier from hibernation than females (see Zingg, 1994).

4.4. Survival and mating strategy

The observed sex-dependent seasonal survival is in accordance with the present knowledge of the mating strategy of the hedgehog. Both males and females are solitary (Reeve, 1994) and non-territorial (Reeve, 1981; 1982; 1994; Boitani & Reggiani, 1984; Kristiansson, 1984). Males as well as females are known to court with different individuals of the opposite sex within a matter of days or even one night (e.g., Reeve, 1981; Kristiansson, 1984; Reeve & Morris, 1986). Up to four males have been seen competing for a female at the same time, and fighting among competing males has also been observed (see Reeve, 1994). Zingg (1994) showed that males may spent 18% (average between March and December) of their nightly time on courting behaviour, whereas for females this was only 6%. Even more marked was the difference he found in the time the animals spent on moving about (excluding feeding related movements): males 21%, females 6%. Males spend much less time feeding than females (males 43%, females 68%) with the greatest differences occurring between May and August, the same period during which the courting behaviour was recorded. Furthermore, males travel much greater distances than females, especially during the mating season. Thus it seems that males attempt to mate with as many females as possible. Not hindered by territorial boundaries their reproductive success is dependent on their ability to find fertile females at the right moment and, possibly, fighting or scaring off competitors that may also be present. However, apparently there are high energetic costs involved for successful males: adult males lose considerable weight during the mating season and the survival rates we found indicate that males may deplete their reserves to the extend that it affects their survival probability.

Although females spend most of their time feeding during the mating season, there seems to be a significant cost of reproduction for females too. Their low survival rate during or just after hibernation may result from suckling their young in late summer and autumn, leaving them little time to store sufficient fat reserves for hibernation (Palm & Stöwer, 1992). If this is indeed the case, it seems that females that have early litters would have a selective advantage. However, in our study area radio-tagged females did not give birth until late summer. Females with young in the nest (the age of the young was ten days at the most) were found between 27 July and 31 August 1995 (N=4) and 6 and 20 September 1996 (N=4). Considering the length of the mating season in this part of Europe (May-September (Reeve, 1981)), there was remarkably little variation in the time of birth within a year, but in 1995 the young were born about a month earlier than in 1996. This difference may have been caused by the fact that 1995 was characterized by a relatively warm and dry summer. Thus climatological factors may prevent females from having their litters earlier in the season. Therefore the females in our study area may have had little choice in accepting reduced survival rates during or just after hibernation.

Other discussions on survival rates (Škoudlín, 1981; Esser, 1984; Kristiansson, 1984; 1990; Morris, 1988b) did not take sex and season into account and were therefore unable to demonstrate sex- and season-dependent survival. However, Kristiansson (1984) did note the possible existence of such effects when he discussed the sex- and season-dependent changes in body weight. By ignoring these aspects, winter mortality for males may have been overestimated in previous studies.

4.5. Traffic victims

In 1994 as well as in 1995 eight hedgehog traffic victims were found in and around the study area (0.63 animals km^{-1} paved road $year^{-1}$). The landscape outside the study area was characterized by other habitat types than the small scale agricultural landscape of the study area. Only the 1 km of paved two-lane secondary road (N309) had through traffic and was fully surrounded by this type of landscape. On this road section 2-3 (1994-1995) traffic victims per km per year were found (Fig. 1). These numbers are higher than those found in other studies, but these had less chance on extreme values since they were often based on far greater road lengths and longer time periods: 1.0 on average in Bavaria (Germany) with 0.6 in agricultural or forested areas (Reichholf & Esser, 1981), 0.52-2.05 in Norfolk (Great-Britain) (Keymer et al., 1991), 1.67 in southern Sweden (Göransson et al., 1976), 1.71 in northern Spain (Garnica & Robles, 1986) and 0.3-0.8 in agricultural areas in Switzerland (Berthoud, 1980).

Most of the traffic victims were male (69%), a figure that matches the sex ratio of animals that were shown to cross one of the two paved roads, and the sex ratio of traffic victims found by Palm & Stöwer (1990). Since sex ratio seems to be equal at birth (Huijser, 1997; Reeve, 1994), the increased activity of males during the summer months is the most probable cause for the high percentage of males among traffic victims.

When the traffic victims with unknown sex are distributed over the sexes according to the sex ratio of the traffic victims with known sex, the traffic mortality within the total losses amounts to 21% for male and 5% for female (sub)adult hedgehogs. Other studies that paid attention to traffic mortality often used radio-telemetry which made it possible to determine the fate of individual animals. Reeve (1981) reported a value of 18% and Doncaster a minimum of 33% (1992) and 17% (1994) for traffic mortality when related to total mortality. In such studies losses consist of mortality only and not of a combination of mortality and dispersal. Therefore the percentage of traffic victims can be relatively high when compared to our study.

In the course of two successive seasons (1994-1995), a minimum of 13% and 14% of the males and 1% and 5% of the females in the (sub)adult population became a traffic victim in our study. Only a limited number of other studies have determined the percentage of traffic victims in relation to population size: Kristiansson (1990): 2-24%, Göransson et al. (1976): 17-22%, Esser (1984): 5-20%. Our values are relatively low, but since the relative impact of traffic mortality depends on many variables (e.g., traffic intensity, road density, composition of the landscape) which were either not reported or given in insufficient detail to enable us to correct for them or to estimate their influence, direct comparisons of the different studies remain problematic.

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CHAPTER 4

THE EFFECT OF ROADS AND TRAFFIC ON HEDGEHOG (*ERINACEUS EUROPAEUS*) POPULATIONS

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THE EFFECT OF ROADS AND TRAFFIC ON HEDGEHOG (*ERINACEUS EUROPAEUS*) POPULATIONS

Abstract - We studied the effect of roads and traffic on hedgehog population density by comparing relative densities in 15 paired road and control plots matched for landscape parameters. Relative hedgehog density was determined by means of footprints in specially designed tunnels. The relative density was closely correlated with the total number of individual hedgehogs that were caught in traps in five of the plots immediately after the tunnels were removed. A power analysis indicated that, with the resources available, we could only detect an effect greater than 35%. We were unable to demonstrate a significant effect, i.e. hedgehog density in areas adjacent to roads is not reduced by more than 35%. However, we did find about 30% fewer tracks in road plots when compared to control plots and the *P*-values were marginally insignificant at the $P \leq 0.05$ significance level. These results suggest that roads and traffic are likely to reduce hedgehog density by about 30%, which may affect the survival probability of local populations.

1. Introduction

The hedgehog (*Erinaceus europaeus* L.) is a common species in The Netherlands and it occurs throughout the country (Hoekstra, 1992; Thissen & Hollander, 1996). Hedgehogs are also frequently reported as traffic victims (see reviews in Reeve, 1994 and Huijser et al., 1998). Huijser and Bergers (1998) estimated that between 113,000 and 340,000 hedgehogs may fall victim to traffic in The Netherlands each year. These numbers may simply reflect the presence of thriving populations, but there is some debate on whether or not local populations are at risk of extinction because of traffic mortality (e.g. Reichholf, 1983; Kristiansson, 1990; Mulder, 1996a; Bergers & Nieuwenhuizen, 1999). Other studies have shown that traffic and the proximity of roads can reduce the survival probability or density of populations of several species including amphibians (Fahrig et al., 1995; Vos & Chardon, 1998), reptiles (Fowle, 1996; Rudolph et al., 1998), birds (Van der Zande et al., 1980; De Bruijn, 1994; Reijnen et al., 1995; 1996) and mammals (Rost & Bailey, 1979; Lyon, 1983; Mech et al., 1988; Lankester et al., 1991; Maehr et al., 1991).

The effects of roads and traffic on animal populations are not restricted to traffic mortality alone. Direct habitat loss and factors related to roads and traffic that may affect habitat quality or animal movements can reduce survival probability or population density too. Isolation, traffic noise, visual stimuli (e.g. lights), pollution (e.g. salt, heavy metals, nitrogen-containing compounds, herbicides), management activities in the road-side verges, increased human access, and erosion and sedimentation (especially in uneven terrain) are generally considered to have the greatest effect on habitat quality (e.g. Forman et al., 1997; Forman & Alexander, 1998; Huijser et al., 1999). The 'effect zone' of these factors is not restricted to the actual road and road-side verges. Depending on the factor concerned, the affected area may be a few metres up to several kilometres wide (Forman et al., 1997).

We aimed to investigate whether the presence of roads and traffic affects hedgehog population density, but we had no prior knowledge of the extent of a possible effect. Fortunately we did have access to data that provided us with estimates of the expected statistical properties of the response variable. Since the power of a given test depends on sample size, and since our sample size was fixed due to limited resources, we conducted a power analysis (Sokal & Rohlf, 1995; Steidl et al., 1997) before starting the study. The power analysis gave us an estimate of the effect we should still be able to detect given our sample size (for details see methods). This then led to the null hypothesis that the effect of roads and traffic on hedgehog population density is absent or smaller than 35%, whereas our alternative hypothesis was that the effect is greater than or equal to 35%.

2. Methods

2.1. General study design

The field work was carried out between May and September 1996 on 15 locations in the provinces of Gelderland and Overijssel, The Netherlands. On each location a paired comparison was made of relative hedgehog densities in areas adjacent to roads (road plots) and areas that, because of their distance from roads, were expected to suffer little or no traffic mortality (control plots) (see also Reijnen & Foppen, 1994; Nieuwenhuizen & Van Apeldoorn, 1995).

The landscape of the study sites was dominated by small scale grasslands and arable land, separated by hedgerows (usually with mature trees) and woodland fragments. In this landscape, hedgehogs have relatively high population density (Huijser, 1999) while road density is low enough to allow for suitable control plots. To ensure valid paired comparisons, road and control plots were checked for similarity in landscape parameters (see analysis).

The roads adjacent to the road plots were characterized by relatively high traffic volumes between dusk and dawn when hedgehogs are most active. During the quietest hours, traffic intensity averaged 15-20 vehicles per hour. Over a 24 h period the average intensity was 7,118 (SD=2,023) vehicles.

The road plots were located on one side of a road and were selected to ensure that there were no barriers (e.g. open water, fences, steep slopes, ribbon-development) between the roads and the road plots or on the other side of the road. The hedgerows and woodland fragments generally continued right up to the road.

2.2. Plot dimensions

The road and control plots had an elongated shape of fixed width and each pair of plots was equal in shape and size; minimum 1000 x 200 m (20 ha), but most of them were 1500 m in length (30 ha). The width of the plots and the minimum distance from a control plot to a paved road was based on the home range size of hedgehogs. Males have larger home ranges (32-47 ha) than females (10-20 ha) (Reeve, 1982; Kristiansson, 1984). Plot width was based on the animals that have the smallest home ranges (10 ha). Assuming a circular home range (which is not unreasonable, see Reeve, 1994), a radius of 180 m was calculated. Thus all animals with a home range centred within a road plot were potential traffic victims.

The distance between the road and control plots was determined by the animals with the largest home ranges (47 ha, diameter 775 m). Owing to high road densities in The Netherlands (Huijser, 1999), a distance of at least 800 m from a paved road was hard to obtain. Therefore we settled for a minimum distance of 400 m. Thus, the animals that had the centre of their home range within a control plot were, at least theoretically, not at risk of becoming a traffic victim. Nevertheless we chose a distance of at least 800 m whenever possible.

In small scale agricultural landscapes one would expect to find a density of ±30 hedgehogs per 100 ha (Huijser, 1999). Thus, in a 20 ha plot (minimum size) six hedgehogs could be expected.

2.3. Footprints and footprint tunnels

Relative hedgehog densities were determined through the presence or absence of their footprints in tunnels. We designed footprint tunnels that were light and easy to transport. A plastic board (50 x 20 cm) served as a base with two holes drilled half-way along the two longest sides at about 1 cm from the edge. Two tent-pegs stuck through these holes secured the tunnel to the ground and held a corrugated PVC roof in its place.

White paper (80 g/m^2) was attached to the plastic board. Then a 12 cm wide strip of the paper was smeared with a mixture of paraffine oil and carbon black on both sides of the tunnel (see also Lord et al., 1970; King & Edgar, 1977; Van Apeldoorn et al., 1993; Ratz, 1997; Brandjes et al., 1998). When a hedgehog entered a tunnel black footprints were left on the white paper in the middle of the tunnel. Tunnels were baited with canned dog food (beef: Saturn Petfood).

2.4. Density, location and checking of footprint tunnels

The number of footprint tunnels was set at 15 per km plot length (0.75 tunnels per ha). The tunnels were distributed throughout the plots according to a grid. However, the grid locations were not always acceptable for practical reasons. Open grasslands and arable land had to be avoided because of disturbance (cattle, people) and farming activities (mowing, etc.). In these situations the tunnels were located on the edge of a field, behind barbed wire, or along or in a ditch. Since we conducted the study in a small scale landscape the tunnels were often located along a hedgerow or a forest's edge.

We sampled each plot pair simultaneously. The tunnels were usually left in the plots for three consecutive nights. However, we settled for two nights when at least five different tunnels (road and control plot combined) had been visited by hedgehogs during the first two nights. The tunnels were checked for footprints and provided with fresh bait every day.

2.5. Analysis

An important assumption of our study design is similarity in landscape of road and control plots within a pair. We updated topographical maps in the field and then measured a number of landscape parameters in both the road and control plots (Table 1). Differences in landscape between road and control plots were not significant ($P>0.05$). However, we did find relatively low P-values for hedgerows ($P=0.06$) and forest edge ($P=0.09$). Both hedgerows and forest edge are characterized by a transition from cover to open habitat and these edges are positively selected by hedgehogs (Huijser, 1999). Thus the greater length of hedgerows in road plots may have been (partially) compensated for by more forest edge in control plots.

Table 1. Comparison of landscape parameters in road and control plots (Wilcoxon matched-pairs signed-ranks, two-tailed test).

	Road plots		Control plots			
Landscape parameter	Mean[a]	SD[a]	Mean[a]	SD[a]	P	N[b]
Agriculture (ha)	13.36	(2.90)	14.98	(3.69)	0.13	15
Forest (ha)	7.04	(4.16)	7.26	(2.70)	0.65	15
Heathland (ha)	0.45	(1.76)	0.02	(0.09)	0.32	1
Farm buildings (ha)	0.47	(0.45)	0.31	(0.34)	0.20	15
Hedgerow (km)	1.39	(0.78)	1.06	(0.50)	0.06	15
Forest edge (km)	0.97	(0.47)	1.18	(0.40)	0.09	15

[a] Means and standard deviations were based on 30 ha plot sizes.
[b] N = number of study areas in which the landscape parameter occurred.

A second assumption is that the number of tunnels in which hedgehog footprints were present reflects the actual population size (see also Stander, 1998). We checked this by capturing hedgehogs in five plots (32 ha each) during two consecutive nights, immediately after the footprint tunnels were removed. We used wooden cages that were located on the exact same spot as the footprint tunnels. The traps were also baited with dog food. The hedgehogs were individually marked by attaching coloured plastic tubes on ten adjacent spines. We analyzed the relationship between the presence of hedgehog footprints and the number of captured hedgehogs in two ways. The 'total' analysis was based on the sum of the total number of tunnels visited by hedgehogs during two or three consecutive nights. The 'different' analysis dealt with the total number of different tunnels that were visited in this period. Thus in the 'different' analysis a particular tunnel had a maximum score of 1 whereas the 'total' analysis allowed for a maximum score of 2 or 3, depending on the length of the sampling period. For both analyses the number of tunnels with hedgehog footprints was significantly correlated with the number of individual hedgehogs that were captured in the same plot (Spearman rank correlation; 'total': $r_s=0.90$, $P=0.02$, $N=5$; 'different': $r_s=0.80$, $P=0.05$, $N=5$).

We used a *t*-test to analyze the difference between road and control plots. As before we did this in two ways; the previously described 'total' and 'different' analyses. The number of tunnels in which hedgehog footprints were present was standardized to numbers per 30 ha (x) for all plots (i). Since x was zero in some cases, a small value was added before we transformed these numbers to a logarithmic scale ($\ln(x+0.03)$; 0.03 was the lowest value that occurred for x/30). We then calculated the difference between all paired road (R_i) and control (C_i) plots ($\ln(R_i)$-$\ln(C_i)$) and tested whether these values differed from zero (*t*-test, one-tailed). A *t*-test was appropriate since the difference ($\ln(R_i)$-$\ln(C_i)$) was distributed normally for both the 'total' and 'different' analysis (Kolmogorov-Smirnov; 'total': $P=0.63$; 'different': $P=0.43$).

We conducted a power analysis to indicate the size of the detectable effect with a sample size of 15 plot pairs (*t*-test, Jansen, 1991). Data from a capture-mark-recapture study of ours in a similar landscape showed a mean of 2.9 (SD=0.9) hedgehogs captured per 20 ha (Huijser et al., unpublished data). Given a significance level (α) of 0.05 (one-tailed test) and a power (π) of 90% we could only expect to detect differences of 35% or more.

3. Results

The median of the number of footprint tunnels visited by hedgehogs in road plots was lower than in the control plots (Fig. 1). Furthermore, the sum of the number of footprint tunnels visited by hedgehogs in all road plots ('total': $N=31$; 'different': $N=22$) was 32.6 and 31.3% lower than in the control plots ('total': $N=46$; 'different': $N=32$). However, the effects were not significant ($P>0.05$): 'total': $P=0.076$; 'different': $P=0.077$ (*t*-test, one tailed).

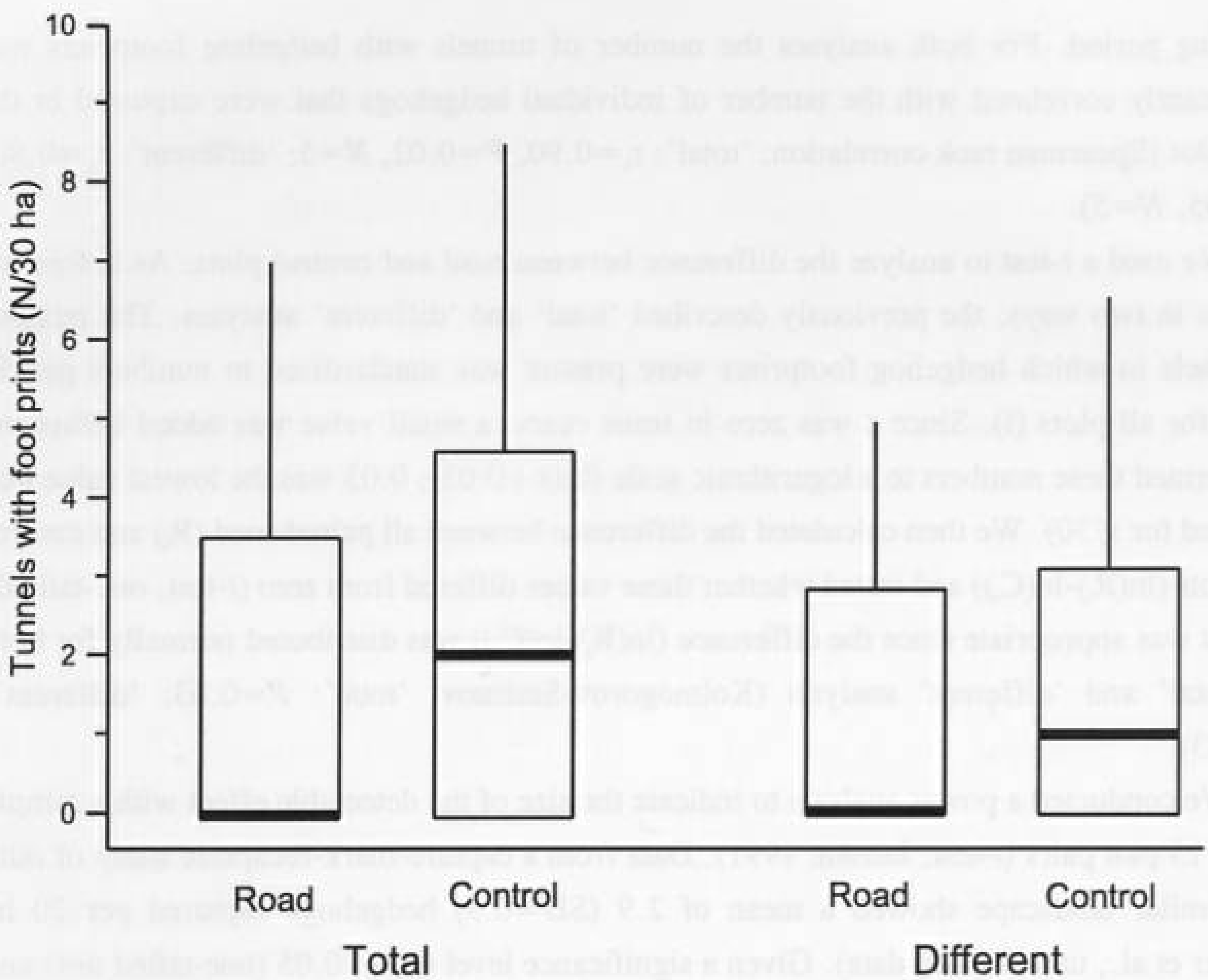

Fig. 1. The number of footprint tunnels visited by hedgehogs in road and control plots (standardized to 30 ha plot sizes). 'Total' = total number of tunnels visited during two or three sampling nights; 'Different' = number of different tunnels visited during two or three sampling nights. The boxes represent the inter-quartile range and the median is indicated by the bold horizontal line. The vertical lines at the top of the boxes extend to the largest value within 1.5 times the interquartile range (Sokal & Rohlf, 1995). In this particular case the vertical lines all reach the maximum value of the variables concerned.

4. Discussion

The power analysis indicated that we would only be able to detect an effect greater than 35%. Since we were unable to demonstrate a significant effect, we conclude that hedgehog density in areas adjacent to roads is not reduced by more than 35%. However, we did find about 30% fewer hedgehog tracks in road plots when compared to control plots and the *P*-values were close to reaching the $P \leq 0.05$ significance level ('total': $P=0.076$; 'different': $P=0.077$). These results suggest that roads and traffic are likely to affect hedgehog density by ±30%.

Although this study was designed to detect a possible effect of traffic mortality, it is important to be aware of the fact that an effect could have been obscured by proximity of some of the control plots to the road (< 800 m) and that traffic mortality could not be isolated from other road-related factors (e.g. those that affect habitat quality). Thus, a reduction in population density is not necessarily caused by traffic mortality alone. Another issue to take into account is that an effect on population density may be hidden when there is a high-overall population size (Van Horne, 1983). In years with many individuals, low quality habitats that are close to roads may also be fully occupied, and the effect of roads and traffic may be seriously underestimated (e.g. Reijnen & Foppen, 1995). However, based on the knowledge we have on the relationship between the presence of footprints in tunnels and absolute population density (Huijser et al., unpublished data) we do not think the median population density in the plots was high for the habitat concerned: seven ('total') or eight ('different') hedgehogs per 100 ha (for comparison see review in Huijser, 1999). Finally, a reduction in hedgehog density due to roads and traffic may not remain constant over the years. We are looking at a snapshot in time and road density and traffic intensity still are very much on the increase in The Netherlands (Huijser, 1999).

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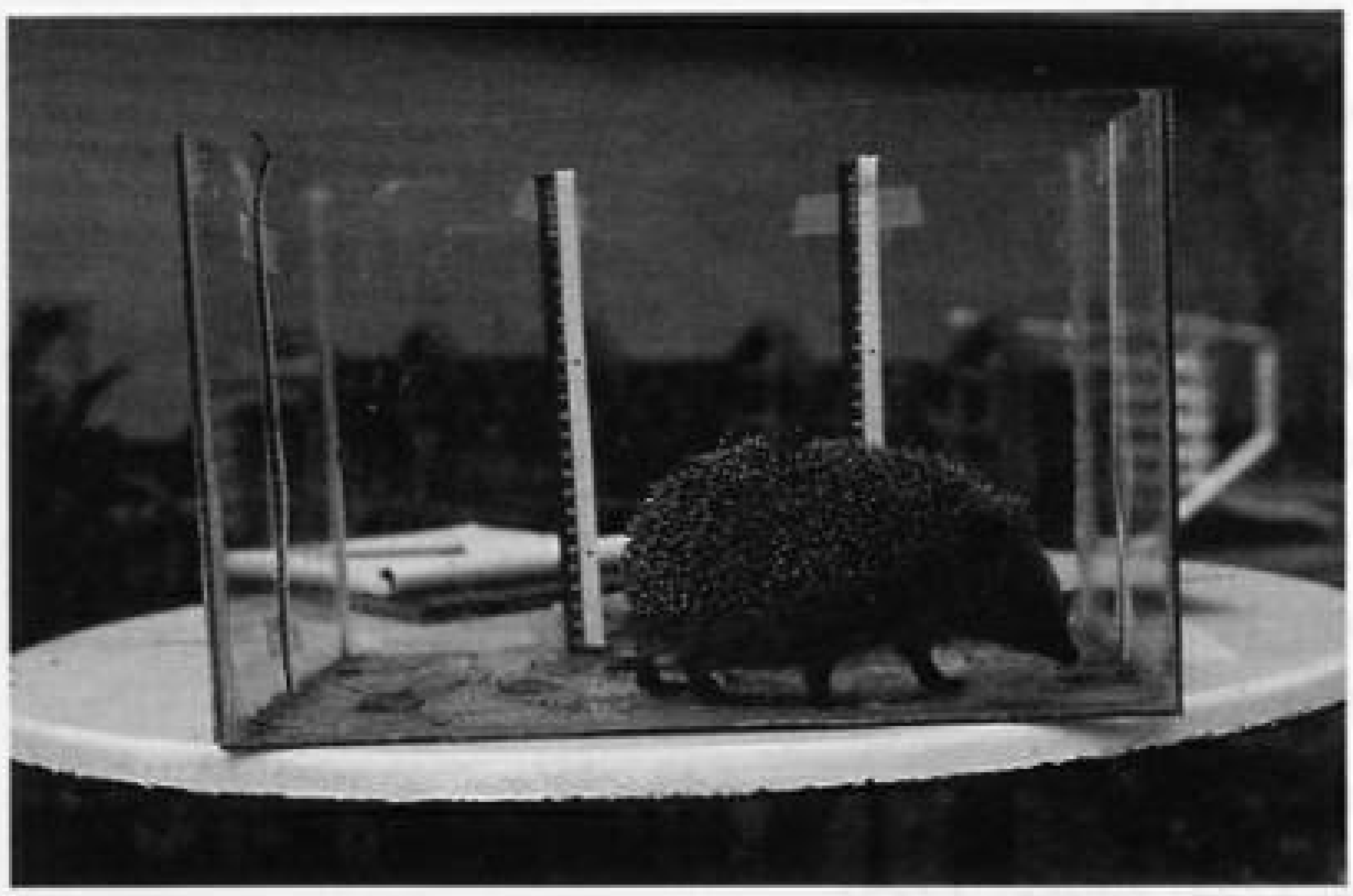
CHAPTER 5

VEHICLE CLEARANCE FROM A HEDGEHOG'S VIEW



Marcel P. Huijser
submitted

VEHICLE CLEARANCE FROM A HEDGEHOG'S VIEW

Several hundreds of thousands of hedgehogs (*Erinaceus europaeus*) become road traffic victims in The Netherlands each year (Huijser & Bergers, 1998). Their population density close to roads is affected by some 30% (Huijser & Bergers, 2000) which may reduce the survival probability of local populations. Furthermore, the casualties are easily identifiable and elicit strong public sympathy. This may explain why the behaviour of hedgehogs on roads has been a popular topic for discussion (Poduschka, 1971; Ellenberg et al., 1982; Morris, 1983; Esser, 1984; Palm & Stöwer, 1990; Hoekstra, 1992; Mulder, 1996b). Hedgehogs are usually stereotyped as slow animals that, instead of running away, freeze and crouch (Reeve, 1994) or roll up completely when a car approaches (Esser, 1984; Hoekstra, 1992). The hedgehogs that stay on the road may then not only be hit by the tyres but could also collide with the underside of the car (Zingg, 1993; Mulder, 1996b). Here it is shown that the airflow underneath and alongside a moving car is not strong enough to lift a hedgehog and have it bounce between the underside or side of a car and the road. However, many passenger vehicles have insufficient clearance and, since hedgehogs that walk are taller than when they crouch, their behaviour may influence their survival probability on a road.

Hedgehogs vary greatly in their reaction to approaching traffic (Bontadina et al., 1993; Mulder, 1996b). Although crouching is a common response, hedgehogs may run at a surprising speed when crossing a road or when a car is detected (Bontadina, 1991; Mulder, 1996b). Speeds of over 50 (Wroot, 1984) and up to 60 m/min (Reeve, 1994) have been recorded, which suggests that hedgehogs can avoid approaching cars if they choose to run. Others have shown that roads are generally avoided by hedgehogs and that they typically cross without lingering (Bontadina, 1991; Zingg, 1994).

Zingg (1993) reported hedgehog traffic victims with no apparent injuries except for broken spines, but closer examination revealed massive internal damage. He hypothesised that the low road-clearance of some cars may not allow them to pass over hedgehogs without making contact. Even with sufficient clearance, the airflow underneath or alongside a car may be strong enough to lift a hedgehog from the road surface, just as has been demonstrated for common toads (*Bufo bufo*) (Scholte, 1982). Hedgehogs may then bounce between the road and the underside or side of the car. The number of hedgehogs killed in this way could easily be underestimated since traffic victims are usually not recorded until the next morning. By that time, the tyres of the vehicles that followed would have flattened most of the already

Table 1. The height of hedgehogs and the percentage of vehicles with insufficient road-clearance. The percentage of passenger cars with insufficient clearance was calculated using the normal distribution depicted in fig. 1. It was determined for both the average height of a hedgehog and the upper limit of the accompanying 95% confidence interval.

	Height of hedgehogs (cm ± SD)		Vehicles with insufficient clearance (%) (mean-upper limit 95% C.I.)	
	Walking	Crouching	Walking	Crouching
Juveniles (N=10)	10.4 ±1.0	10.4 ±1.1	2-15%	2-17%
Subadults and adults (N=10)	13.2 ±0.8	11.9 ±0.7	26-54%	10-23%

dead or dying animals. In this study, I tested the hypothesis that hedgehogs can be killed by insufficient vehicle clearance and airflow.

Height measurements of live animals in wildlife hospitals showed that subadult and adult hedgehogs (i.e. those that survived ≥1 hibernation) were taller than juveniles (2-3 months of age), both when walking (t-test, significance level $P<0.001$) and when crouching (t-test, $P=0.002$) (Table 1). There was no indication of difference in height between the two postures for juveniles (paired t-test, $P=1.000$), but the subadults and adults were significantly taller when walking (paired t-test, $P=0.002$).

The average minimum clearance of 100 passenger cars at a used car dealer was 14.6 cm (standard deviation SD=2.1) (Fig. 1). A normal distribution (Kolmogorov-Smirnov goodness of fit test, $P=0.08$) was fitted to these data to estimate the percentage of vehicles with insufficient clearance to pass over a hedgehog (Table 1). About 26% of the vehicles may hit a walking subadult or adult of average height (Table 1). Juveniles run less risk.

In tests of the effects of airflow underneath and alongside vehicles, I used the bodies of a subadult (i.e. one that survived 1 hibernation) and an adult hedgehog (i.e. one that survived ≥2 hibernations) which had both died in a wildlife hospital. A video camera was aimed at the animals which had their bellies touching the road surface. The bodies were never lifted from the road surface when a small passenger vehicle (Ford Fiesta, model last manufactured in 1996, clearance 14 cm) passed over them with speeds between 60 and 140 km/hr. The speed was increased in four steps of 20 km and each speed was repeated five times. Although the animals were never actually lifted from the road surface, the position of

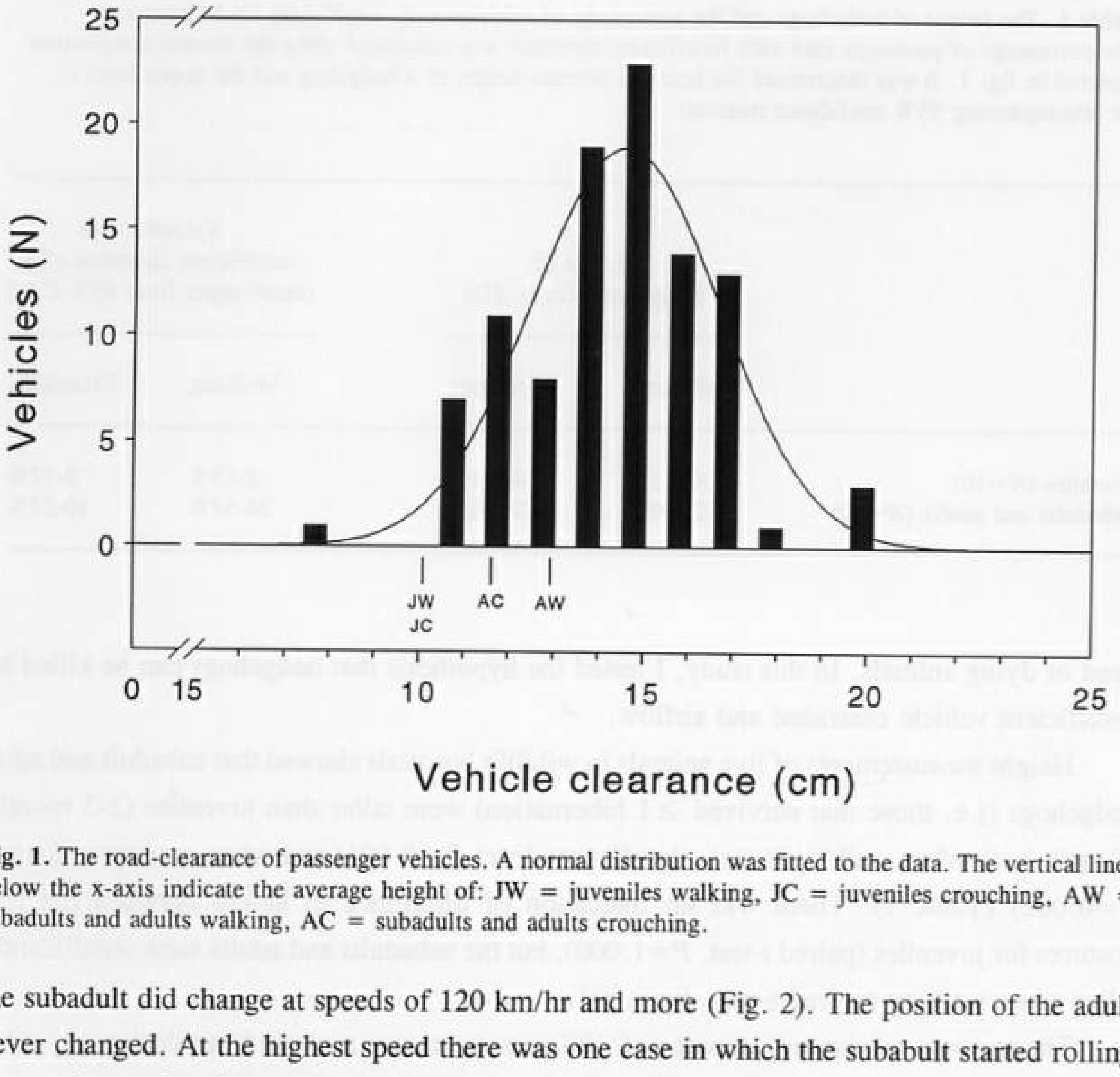


Fig. 1. The road-clearance of passenger vehicles. A normal distribution was fitted to the data. The vertical lines below the x-axis indicate the average height of: JW = juveniles walking, JC = juveniles crouching, AW = subadults and adults walking, AC = subadults and adults crouching.

the subadult did change at speeds of 120 km/hr and more (Fig. 2). The position of the adult never changed. At the highest speed there was one case in which the subabult started rolling across the surface instead of sliding. The other four runs at 140 km/hr did not result in rolling. In another test, with the vehicle not passing over the animals but just to the side of them at a distance of approximately 70 cm, no body movement was recorded at all.

The airflow underneath and alongside the car was not strong enough to lift the hedgehogs from the road surface. Although hedgehogs that walk may be more susceptible to airflow, it is unlikely that they will be bounced between the underside or side of a car and the road surface. Furthermore, the small horizontal movements that were recorded for the subadult are unlikely to result in injury in live hedgehogs. Nonetheless, many passenger cars do have insufficient clearance to drive over hedgehogs without hitting them. Vehicles that carry a heavy load will decrease the clearance even further. Due to variability in height of different sections of a car and a load that may be uneven, it also depends on chance whether some cars will really hit a hedgehog as they drive over it.

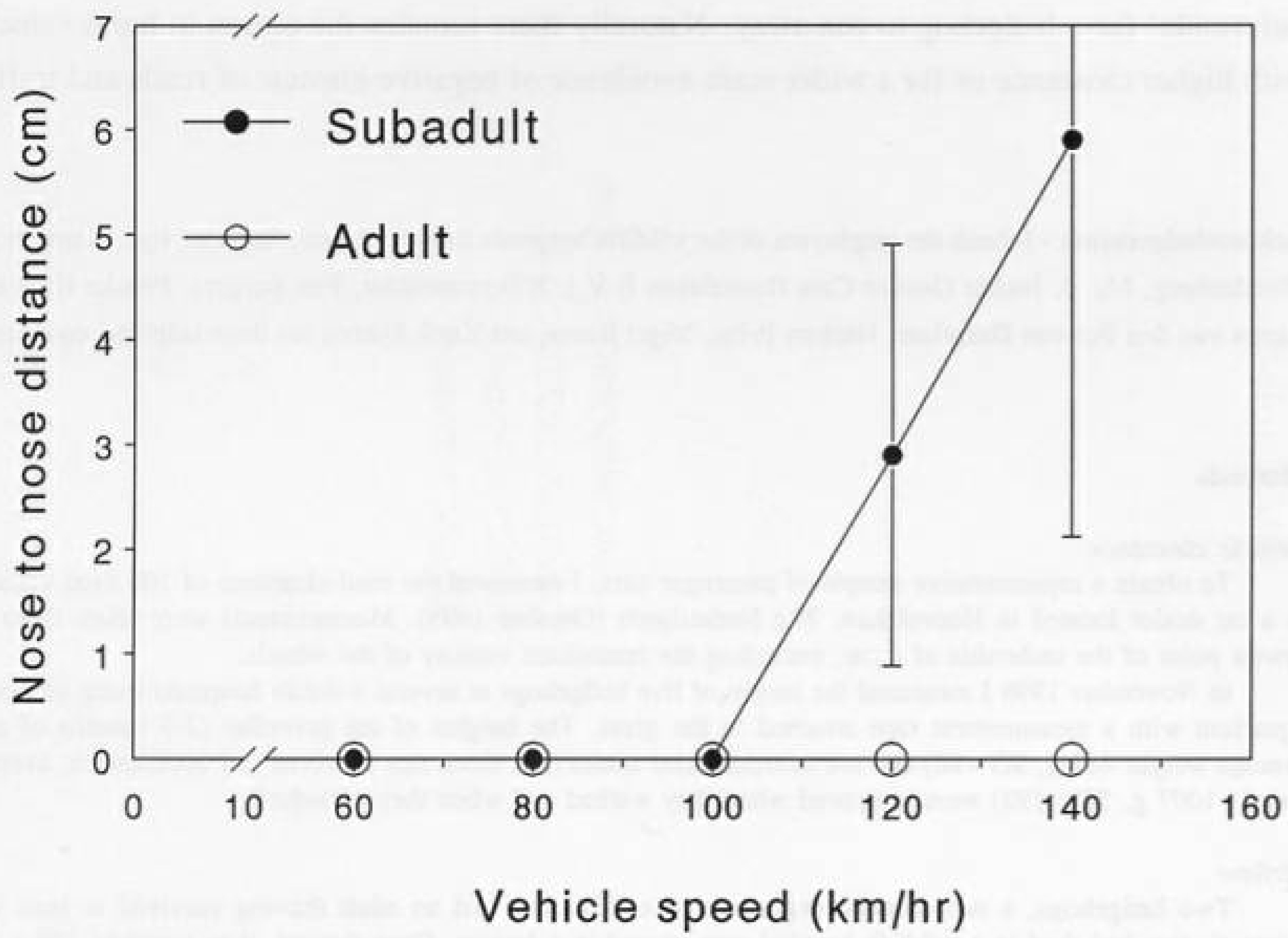


Fig. 2. Horizontal movement of a subadult and adult hedgehog as a result of airflow underneath a car. The distance (± SD) refers to the space between the original and the new position of an animal's nose after a car had past over.

Unfortunately extensive quantitative data on how hedgehogs react to an approaching car are lacking. But from the literature (Bontadina et al., 1993; Mulder, 1996b) and my own observations it is clear that their reaction may vary greatly. It seems that behaviour in such situations is largely determined by the disposition of a hedgehog that may be classified as either bold or cautious (see e.g., Verbeek, 1998). Since subadult and adult hedgehogs are relatively tall when walking, their behaviour is likely to affect their survival probability on a road. On the other hand, walking or running hedgehogs may get out of the way in time while a crouching hedgehog may be hit by a car despite its relative advantage in height. The balance between the two is unknown but it may lead to a selective advantage for one of the two behaviour types. It is likely that if many vehicles travel close together, a crouched hedgehog may never get off the road, and that it will eventually be run over. Thus, with the continuing growth in traffic intensity (Huijser, 1999) it may become more and more 'advisable' for a hedgehog to run away. Naturally there remains the option to build vehicles with higher clearance or for a wider scale avoidance of negative impacts of roads and traffic.

Acknowledgements - I thank the employees of the wildlife hospitals in Amstelveen, Bussum, Epe, Kampen and Woudenberg, Mr. J. Jonker (Jonker Cars Hoevelaken B.V.), Rijkswaterstaat, Piet Bergers, Frouke Hofstede, Agnes van den Pol-van Dasselaar, Herbert Prins, Nigel Reeve and Karlè Sýkora for their help and comments.

Methods

Vehicle clearance

To obtain a representative sample of passenger cars, I measured the road-clearance of 100 used vehicles at a car dealer located in Hoevelaken, The Netherlands (October 1998). Measurements were taken from the lowest point of the underside of a car, excluding the immediate vicinity of the wheels.

In November 1998 I measured the height of live hedgehogs at several wildlife hospitals using an empty aquarium with a measurement tape attached to the glass. The heights of ten juveniles (2-3 months of age, average weight 467 g, SD=80) and ten subadults and adults (i.e. those that survived ≥ 1 hibernation, average weight 1007 g, SD=192) were measured when they walked and when they crouched.

Airflow

Two hedgehogs, a subadult (having survived one winter) and an adult (having survived at least two winters), that had died in a wildlife hospital were stored in a freezer. Once thawed, they weighed 350 g and 850 g respectively, several hundreds of grams lighter than healthy individuals would have been in The Netherlands without additional dehydration in the freezer (Reeve, 1994). They were then used as a model for live hedgehogs, although their relatively low weights made them more susceptible to the effects of airflow than normal individuals.

On 23 April 1998 a test was performed on a newly build stretch of motorway (A4, near Delft) that was still closed to the public at that time. While the animals' bellies touched the road surface, two tight circumferences were drawn around them on the road surface with a crayon. A dot on the line indicated the position of the animals' nose. A small passenger car (Ford Fiesta, model last manufactured in 1996) was used to test whether the airflow underneath and alongside the car was strong enough to move the animals from their original position on the road. The minimum height of the car was 14 cm. The height of the subadult and adult hedgehog was 8.5 and 9.0 cm respectively. Therefore the test vehicle was not able to make contact unless the animals were lifted first. The trials started at a vehicle speed of 60 km/hr. The speed was increased in four steps of 20 km up to 140 km/hr. Each speed was repeated five times. I aimed for the animals to be precisely in the middle of the car, halfway between the tyres.

A video camera was aimed at the two hedgehogs. The camera recorded possible lift of the animals from the road surface and contacts with the body or underside of the car. After each run, the position of the animals was carefully checked. If the hedgehogs had been moved from their original position, both the nose to nose distance and the circumference to circumference distance were measured. The nose to nose distance was defined as the distance between the point on the circumference line (original position of the animal's nose) and the new position of the nose. The circumference to circumference distance referred to the shortest possible distance between the original circumference line and an imaginary one around the animal's new position.

A second test was held by passing not over, but just to the side of the animals. The distance between the wheels of the vehicle and the animals was approximately 70 cm. Shorter distances were hard to accomplish since this second test was only done at speeds of 120 and 140 km/hr (five times each).

CHAPTER 6

HABITAT USE OF HEDGEHOGS IN A SMALL SCALE AGRICULTURAL LANDSCAPE

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Submitted

HABITAT USE OF HEDGEHOGS IN A SMALL SCALE AGRICULTURAL LANDSCAPE

Abstract - We used radio tracking to study the habitat use of hedgehogs (*Erinaceus europaeus*) in a small scale agricultural landscape in The Netherlands. We investigated whether hedgerows can be used in mitigation strategies to decrease the number of hedgehog traffic victims while maintaining or increasing connectivity between populations subdivided by roads. We examined habitat selection at different spatial scales. The habitat composition of the home ranges did not differ from that of the study area, but selection was found when radio locations were examined in relation to both home range and the study area. Hedgerows received greater relative use than all other habitats. During the night hedgehogs spent about 30% of their time in hedgerows, whereas they only comprised some 10% of the study area or their home ranges. Over 60% of all day nesting sites were also found in hedgerows, mostly under bramble bushes amongst tightly packed fallen leaves. Although 53% of time spent during nocturnal activity was in grasslands, more than half of these locations were within 5 m distance from a hedgerow or a forest's edge. The results indicate that hedgerows can be used to identify risk locations and that wildlife passages can be made more effective by hedgerows oriented perpendicular to a road.

1. Introduction

The hedgehog is one of the most frequently recorded mammal species in traffic victim surveys throughout western Europe (reviews by Reeve, 1994; Mulder, 1996a; Huijser, 1999). It was estimated that between 113,000 and 340,000 hedgehogs fall victim to traffic on the Dutch roads each year (Huijser & Bergers, 1998). Furthermore, roads and traffic may reduce hedgehog population density by about 30% (Huijser & Bergers, 2000).

Fences and other physical barriers can be used to prevent hedgehogs from getting onto a road. However, apart from their effect on other species, barriers also affect the viability of hedgehog populations on either side of a road (Bergers & Nieuwenhuizen, 1999). To maintain a certain degree of connectivity between wildlife populations intersected by roads, such barriers are generally accompanied by wildlife passages (e.g., Foster & Humphrey, 1995; Clevenger & Waltho, 2000).

In recent decades hundreds of passages, ranging from pipes to ecoducts, have been put into place for various species in The Netherlands (De Vries, 1999). It is clear that wildlife passages should be located where animals are most likely to cross. The use of passages can be further increased by optimizing their dimensions and other technical features (e.g., Yanes et al., 1995; Jackson & Griffin, 1998; Philcox et al., 1999; Clevenger & Waltho, 2000), restricted human use (e.g., Clevenger & Waltho, 2000) and landscape elements that guide the animals towards or through the structure (e.g., Singer & Doherty, 1985; Broekhuizen et al., 1986; Mansergh & Scotts, 1989; Rodríguez et al., 1996; Van der Linden, 1997; Clevenger & Waltho, 2000). In addition, the area in the immediate vicinity of a passage can be made particularly attractive to animals, e.g., by making water available (e.g., Anonymous, 1997d).

Hedgehogs seem to favour edge habitat characterized by a transition of shrubs and trees to grasslands (review by Huijser, 1999). We aimed to determine if wooded landscape elements and edge habitat do indeed play a key role in the way hedgehogs move through the landscape. If this proves to be the case, possible risk locations could be identified, wildlife passages could be put into place, and the effectiveness of a passage could be increased by guiding hedgehogs towards a passage through changes in the landscape.

Hedgehogs are not only killed by collisions with vehicles, but also by management activities in road-side verges. About 22% of all hedgehog deaths in wildlife hospitals are related to unnatural injuries which include wounds inflicted through e.g., mowing activities (Reeve & Huijser, 1999). Such injuries usually occur during the day when hedgehogs are inactive and remain in a well hidden nest of fallen leaves or other material (Reeve & Morris, 1985). Direct evidence for the hazards of management activities in road-side verges comes from two hedgehogs that carried a radio-transmitter during a pilot study (L.T.J. Meuwissen, unpublished data). Both animals were found dead in a road-side verge the day after the vegetation was mowed. In order to identify risk locations for mowing and other management activities in road-side verges we also focused on nest site characteristics.

2. Study area

The study area (202 ha) was located on the estates of Schouwenburg and Zwaluwenburg near Elburg, The Netherlands (52°26'N, 5°52'E). The landscape was dominated by small scale grasslands and arable land, separated by hedgerows and woodland fragments. The hedgerows usually had both mature trees and a shrub layer. Hedgerows and woodland fragments were dominated by broad-leafed species as oak (*Quercus robur*), beech (*Fagus sylvatica*) and alder (*Alnus glutinosa*), with serviceberry (*Amelanchier lamarckii*) and rowan (*Sorbus aucuparia*) in the shrub layer. Brambles (*Rubus* spp.) were also abundant, especially along the edges. Most of the hedgerows were 10-20 m wide and had ditches on either side. It was unusual for the ditches to carry water during the summer months.

A capture-mark-recapture study had previously shown that hedgehogs occur throughout the study area (Huijser & Bergers, 1997). We produced a habitat map of the 202 ha area to determine the availability of the various habitat types. We distinguished grassland, hedgerow, forest, premises (farm buildings, houses, sheds and gardens), arable land (maize, wheat and flowers), and other (paved and gravel roads, road-side verges and water).

3. Methods

3.1. Study Animals and Study Period

In July 1995 we radio-tagged five male and five female resident adult hedgehogs (i.e. survived ≥ 2 hibernations) to study habitat selection during the night. Between 27 July and 25 October 1995 the animals were tracked for a total of 47 nights or nightly periods. In addition, we determined the location of their nest sites during the day between 18 July and 15 September 1995. We also looked for nest sites during the summer of the next season (19 April - 20 September 1996), but at that time we had radio-tagged 16 adult hedgehogs (7 males, 9 females). This study was reviewed by an ethical commission on animal experiments and was found to be in accordance with Dutch law and regulations.

Nest sites used for hibernation and breeding nests with young were treated separately from ordinary day nesting sites. Eight animals (2 adult males, 5 adult females and 1 subadult female (i.e. survived 1 hibernation, born in 1994)) carried a transmitter while in hibernation (November/December 1995 - April/May 1996). Eight adult females were found with young in the nest. At the time of discovery the young were all less than 10 days old. They were found between 27 July and 31 August 1995 (N = 4 nests) and between 6 and 20 September 1996 (N = 4 nests).

3.2. Radio Telemetry

The hedgehogs were caught in wooden box traps that were baited with canned dog food (with beef: Saturn Petfood). The traps were checked at sunrise and as soon as a radio transmitter was attached (model TW3, Biotrack, UK, frequencies between 153 and 154 Mhz, life expectancy 8 months) the animals were released. The transmitters (3.5 x 1.5 x 1.5 cm, l x w x h) were glued onto the dorsal spines, medially between the scapulae. They weighed 10.1 g (SD = 0.4) on average; <1.5% of an animal's body weight.

When the hedgehogs were tracked during the night they were initially located using a hand held receiver and antenna (customized YAESU 2M FT-290RII receiver, H-shaped antenna). Then two small plastic rods (39 x 4.5 mm (l x ϕ)) were attached with strong adhesive tape to the spines just above an animal's tail. The plastic rods (Cormoran) contained fluids that emitted light when mixed. The light could easily be spotted from a distance of 15-20 m in the dark (in open areas at even greater distances) and lasted until dawn. The lights enabled us to obtain visual locations of the animals while keeping our distance to ensure undisturbed behaviour. When an animal was tracked we determined its position at 5 minute intervals. The lights were removed at the end of a tracking session or in the course of the following day.

3.3. Habitat Selection

Each radio location was assigned to one of the six habitat types (see 'study area'). In addition we determined the distance towards the nearest hedgerow or forest's edge. The distance was measured in four 5 m intervals up to 20 m distance, and three additional categories with a wider interval: 20-30 m, 30-50 and >50 m. A final category was reserved for those locations that were in a hedgerow or forest. A few locations were just off the habitat map and were excluded from all analyses. Habitat use versus availability was investigated with compositional analysis (Aebischer et al., 1993). This analysis assumes that 1. habitat use of the study animals is independent and 2. habitat use of each individual is determined with equal accuracy. Assumption 1. holds for hedgehogs since they are solitary and non-territorial (Kristiansson, 1984; Reeve, 1994). Assumption 2. depends on the number of radio locations obtained for each animal. Since a certain degree of autocorrelation was to be expected with 5 minute intervals, and animals may differ in habitat usage, using the full number of locations from each would place too much emphasis on the most frequently observed animals. Therefore we weighted the data from individual hedgehogs by the square root of the number of radio locations in all further tests and other calculations. In total there were 1,718 and 1,735 locations available for the habitat and distance analysis respectively.

There was no significant difference in habitat use between the two sexes (MANOVA $F_{5,4} = 1.523$, $P = 0.352$). Therefore these data were combined for further analyses. Habitat use versus habitat availability was analyzed in three ways at different spatial scales. For the first analysis a minimum convex polygon was drawn around the locations of each individual. The habitat composition within these home ranges was compared to that of the study area as a whole. In the second analysis we compared the distribution of the radio locations across the habitat types with the habitat composition of the study area. The third analysis involved a comparison of the distribution of the radio locations across the habitat types with the habitat composition of the home ranges of the animals.

If a habitat type was not present within an animal's home range, or if no radio locations were recorded within a certain habitat type, the zero values were replaced by 0.01 (a trivial value) to permit the transformations required for compositional analysis. This correction was appropriate for the first and second analysis since all habitats were available in the study area as a whole but was required only for certain habitat types and a few animals. For the third analysis a different approach was needed since an artificial increase in availability of a habitat type from 0 to 0.01 would give an incorrect result. Therefore the number of habitat types was decreased to three: grassland, hedgerow and all other habitat types combined.

For the analysis of distance to a hedgerow or forest's edge, the data from both sexes were combined since they had a similar distribution over distance categories (MANOVA $F_{3,6} = 0.754$, $P = 0.559$). For this analysis the categories were regrouped into 10 m interval categories up to 20 m distance, and an additional category for distances >20 m. For one of the original distance categories (0-5 m) we determined its area within in the study area. This enabled us to determine whether this distance category was positively or negatively selected by the hedgehogs.

3.4. Nesting Sites

All three types of nesting sites were described at two different levels: 1. the previously described habitat types (see 'study area') and 2. a more detailed description of the site. The latter had the following categories: brambles (*Rubus* spp.), shrubs or young trees, grasses, pile of branches, and 'other' (e.g., pile of planks or other material on the premises surrounding farm buildings, partially-open sheds, abandoned rabbit burrow). In 1996 a third level was added to describe the nesting site. It was determined whether a hedgehog had actually made a nest of compact layers of litter (usually fallen leaves, grasses, mosses etc.), other material, or whether it lay in the open under e.g., dense shrubs or a pile of branches. It was also recorded if the nest was located in or on the slope of a ditch.

Consecutive observations of nests used for hibernation were clearly dependent. However, some animals did wake up during the winter period and chose a different site to continue their hibernation. This behaviour is not unusual (Morris, 1973; Waldhovd, 1979). To ensure independence of the data we only included observations from different individuals or those that came from different locations.

Young hedgehogs usually do not accompany their mother on foraging trips until they are at the age of 3 to 4 weeks (Reeve, 1994). Although adult female hedgehogs do leave the nest during this period, they return to suckle their young and spend the day in or close to the nest with young. Therefore the observations of a nesting site of a female with young were clearly dependent and were treated in the same way as those of hibernation sites. Male hedgehogs do not take part in rearing or protecting the young and remain solitary throughout the summer.

Ordinary day nesting sites were treated as independent observations since there were no obvious reasons for a hedgehog to return to the same site the next morning. Hedgehogs may use as many as eight different nests within a 2 week period (Reeve & Morris, 1985). However, it is not unusual for a hedgehog to return to the same site for several days in a row (Reeve & Morris, 1985). Even if a break occurs, the same site may be used again at a later time.

The descriptions of all three types of nesting sites were summarized in contingency tables (habitat type vs. a more detailed description, see above).

4. Results

4.1. Habitat Selection

Grasslands and hedgerows were the most important habitat types in the study area (Table 1). During the night hedgehogs spent about 30% of their time in hedgerows which only comprised some 10% of the study area or their home ranges (Table 1). Although they spent an additional 53% of their time on grasslands, this habitat type was used less than one would expect from its availability. The use of each of the remaining habitats was less than 5%, except for 'other'.

Habitat selection analysis showed that there was no significant difference between the habitat composition of the home ranges and that of the total study area (MANOVA $F_{5,5}$ = 1.067, P = 0.473). However, the distribution of the radio locations across the habitat types did differ from the habitat composition of the study area (MANOVA $F_{5,5}$ = 5.363, P = 0.045). Further analysis showed that the relative use of the habitats was ranked in the following order: hedgerow > grassland > other > premises > forest > arable land. Hedgerows were the most strongly selected habitat type (t-tests, 9 d.f., $P < 0.05$). Grassland was selected more strongly than premises, forest and arable land (t-tests, 9 d.f., $P < 0.05$), but there was no significant difference with 'other' ($P > 0.05$). Selection of the remaining habitat types (other, premises, forest, arable land) did not significantly differ ($P > 0.05$).

Table 1. Nocturnal habitat use of adult hedgehogs in a Dutch agricultural landscape: 1. relative distribution of the individuals ($x \pm$ SE, N = 10) across the habitat types based on the radio locations; 2. relative abundance of the habitat types within the home ranges ($x \pm$ SE, N = 10); 3. relative availability of the habitat types within the study area (202 ha).

Habitat type	1. Radio locations Mean (%)	SE	2. Home range Mean (%)	SE	3. Study area (%)
Grassland	53.0	4.8	64.6	3.0	59.1
Hedgerow	28.6	5.1	10.4	1.7	11.2
Forest	4.8	2.0	3.9	0.9	8.2
Premises	3.6	1.7	4.7	1.3	6.1
Arable land	3.4	2.3	6.5	1.8	5.1
Other	6.6	2.3	9.9	1.5	10.3

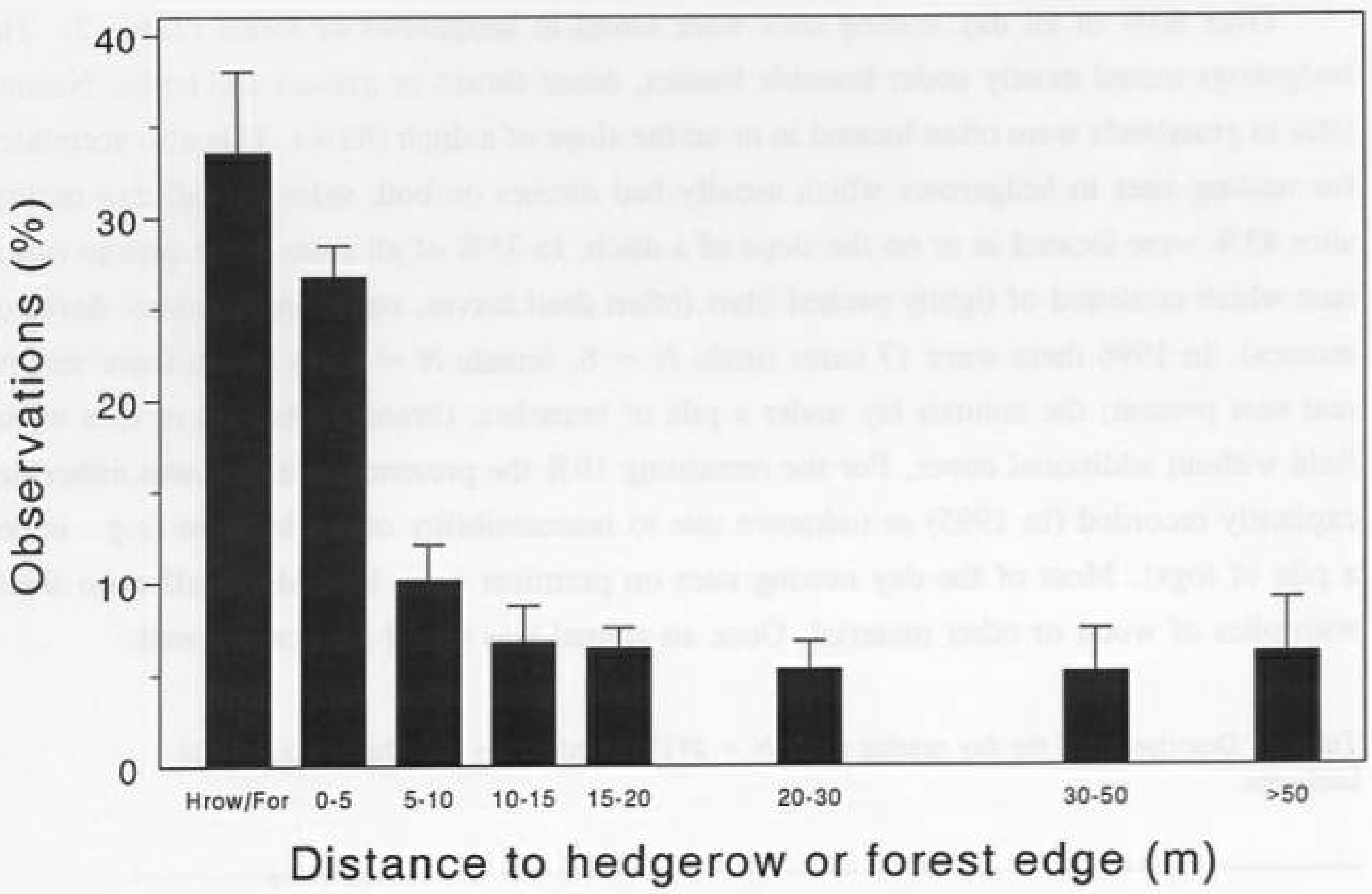

Fig. 1. The relative distribution of adult hedgehogs (N = 10, ±SE), based on the radio locations, with respect to the distance to a hedgerow or forest's edge in a Dutch agricultural landscape. Hrow/For = in a hedgerow or forest.

The distribution of the radio locations across the habitat types differed from the habitat composition of the home ranges of the animals (MANOVA $F_{2,8} = 23.296$, $P < 0.001$). The relative use of the habitats was ranked in the following order: hedgerow > grassland > other. Hedgerows were more strongly selected than grasslands and 'other' (t-tests, 9 d.f., $P < 0.01$). The selection of grasslands did not significantly differ from 'other' ($P > 0.20$).

The hedgehogs spent about 33% of their time in hedgerows or woodland fragments (Fig. 1). Once the animals left these habitat types, they usually stayed close to a hedgerow or forest's edge. Over 26% of all observations were made within the first 5 m from these edges. This was 3.8 times more than expected based on the area of the 0-5 m zone in the study area. Fewer observations occurred with increasing distance from a hedgerow or forest's edge.

4.2. Nesting Sites

Over 80% of all day nesting sites were found in hedgerows or forest (Table 2). The hedgehogs nested mostly under bramble bushes, dense shrubs or grasses and herbs. Nesting sites in grasslands were often located in or on the slope of a ditch (83%). This also accounted for nesting sites in hedgerows which usually had ditches on both sides. Of all day nesting sites 43% were located in or on the slope of a ditch. In 75% of all cases there was an actual nest which consisted of tightly packed litter (often dead leaves, sometimes grasses, herbs or mosses). In 1996 there were 17 cases (male $N = 8$, female $N = 9$) in which there was no real nest present; the animals lay under a pile of branches, (bramble) bushes or in a wheat field without additional cover. For the remaining 19% the presence of a nest was either not explicitly recorded (in 1995) or unknown due to inaccessibility of the location (e.g., under a pile of logs). Most of the day nesting sites on premises were located in half open sheds with piles of wood or other material. Once an animal was found in a cavity wall.

Table 2. Description of the day nesting sites ($N = 271$) of hedgehogs in a Dutch agricultural landscape.

	Hedgerow	Forest	Grassland	Premises	Other	Total (%)
Brambles	83	23	7	0	0	41.7
Shrubs	33	20	0	0	0	19.6
Grasses	26	7	16	0	1	18.5
Branches	18	9	1	3	0	11.4
Other	2	0	0	20	0	8.9
Total (%)	60.5	21.8	8.9	8.5	0.4	100

Only a limited sample size was available for winter nesting sites and nests with young (Tables 3 and 4). Their characteristics were similar to those of day nesting sites, except for the possibility that forest may be a relatively popular place to spend the winter for hedgehogs. The hibernation sites under grasses in hedgerows and forest consisted of a hole dug under the root system of wavy hair-grass (*Deschampsia flexuosa*). The grass nest on premises was in the centre of a tussock of pampas grass (*Cortaderia selloana*). Furthermore, one of the females and her young used an abandoned rabbit burrow.

Table 3. Description of the hibernation nesting sites (N = 15) of hedgehogs in a Dutch agricultural landscape.

	Hedgerow	Forest	Premises	Total (%)
Brambles	2	4		40.0
Shrubs	1	1		13.3
Grasses	3	1	1	33.3
Branches	1			6.7
Other			1	6.7
Total (%)	46.7	40.0	13.3	100

Table 4. Description of the breeding nest sites (N = 8) of hedgehogs in a Dutch agricultural landscape.

	Hedgerow	Forest	Total (%)
Brambles	3	1	50.0
Shrubs	1		12.5
Grasses	1		12.5
Branches		1	12.5
Other	1		12.5
Total (%)	75.0	25.0	100

5. Discussion

5.1. Habitat Selection

The hedgehogs spent much of their time during the night in hedgerows or on grasslands, particularly along hedgerows or a forest's edge. This corresponds with the findings of other habitat use studies (e.g., Esser, 1984; Zingg, 1994). Furthermore, Wroot (1984), Zingg (1994), Micol et al. (1994) and Cassini and Föger (1995) showed that grasslands are important for foraging and Esser (1984), Morris (1986) and Huijser (1999) all stressed the importance of edge habitat. Our study showed that hedgehogs may spend about 55% of their time in hedgerows and an adjacent 5 m wide zone on either side, and that they do indeed strongly select this edge habitat.

The importance of edge habitat was further illustrated by the difference in relative use between hedgerows and forest. Both habitats are characterized by woody vegetation and abundant cover, but since hedgerows are linear they differ in edge effects by definition. Other studies have also found that forests are used relatively little (review in Huijser, 1999). The same accounts for arable land. The fact that premises also received little use may seem surprising since urban areas with many gardens and parks usually have very high hedgehog densities (review in Huijser, 1999). However, Wroot (1984) and Zingg (1994) showed that urban hedgehogs spend most of their time on lawns. Urban lawns are often separated by trees and shrubs and form a dense pattern of edge habitat while most of the premises in our study area were isolated from one another. Furthermore, the greater part of the premises consisted of buildings, asphalt or other hard or bare surfaces which have little to offer to hedgehogs.

Within the heterogeneity of a small scale agricultural landscape, the habitat composition of the home range of the animals did not significantly differ from that of the study area as a whole. This may be due to the fact that most of the habitats were available throughout the area. This is particularly true for grasslands and hedgerows which were used most intensively. Furthermore, hedgehogs have home ranges that may amount to several dozens of hectares (Reeve, 1982; Kristiansson, 1984). Because the scale of heterogeneity in the study area was small, the large home ranges automatically included most of the habitat types in quantities similar to those in the study area as a whole.

5.2. Nesting Sites

The hedgehogs had their day nesting sites predominantly in hedgerows and forest which both have abundant cover. The positive selection of hedgerows may also be related to the fact that the hedgehogs spent much of their nightly time in or very close to this habitat to begin with, and that hedgerows were never far off in the morning when the animals were in need of a suitable nest site. Furthermore, the linear nature of hedgerows also ensured that they were readily available throughout the study area.

The nests were often located underneath bramble bushes which is similar to the findings of Morris (1973), Reeve and Morris (1985) and Zingg (1994). Bramble bushes were particularly abundant in and along the hedgerows and adjacent ditches, but the selection of bramble bushes may also be related to two other factors: 1. the animals are less likely to be disturbed by predators (e.g., badgers, dogs) or people, and 2. nests that are built against low lying thorny branches remain intact for longer and may also serve as a nesting site at a later time (Morris, 1973).

Many of the nests were located in or on the slope of a ditch. This may be related to the abundance of bramble bushes that grow there, but fallen leaves also tend to accumulate in these depressions. Fallen leaves are the main material for the majority of the actual nests. Cooler temperatures due to the relatively moist ground in ditches may also have been a factor. The rare instances when animals did not have a nest of compact layers of litter were all on days with hot weather (> about 25°C).

Apart from the occurrence of holes dug underneath grassroots, and possibly a stronger selection of forest as opposed to hedgerows, the hibernation sites were very similar to ordinary day nesting sites. Forests are less exposed than hedgerows and provide better protection from the elements. We did not measure how thick and tightly packed the walls of the nests were, but the hedgehogs may have put more effort into winter nests since leaf layers offer a certain degree of protection against low temperatures (Waldhovd, 1979). Nests with young did not appear to be different from ordinary day nests apart from the fact that they were larger to fit both the mother and the young.

6. Management implications

Our study showed that wooded landscape elements and edge habitat are very important for hedgehogs, both when active and resting. At night, hedgehogs spent much of their time in or along hedgerows. Since hedgerows guide the animals through the landscape we may expect a concentration of hedgehog traffic victims wherever hedgerows occur close to a road and are oriented perpendicular to it.

There are several implications for mitigation strategies. Firstly, hedgerows close and perpendicular to roads could be removed in order to reduce the number of hedgehog traffic victims. However, by doing so the barrier effect of roads would increase. This is something to be avoided since connectivity is very important to the viability of hedgehog network populations (Bergers & Nieuwenhuizen, 1999). Thus, hedgerows should only be removed if effectively functioning wildlife passages have been put into place and if the habitat loss is compensated for elsewhere (see e.g., Cuperus et al., 1999). Locations where hedgerows are oriented perpendicular to the road are of course the best places to build them. The hedgerows would then guide the animals towards the passages. New hedgerows planted next to newly built or existing passages are also an option.

Additional physical barriers will probably remain necessary since hedgehogs are not restricted to hedgerows and their immediate surroundings. Furthermore, hedgehogs may also decide to cross over the road surface rather than through or over a passage. If the physical barriers are not absolute, it is also important to design the corridor in such a way that movement is enhanced and that the animals do not stay near the road. A wider hedgerow is not necessarily a better corridor since this may then be conceived as permanent habitat (see e.g., Andreassen et al., 1996). Animals that stay close to a road with only partial physical barriers may end up as traffic victims after all. It is probably wise to have relatively narrow hedgerows close to a passage and they should be oriented perpendicular to the road. This should minimize the time that hedgehogs are close to traffic.

It is important to be aware of the possible presence of hedgehogs in nests when conducting management activities in the road side verges. The mowing or cutting of bramble bushes and the clearing of ditches filled with fallen leaves are particularly dangerous to hedgehogs at all times of the year. Mowing, cutting and clearing activities could be reduced to an absolute minimum. Alternatively, the road-side verges could be divided into sections that are mowed or cleared at different times. This would spread the risk of killing or injuring hedgehogs.

Naturally, changes in the landscape should carefully be evaluated before they are carried out. Hedgerows may be used in mitigation strategies in landscapes that are dominated by humans already, such as agricultural areas. However, great caution should be taken in relatively undisturbed landscapes or areas of special conservation interest; such areas may require very different mitigation strategies.

Hedgerows have been shown to be important to the movement of a range of species including mammals (e.g., Taylor, 1978; Bennett, 1990; Verboom & Huitema, 1997; Bright, 1998), birds (e.g., Wegner & Merriam, 1979; St. Clair et al., 1998), amphibians (e.g., Vos, 1999), reptiles (e.g., Durner & Gates, 1993) and insects (e.g., Gruttke, 1994; Charrier et al., 1997; Tischendorf et al., 1998). However, when changes in the landscape are considered for hedgehogs, care must be taken that no serious side effects occur for other species. The changes should always be based on an integrated approach.

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CHAPTER 7

ROAD, TRAFFIC AND LANDSCAPE CHARACTERISTICS OF HEDGEHOG TRAFFIC VICTIM SITES

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Submitted

ROAD, TRAFFIC AND LANDSCAPE CHARACTERISTICS OF HEDGEHOG TRAFFIC VICTIM SITES

Abstract - Wildlife traffic mortality needs to be reduced because of human safety and property damage issues as well as the prevention of mass wildlife mortality and negative effects on the population level. Since physical barriers lead to further fragmentation of the remaining wildlife populations, fences are often combined with wildlife passages. Here we investigate whether certain road, traffic and landscape characteristics are associated with hedgehog (*Erinaceus europaeus*) traffic victim sites and whether wildlife passages can be made more effective through changes in the landscape.

Hedgehog traffic victims, although widely dispersed along roads, were not randomly distributed along 20 monitoring routes (514.5 km and 942 victims in total) located throughout The Netherlands. Wide roads and street lights were associated with fewer victims, probably because of an increased barrier effect. Forests and urban areas had more victims than agricultural areas, salt marshes or open sand dunes. When hedgerows, a forest's edge, a row of trees or urban green are present adjacent to a road, 36-47% more victims can be expected compared to when these elements are at least 100 m away from the road. Grass verges also led to an increase in traffic victims. If linear elements such as hedgerows, a forest's edge, or grass verges are oriented perpendicular to a road, 20-27% more victims are expected to occur compared to a situation where these elements are oriented in a more parallel way. Arable land and moorland resulted in fewer victims.

Our study suggests that existing and new wildlife passages can be made more effective for hedgehogs when their location in the landscape is considered. Their use can further be increased through changes in the landscape that guide animals towards a passage and keep them away from the road at sections between passages.

1. Introduction

Roads and the vehicles that travel on them are known to have many negative impacts on ecosystems, animal populations, and individuals (see reviews by Forman & Alexander, 1998; Trombulak & Frisell, 2000). Over the past decades greatest attention has been given to the most visible and direct effect of infrastructure: wildlife mortality from collision with vehicles. Most of the studies focus on road mitigation measures for animal species that either have large body sizes or those that are rare. This is often based on human safety and property damage issues (e.g., Groot Bruinderink & Hazebroek, 1996; Putman, 1997; Wu, 1998) and on the possible local, regional or absolute extinction of the species concerned (e.g., Mansergh & Scotts, 1989; Van der Zee et al., 1992; Foster & Humphrey, 1995). Currently, a growing number of mitigation and compensation efforts address direct mortality as well as habitat loss, habitat degradation and population isolation, and tend to have a multi-species or ecosystem approach (cf. Cuperus et al., 1999; Clevenger & Waltho, 2000). However, the measures taken remain based on our current knowledge of how individual species interact with their environment and with infrastructure in particular. Species that require special attention in the multi-species or ecosystem approach are not just those that are rare already. High casualty rates or reduced population density should be avoided, mitigated or compensated for, regardless of whether population viability is seriously affected.

In western Europe, the hedgehog (*Erinaceus europaeus*) is not a threatened species and is likely to have benefited from human induced changes in the landscape (Huijser, 1999). Nevertheless, hedgehog traffic victims are common throughout the species' range (see reviews by Reeve, 1994; Huijser, 1999) and an estimated 113,000 - 340,000 individuals die on the Dutch roads annually (Huijser & Bergers, 1998). Furthermore, roads and traffic may reduce their population density by an estimated 30% (Huijser & Bergers, 2000). Thus high mortality rates combined with possible effects on hedgehog populations call for measures that reduce the negative effects of roads and traffic, and particularly traffic mortality.

In The Netherlands, the density of paved roads averages 3.38 km per km^2 land. This figure is much lower for most other countries: Russia 0.02, Australia 0.05, United States 0.43, United Kingdom 1.54, France 1.64, Denmark 1.68, Germany 1.86, Japan 2.29, but Belgium 4.74 (Anonymous, 1999). Traffic intensity in The Netherlands is high too, with an estimated 7,319,000 motor vehicles using a total of 116,093 km of paved roads (Anonymous, 2000). In this region both road density and traffic intensity have shown a strong and consistent increase over the past decades (Huijser, 1999). Since it is unlikely that road density and traffic volume will stabilize or decrease in the near future, efforts tend to focus on mitigation and compensation measures (see e.g., Cuperus et al., 1999). Hedgehog traffic victims are usually widely scattered over several kilometres or more (Smit & Meijer, 1999). The absence or rarity of clear mortality hot spots makes it difficult to reduce casualties through the construction of a limited number of wildlife passages alone. Additional measures that would guide the animals towards the passages and keep them from getting onto the road between passages remain necessary.

In this study we investigated whether certain road, traffic and landscape characteristics were associated with hedgehog traffic victim sites. We were especially interested in landscape features that may guide animal movements to or away from the roadway. This information is needed to determine the most appropriate location of new wildlife passages, increase the use of existing passages, and reduce the animals' access to roads in areas between passages (cf. Finder et al., 1999). Such changes in the landscape would then lead to reduced traffic mortality while increasing connectivity between populations on either side of the road and so help to ensure viable populations (see Bergers & Nieuwenhuizen, 1999).

2. Methods

2.1. Monitoring routes

Volunteers and road maintenance crews gathered data on the location of hedgehog traffic victims (*N* = 942) along 20 monitoring routes during 1995, 1996 and 1997 (Table 1). The routes were located throughout The Netherlands and included 514.5 km of motorways, secondary roads, and country roads (Table 2). The location of the victims was determined

Table 1. Frequency distribution of the number of hedgehog traffic victims per 100 m road length.

	Hedgehogs (*N*)	100 m road length units (*N*)
	0	4,391
	1	632
	2	93
	3	18
	4	5
	5	3
	6	1
	7	1
	22	1
Total	942	5,145

Table 2. The length of the monitoring routes, the number of reported hedgehog traffic victims, and their distribution across three road classes.

Road class	Routes (*N*)	Route length (km) Median	Min-max	Total	Victims (*N*) Median	Min-max	Total
All road types (km)	20	25.3	6.3-68.8	514.5	31	12-157	942
Motorways (km)	4	24.1	9.1-50.9	108.2	29.5	7-63	129
Secondary roads (km)	18	20.9	5.1-37.2	377.8	26.5	12-157	762
Country roads (km)	3	10.7	6.6-11.2	28.5	12	8-31	51

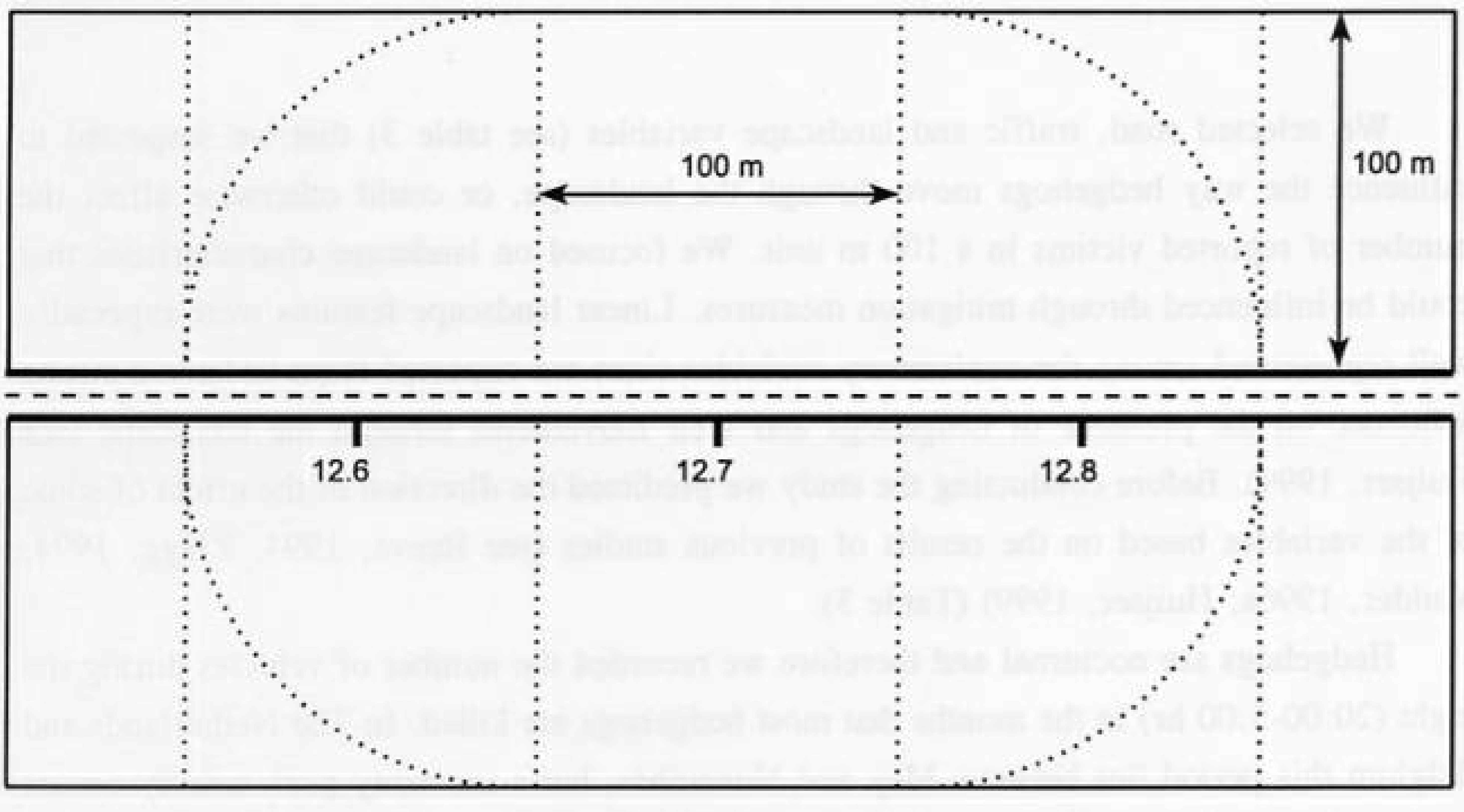

Fig. 1. A hypothetical example of a road stretch with hectometre sign posts, the 100 m road length units in which hedgehog traffic victims were recorded, and a 100 m wide zone and a 100 m radius on either side of the road in which road, traffic and landscape variables were determined (see text).

with 100 m accuracy. In most cases the description of the location was based on the hectometre sign posts that are present along all major roads (see fig. 1).

Between September and December 1997 we visited all 100 m road length units (N = 5,145) to determine road, traffic and landscape characteristics. A road length unit started and ended halfway between the hectometre sign posts (Fig. 1). Landscape characteristics were measured in sections that extended up to 100 m from both sides of each road length unit. Thus a section measured 100 m by 200 m plus the road width (see fig. 1). The 100 m zone on both sides of a road is a fraction of the radius of a hedgehog home range (males = 319-387 m, females = 178-252 m) and should be relevant to hedgehogs approaching a road (Reeve, 1982; Kristiansson, 1984). In case certain road or landscape features were nearby but not present within a section, we also examined the two adjacent sections with a 100 m radius (measured from the edge of the pavement at the beginning or end of a road length unit) as a maximum (see later).

2.2. Road, traffic and landscape characteristics

We selected road, traffic and landscape variables (see table 3) that we suspected to influence the way hedgehogs move through the landscape, or could otherwise affect the number of reported victims in a 100 m unit. We focused on landscape characteristics that could be influenced through mitigation measures. Linear landscape features were especially well represented among the explanatory variables since we expected them to have a strong influence on the presence of hedgehogs and their movements through the landscape (see Huijser, 1999). Before conducting the study we predicted the direction of the effect of some of the variables based on the results of previous studies (see Reeve, 1994; Zingg, 1994; Mulder, 1996a; Huijser, 1999) (Table 3).

Hedgehogs are nocturnal and therefore we recorded the number of vehicles during the night (20:00-5:00 hr) in the months that most hedgehogs are killed. In The Netherlands and Belgium this period lies between May and November, but a mortality peak usually occurs between June and August (Huijser & Bergers, 1998; Holsbeek et al., 1999; Smit & Meijer, 1999). Along with the width of a road and central verge, we expected traffic intensity to have an influence on the number of traffic victims, but we were uncertain of the direction of the possible effect. Wide and busy roads with potential foraging habitat between the lanes are

Table 3. Road, traffic and landscape variables that were recorded in each section. P = the presence of a habitat type or landscape element (0/1), D = distance to road (m), Q = quantity (% for both sides combined along a 100 m road length unit), O = perpendicular orientation (0/1), W = width (m), S = presence of shrub layer (0/1), L = length (see text and fig. 1 for further explanation).

Variable	Description and expected direction of effect						
VEHICLES	Vehicles ($N^?$) between 20:00-5:00 hr						
WIDTH	Width of road ($m^?$)						
CENTRAL_VERGE	Width of central verge ($m^?$)						
PASSAGE	Presence of non-inundated over- or under passage ($0^+/1^-$)						
LANDSCAPE	Landscape type* 1. salt marshes$^?$, 2. open coastal dunes$^?$, 3. heathland and inland sand dunes$^-$, 4. agricultural lands$^?$, 5. forest and woodland$^?$, and 6. urban areas$^+$.						
FOREST	Presence of forest or woodland ($0^?/1^?$)						
FOREST_TYPE	Deciduous, pine or mixed forest ($1^+/2^-/3^?$)						
FOREST_SHRUB	Presence of shrub layer in forest ($0^-/1^+$)						
GRASS	Meadow or pasture	$P^?$	$D^?$	$Q^?$			
LIGHTS	Street lights	$P^?$	$D^?$	$Q^?$	$O^?$		
GRASS_VERGE	Grass verge, width is sum of both sides	$P^?$	$D^?$	$Q^?$	$O^?$	$W^?$	
ORCHARD	Orchard	P^+	D^-	Q^+			
GREEN	Urban green, garden or premises	P^+	D^-	Q^+			
DITCH	Ditch or shore of water body	P^+	D^-	Q^+	O^+		
FOREST_EDGE	Forest edge, W > 20 m or L:W < 10:1	P^+	D^-	Q^+	O^+		
TREE_LINE	Line of trees	P^+	D^-	Q^+	O^+		
HEDGEROW	Hedgerows, width ≤20 m and L:W ≥ 10:1	P^+	D^-	Q^+	O^+	W^+	S^+
ARABLE	Arable land, horticulture, tree nursery	P^-	D^+	Q^-			
HEATH	Heathland	P^-	D^+	Q^-			
FENCE	Fine mesh fence, barrier to hedgehogs	P^-	D^+	Q^-	O^+		
WATER	Water (> 3 m wide)	P^-	D^+	Q^-	O^+		
ROAD	Other hard surfaced road	$P^?$	$D^?$	$Q^?$	O^+		
RAILROAD	Railroad	$P^?$	$D^?$	$Q^?$	O^+		

$^+$ = increase in victims expected if feature is present or increases.
$^-$ = decrease in victims expected if feature is present or increases.
$^?$ = direction of possible effect is unknown, or was not determined before the study.
* = The list only includes the landscape types that were encountered.

more risky to a crossing or foraging hedgehog (more victims), but the traffic intensity, width of a road and the open habitat may also keep the animals from even trying (fewer victims). Furthermore, hedgehogs are known to use several types of non-inundated under- and overpasses (see review by De Vries, 1999) and the presence of such structures may lead to fewer traffic victims. However, it is important to note that we included all possible passages, and not just those that were put in place and designed for wildlife, or hedgehogs in specific.

We determined the effect of landscape characteristics at two levels: 1. through a classification of major landscape types (LANDSCAPE), and 2. through a range of landscape features present (FOREST through RAILROAD) (Table 3). The size of forest (FOREST) could influence the number of traffic victims. Forests typically have low hedgehog density, but forest edges seem to be positively selected and could lead to more victims (see review by Huijser, 1999). The presence of forest is not restricted to within the major landscape type (LANDSCAPE). In our study a forest (FOREST) could also be a forest fragment in an agricultural landscape. In order to be classified as a forest landscape (LANDSCAPE), the trees and shrubs had to cover over 50% of a section, and at least one of the two adjacent sections also had to qualify as a forest landscape. Apart from possible differences in food availability between deciduous and pine forests, leaves of deciduous trees are the most important material for hedgehog nests which are often located under bramble bushes (*Rubus spp.*) (Reeve & Morris, 1985; Zingg, 1994). Therefore deciduous forests and the presence of a shrub layer may increase the number of traffic victims.

We also measured several aspects of landscape features that were divided into P, D, Q, O, W and S variables (see table 3). The presence of a landscape feature (a P variable) corresponds to its presence in the section concerned, or to its presence in one of the adjacent sections within a 100 m radius from the edge of the original section (see fig. 1). The distance (a D variable) was measured with an optical range finder (Ranging, Bushnell TLR 75, Overland Park, Kansas, USA) and relates to the minimum distance from the landscape feature to the edge of the road surface. If the landscape feature was only present in one of the adjacent sections, the minimum distance was measured from the edge of the road surface of the original section, with the 100 m radius as a maximum. If the landscape element was not present there either, the distance was set at 101 m. Quantity (a Q variable) was defined as the percentage of the 2 x 100 m road length that a landscape feature could be present on either side of a road length unit. A perpendicular orientation (an O variable) of a linear landscape feature corresponded to it lying at a 45-90° angle from the road. The landscape feature had to be present in the section concerned or in one of the adjacent sections within a 100 m radius of the original section. The width and shrub variables (W and S variables) are self explanatory. Finally, it is important to note that the values of the P, D, O, W and S variables were not only influenced by the situation in the road section concerned, but also by the two adjacent sections. The same applied to the PASSAGE, FOREST, FOREST_TYPE and FOREST_SHRUB variables.

Grassland is an important foraging habitat for hedgehogs. However, extensive grasslands seem to be avoided and grass verges may not be attractive because of the nearby road and disturbance from it. This makes it hard to predict the direction of their possible effect. The same accounts for street lights that may either attract ground dwelling invertebrates and foraging hedgehogs, or could deter them. Orchards, urban green, ditches, forest edges, lines of trees and hedgerows are usually positively selected by hedgehogs and the direction of their expected effect is clearly positive (see Reeve, 1994; Zingg, 1994; Mulder, 1996a; Huijser, 1999). Arable land and heathland are avoided, and barriers such as fences and wide water bodies can be expected to keep hedgehogs from getting onto or close to the road. On the other hand, barriers (FENCE, WATER, ROAD, RAILROAD) that are oriented perpendicular to a road may force the animals towards the road and could lead to an increase in victims. It is unclear what the effect would be of the presence, distance and quantity of a railroad or another road since they may either form a death-trap (more victims), or they could prevent hedgehogs from reaching the road (fewer victims).

2.3. Analyses

The data were hierarchical with the 20 monitoring routes at the first, and the 5,145 sections at the second level. The response variable, the number of recorded hedgehog traffic victims in a section, was non-normally distributed and had many zero values (see table 1). Therefore the data were analyzed with a quasi-Poisson loglinear mixed model (Schall, 1991; Breslow & Clayton, 1993; Engel & Keen, 1994). 'Quasi' refers to the fact that the model does not use the Poisson distribution itself, but only the property that the variance is proportional to the mean. Because in our data the response variable had predominantly 0 and 1 values, the constant of proportionality was hard to determine and therefore set to zero, the value it takes in the Poisson distribution. The model accounted for the hierarchical structure of the data by including 'route number' as an extra random factor. This factor corrected for differences between routes and observers. The analysis was carried out using the GENSTAT procedure IRREML (Iteratively Reweighted Residual Maximum Likelihood) (Anonymous, 1993b; Engel & Keen, 1994; Keen, 1996; Engel, 1997).

The number of recorded hedgehog traffic victims in a section was expected to be proportional to the frequency a monitoring route was sampled and the relative chance of finding victims in the period concerned. This chance was derived from the seasonal distribution of the victims, see Huijser and Bergers (1998). The relationship was accounted for in the IRREML analysis by defining the sum of the logarithms of the frequency variable and the chance variable as an offset variable (an offset variable is an explanatory variable with a regression coefficient of 1).

There was one extreme value for y (22 victims recorded in the same 100 m road length unit, see table 1). To prevent this section from having a very substantial impact on the results we changed this value to 10 victims, which was still higher than all other values of y.

The VEHICLES, WIDTH, CENTRAL_VERGE, and all D, Q and W variables were first transformed to their natural logarithm ($\ln(x+1)$). Prior to the analysis we checked for variables that were strongly correlated ($r \geq 0.80$ or $r \leq -0.80$) since they could hide each other's effect. So that correlation coefficients could be calculated, all factor variables were split into 0/1-variables. WIDTH and CENTRAL_VERGE, P_FOREST_EDGE and FOREST, P_FOREST_EDGE and DECIDUOUS (FOREST_TYPE), P_HEDGEROW and W_HEDGEROW, P_FENCE and O_FENCE, and the vast majority of all P and Q variables were strongly positively correlated. Most of the P and D variables and the D and Q variables had strongly negative coefficients. These strong correlations were partly due to extreme values (e.g., P=0 then Q=0, or P=0 then D=101, or Q=0 then D=101), and not based on a true correlation over the full range.

Because of the correlations, and a software-dictated maximum number of variables, we conducted a number of separate analyses on different levels for just the main effects. However, three forced variables (VEHICLES, WIDTH and PASSAGE) were included in all analyses to allow for a better estimate of the influence of landscape features. We excluded CENTRAL_VERGE from the analyses since the width of the central verge was strongly correlated to the total width of a road (WIDTH).

We conducted six types of analyses. The type 1 analyses consisted of a series of separate analyses for the effect of a. VEHICLES, b. WIDTH, c. PASSAGE, d. LANDSCAPE, e. FOREST, and f. the combined effect of the P, D, Q, O, W and S variables concerning a particular landscape feature (Wald tests). Thus these type 1 analyses did not take the possible effects of the other, excluded, landscape features into account. However, the analyses always included the three, or the two remaining, forced variables. Furthermore, we only determined whether an effect was present for the combined P, D, Q, O, W and S variables. We did not calculate the direction and magnitude of the effect since we expected the P, D, Q, O, W and S variables to differ in direction and to hide each other's individual effect due to strong correlations. This did not apply to the forced variables, LANDSCAPE and FOREST for which we not only determined whether an effect was present, but also the direction and magnitude. Since LANDSCAPE is a factor variable we expressed the effect relative to a 'standard' for which we selected the most frequently recorded category: agricultural lands.

Analysis 2 concerned an analysis for all P variables combined. First we determined whether the presence of a certain landscape feature had an effect on the number of victims, given the presence of absence of the other landscape features (Wald tests). If an effect was present, the direction and magnitude were then calculated. Analyses 3 and 4 are similar to 2, but they were for the distance (D) and quantity (Q) variables respectively. Analysis 5 determined the effect of the perpendicular orientation of linear landscape features to the road given the presence of that feature and the orientation of the other landscape features.

Type 6 analyses consisted of a group of separate analyses customized for the variables concerned. We determined the effect of forest type (FOREST_TYPE) given the presence of forest, but since forest type is a factor variable we expressed the effect relative to a 'standard': deciduous forest. The remaining type 6 analyses concerned the effect of a. the presence of shrubs in a forest (FOREST_SHRUB) given the presence of forest, b. the presence of shrubs in a hedgerow (S_HEDGEROW) given the presence of a hedgerow, c. the width of a hedgerow (W_HEDGEROW) given the presence of a hedgerow, and d. the width of a grass verge (W_GRASS_VERGE) given the presence of a grass verge.

3. Results

Traffic intensity and the presence of passages did not have a significant effect on the number of hedgehog traffic victims in a section (Table 4). However, wide roads had relatively few victims: roads twice as wide had 19% fewer victims. Landscape type also had a considerable effect (Tables 4 and 5). Far more victims occurred in forests (+96%) and urban areas (+32%) than in agricultural areas. On the other hand, open sand dunes had very few victims (-70%) compared to agricultural lands. The same applied to salt marshes and heathland but for these landscapes the differences were not significant. However,

Table 4. The effect of individual variables (corrected for the 'forced variables') on the expected number of hedgehog traffic victims based on type 1 and 6 analyses (see methods). If an effect was demonstrated (two-tailed Wald test, * = $P \leq 0.05$, ** = $P \leq 0.01$, ns = not significant) the direction and magnitude of the effect (including 95% confidence interval (CI)) are also shown. The effect is expressed as a multiplication factor for the expected number of victims when 1. the variable concerned is present, or 2. the variable concerned doubles in value. If the effect is <1 then fewer victims are found, if the effect is >1 then more victims are found.

	Sign.	Effect	95% CI
VEHICLES	ns		
WIDTH	**	0.81	0.71-0.91
PASSAGE	ns		
LANDSCAPE	**	see table 5	
FOREST	**	1.39	1.19-1.62
FOREST_TYPE[a]	**	see table 5	
FOREST_SHRUB[a]	ns		
S_HEDGEROW[b]	**	1.94	1.25-3.00
W_HEDGEROW[b]	*	1.13	1.03-1.25
W_GRASS_VERGE[c]	ns		

[a] = given the presence of forest.
[b] = given the presence of a hedgerow.
[c] = given the presence of a grass verge.
Note: A one-tailed Wald test (see hypotheses in table 3) did not result in more variables reaching the $P = 0.05$ significance level.

significantly fewer victims occurred in salt marshes and open dunes compared to forests and urban areas.

The presence of forest or forest fragments led to a 39% increase in hedgehog traffic victims (Table 4). Far fewer victims occurred in or close to pine forests than in or close to deciduous or mixed forest (Table 5). Mixed forest had the highest casualty numbers. In contrast to the presence of shrubs in hedgerows (+94%), the occurrence of shrubs in forests did not have a significant effect (Table 4). Furthermore, hedgerows that were twice as wide resulted in more victims (+13%), but we could not demonstrate an effect of an increase in grass verge width.

Table 5. The effect of landscape- and forest type (corrected for the 'forced variables') on the expected number of hedgehog traffic victims based on type 1 and 6 analyses (see methods). The effect is expressed as a multiplication factor for the expected number of victims in the landscape or forest type concerned compared to agricultural land or deciduous forest (two-tailed Wald test, * = $P \leq 0.05$, ns = not significant). If the effect is <1 then fewer victims are found, if the effect is >1 then more victims are found. We also determined whether the effect of the landscape- and forest types differed from landscape- or forest types other than agricultural lands or deciduous forest.

	Effect compared to agricultural land or forest	Sign.	Significant difference (*) with other types
Landscape type			
1 Salt marshes	0.24	ns	5,6
2 Open dunes	0.30	*	5,6
3 Heathland	<0.01	ns	
5 Forest	1.96	*	1,2,6
6 Urban areas	1.32	*	1,2,5
Forest type			
2 Pine forest[a]	0.39	*	3
3 Mixed forest[a]	1.50	*	2

[a] = given the presence of forest.
Note: For heathland a one-tailed Wald test (see hypotheses in table 3) did not result in reaching the $P = 0.05$ significance level.

There was no effect of any of the orchard, grassland and ditch variables on the number of hedgehog traffic victims (Table 6). Heathland, streetlights and arable land were all associated with fewer victims. The presence of arable land resulted in 13% fewer in victims. When arable land was located twice as far from a road 11% more victims occurred, whereas a two fold increase in quantity of this land use type resulted in 4% fewer victims. Similar effects were found for the distance of heathland and the distance and the quantity of streetlights.

Landscape features that were expected to function as barriers (fences, water, railroads, roads) only had a limited effect on the number of hedgehog traffic victims. Fences had no demonstrable effect at all, and although the combined water variables did, none could be shown for the individual presence, distance, quantity or orientation variables that were

Table 6. The effect of the combined variables for a certain landscape feature (corrected for the 'forced variables') on the expected number of hedgehog traffic victims based on type 1 analyses (see methods) and the effect of the presence (P), distance (D), quantity (Q) and perpendicular orientation (O) of a landscape feature given the presence, distance, quantity or orientation of the other landscape features (corrected for the 'forced variables') based on type 2, 3, 4 and 5 analyses respectively. The results of the type 1 analyses are indicated by * = $P \leq 0.05$, ** = $P \leq 0.01$ or ns = not significant (two-tailed Wald tests). - = non-existent parameter. If an effect was found (two-tailed Wald tests, $P \leq 0.05$) for a type 2 through 5 analysis the magnitude and direction were determined, including the accompanying 95% confidence interval (CI). The magnitude of the effects is expressed as a multiplication factor for the expected number of victims when the variable concerned is present (P and O variables) or doubled (D and Q variables). If the effect is <1 then fewer victims are found, if the effect is >1 then more victims are found.

	Anal. 1	Anal. 2 (P-var.)		Anal. 3 (D-var.)		Anal. 4 (Q-var.)		Anal. 5 (O-var.)[1]	
	Sign.	Eff.	95% CI	Eff.	95% CI	Eff.	95% CI	Eff.	95% CI
ORCHARD	ns	ns		ns		ns		-	
GRASS	ns	ns		ns		ns		-	
DITCH	ns	ns		ns		ns		ns	
HEATH	*	ns		1.89[2]	0.88-4.04	ns		-	
LIGHTS	**	ns		1.06	1.02-1.09	0.96	0.94-0.99	ns	
ARABLE	**	0.87[2]	0.73-1.02	1.11	1.05-1.17	0.96	0.93-0.98	-	
FENCE	ns	ns		ns		ns		ns	
WATER	**	ns		ns		ns		ns	
RAILROAD	ns	ns		ns		ns		2.40[2]	0.90-6.35
ROAD	**	ns		ns		1.03	1.00-1.06	0.58	0.44-0.76
HEDGEROW	**	1.36	1.17-1.58	0.89	0.86-0.93	1.06	1.04-1.09	1.20	1.01-1.44
FOREST_EDGE	**	1.40	1.20-1.63	0.90	0.86-0.94	1.07	1.03-1.11	1.26	1.11-1.92
TREE_LINE	**	1.41	1.20-1.65	0.93	0.90-0.97	1.04	1.02-1.07	ns	
GREEN	**	1.47	1.26-1.71	0.91	0.87-0.95	1.08	1.05-1.11	-	
GRASS_VERGE	**	5.91	1.40-24.86	0.82	0.71-0.94	1.21	1.07-1.36	1.27	1.01-1.58

[1] Given the presence of the landscape feature concerned.
[2] Based on a one-tailed Wald test (see hypotheses in table 3).

corrected for the possible influence of other landscape features. At locations where a railroad was oriented perpendicular to a road we found 140% more victims than in situations where a railroad had a more parallel orientation. However, this was only significant with a one-tailed test and the accompanying confidence interval is relatively wide. There was a slight positive effect of an increase in the quantity of roads while a perpendicular orientation of an intersecting road led to considerable fewer victims.

The presence, vicinity and an increase in quantity of hedgerows, forest edge, lines of trees, premises, urban green, and grass verges all had a positive effect on the number of hedgehog traffic victims. The same applied to a perpendicular orientation of hedgerows, forest edge and grass verges, but we did not find a significant effect for tree lines. The presence of grass verges had a very strong effect, but the accompanying 95% confidence interval was very wide.

4. Discussion

4.1. Road and traffic characteristics

One might logically expect a positive association between traffic intensity and the number of traffic victims. However, traffic intensity on the Dutch roads is high (Huijser, 1999) and mortality may no longer increase above a certain threshold (Clarke et al., 1998), which may have confounded a possible association in our study. Another factor to consider is that the disturbance from noise could have deterred hedgehogs and discouraged them from crossing. Some individuals crouch or run away as a response to approaching traffic (Bontadina et al., 1993; Mulder, 1996b) which indicates that high traffic volumes may indeed increase the barrier effect of a road. The relationship between traffic volume and traffic victims is often unclear (e.g., Case, 1978; Rolley & Lehman, 1992; Groot Bruinderink & Hazebroek, 1996), but positive correlations have been found for the proportion of dead amphibians (Fahrig et al., 1995) and the number of killed armadillos (*Dasypus novemcinctus*) (Inbar & Mayer, 1999) as well as white-tailed deer (*Odocoileus virginianus*) (Allen & McCullough, 1976).

Wide roads have fewer hedgehog traffic victims than narrow roads, which suggests that hedgehogs perceive a road as a barrier (cf. Oxley et al., 1974; Mader, 1984). Thus, hedgehogs seem less likely to cross this potentially hostile habitat when it is wide. This is supported by the fact that hard surfaced roads are generally avoided by hedgehogs (Bontadina, 1991; Zingg, 1994) and that they cross wide roads more quickly than narrow ones (Bontadina, 1991). The slight rise in numbers of victims as the quantity of other roads close to the monitoring routes increased may have been caused by more and wider grass verges which attract hedgehogs (see later). A perpendicular orientation of railroads did lead to more victims, but this could have been due to either a true barrier effect of the railroad or the possible selection of the vegetation in the railroad verges by hedgehogs.

The presence of non-inundated passages did not reduce the number of traffic victims. However, we included all possible under- and overpasses which were not necessarily located in the best place for wildlife, or hedgehogs in particular. Furthermore the dimensions and other technical aspects such as a hard and barren concrete surface were not optimized for wildlife, and we did not correct for possible barriers between the passage and the surrounding landscape. Other studies have shown that hedgehogs use a variety of passage types (see review by De Vries, 1999), but fences or other barriers along road edges between passages probably remain necessary to obtain a strong reduction in mortality.

We could not demonstrate a barrier effect of fences. This could well be related to the close correlation of the presence of fine mesh fences and the presence of perpendicularly orientated fences for which we expected the effect to be opposite. Furthermore, many of the fences were only placed parallel to the road for a very short distance. They were mostly used to fence off a garden or a small parcel of land and were not erected to prevent wildlife from getting onto the roads.

Our study showed that street lights increased the barrier effect of a road and that they should preferably be absent or turned off close to hedgehog or other wildlife passages to enhance connectivity. This is contrary to the findings of Bontadina (1991) who could only demonstrate avoidance of street lights for one of his study animals while the other hedgehogs seemed indifferent.

4.2. Landscape, land use and vegetation characteristics

The abundance of hedgehog traffic victims in the various landscape types matches our knowledge of hedgehog population density and road mortality in a range of landscape types (see review by Huijser, 1999). Hedgehogs reach higher population densities in urban areas with parks and gardens than in any other habitat. The presence of trees and shrubs combined with a transition to a more open habitat is also associated with high densities. Large scale forests with little edge habitat have relatively low hedgehog population density. However, in our study the presence of forest as a landscape feature was strongly correlated with the occurrence of a forest edge which may explain why mortality was so high in forested areas.

As expected, deciduous forests had more traffic victims than pine forests. We could have expected an intermediate position of mixed forests, but instead they had the highest mortality. One of the possible explanations is that the mixed forests tended to have large areas compared to deciduous forests as most of the very small and isolated forest fragments in an otherwise agricultural environment consisted of deciduous trees. Here isolation may have been more important than the presence of edge habitat. Finally, in contrast to hedgerows, there was no positive effect of a shrub layer in forests. This may be related to the availability of suitable nest sites or foraging opportunities in the litter layer. Fallen leaves are more abundant in forests than in hedgerows but a shrub layer in hedgerows may enhance their accumulation. Naturally, the shrubs themselves also provide shelter.

Typical edge habitat landscape features (hedgerows, forest edges, lines of trees) were all associated with a strong increase in hedgehog traffic victims. The same is true for urban green areas which are often a matrix of edge habitat. A grass verge can be seen as a small scale grassland which is an important foraging habitat for hedgehogs (e.g., Zingg, 1994). However, we did not distinguish between large and small scale grasslands along the monitoring routes which may explain why we could not demonstrate a significant effect of this land use type.

Most of the orchards along our monitoring routes were fenced off which explains the absence of an effect on the number of hedgehog traffic victims. Ditches did not seem to influence the number of road-kills either, but the data had a very skewed distribution with respect to this variable because most roads had ditches on both sides. Heathland and arable land are not normally favoured habitats for hedgehogs and, as expected, had fewer traffic victims. Although water had an effect too, we could not determine the direction and whether it was based on the presence, distance, quantity or perpendicular orientation or a combination of these variables.

4.3. Mitigation measures

Hedgehog traffic victims are widely dispersed (Smit & Meijer, 1999), but we found them to be non-randomly distributed with respect to landscape characteristics. Some landscape elements were associated with many victims, others with relatively few. The presence and orientation of most of the landscape features had a much greater effect than their distance or quantity. The presence of relatively small amounts of certain landscape features was enough to increase the chance of hedgehogs ending up as traffic victims on a nearby road.

It is clear that wildlife passages for hedgehogs have greatest chance of being successful when they are located close to or in areas with urban green, forests, forest edges, hedgerows or lines of trees. Furthermore, new wildlife passages should carefully be positioned with respect to existing landscape features. Passages that lie in the path of a hedgerow, forest edge or grass verge that abuts the road are likely to be used more than passages that have arable or open land on either side, and no adjacent wooded elements. Street lights, or any other lights, should preferably be absent or turned off in the direct vicinity of a passage.

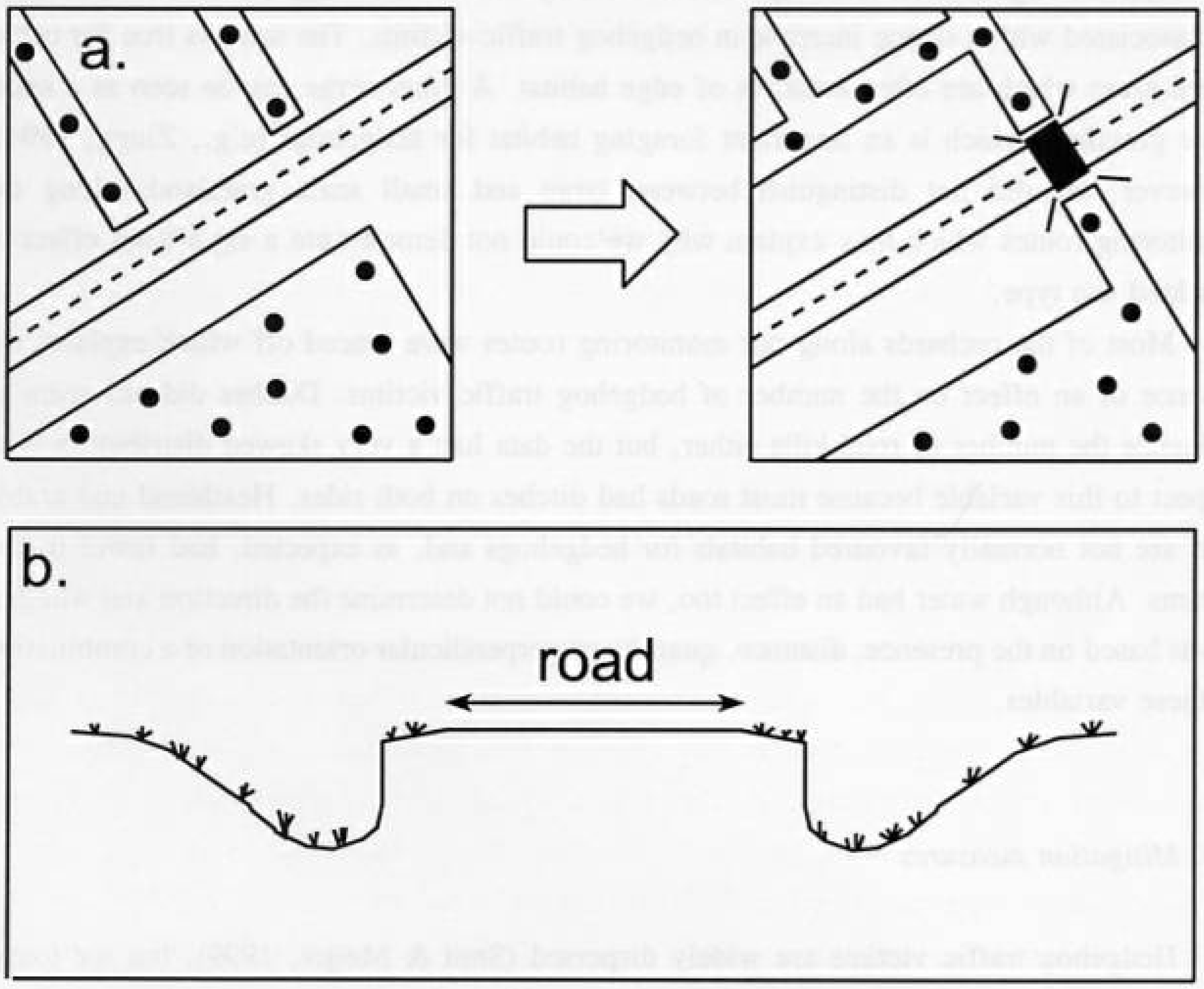

Fig. 2. a. Schematic changes in the landscape which would reduce the number of hedgehog traffic victims while maintaining connectivity between populations on either side of a road. The hedgerows and forest edge guide the animals towards a passage while the arable land keeps them from coming close to a road at sections between passages. b. A cross section of a road and its verges with a barrier integrated into the ditches that run parallel to the road.

Existing or new wildlife passages can be made more effective by minor modifications to the landscape in areas adjacent to a road. In this study we used a 100 m wide zone for our analyses, but possibly changes in the landscape do not necessarily relate to the same width. A detailed habitat use study showed that in a small scale agricultural landscape, hedgehogs were found mainly in hedgerows (29% of all observations) or in an adjacent 5 m wide zone (an additional 26%) (Huijser, Buitenkamp, Dulos and Lips, unpublished data). Certain landscape elements such as hedgerows, a forest edge or grass verges can guide hedgehogs towards a passage, while other features such as arable land or heathland, and possibly also large scale grasslands, will help to keep the hedgehogs away from the road at sections between passages (Fig. 2a). Nevertheless, wildlife passages combined with changes in the landscape are unlikely to be enough to obtain a strong reduction in traffic mortality. Physical barriers between the road and the surrounding landscape will probably remain necessary. Fences are costly, require constant maintenance, and deface the landscape in some situations (Foster & Humphrey, 1995; Boarman & Sazaki, 1996; Janssen et al., 1997; Putman, 1997). Relatively low barriers from concrete that are on the same level as the road on the road side and have a steep drop-off at the other (Fig. 2b), are probably cheaper, require less maintenance and do not stand out in the landscape. A design of this type would also allow animals to get off the road if they happened to get on it despite all efforts. Such barriers could also be integrated into existing ditches that run parallel to most roads.

4.4 Mitigation and compensation considerations

Changes in the landscape surrounding roads should be carefully evaluated before they are carried out. In landscapes that have already received heavy human impact (e.g., agricultural areas) landscape changes may be an option, whereas relatively undisturbed areas should preferably be left intact. Furthermore, physical barriers should never be erected without the presence of wildlife passages that have proven to be effective (see e.g., Putman, 1997). Whether a passage is effective is usually measured in terms of frequency of use. However, a few individuals that live close to a road, and have adapted to the passages, may well be responsible for the vast majority of the crossings while dispersers who are new in the area may decide not to use them. Thus the mere frequency of use does not necessarily translate into a species' ability to colonize or recolonize areas at relatively great distances on the other side of a road. Finally, care must be taken that landscape changes, physical barriers, and passages designed for hedgehogs do not adversely affect other species and that the mitigation measures are based on an integrated approach that improves the situation for a wide range of species.

Landscape changes that increase the barrier effect of a road at sections between passages create a new problem because of the habitat loss or decrease in habitat quality. These effects should then be compensated for elsewhere (cf. Cuperus et al., 1999). However, even then there remain other negative effects of existing roads and traffic such as: reduced habitat quality because of e.g., disturbance through noise (Reijnen et al., 1995), disruption of the physical environment, alteration of the chemical environment, spread of exotic species, and changes in human use of land and water (see review by Trombulak & Frisell, 2000). More drastic measures such as elevating roads or putting them under ground over long distances would solve some of these problems and reduce others. Such measures may seem very costly, but they could be restricted to the most intensively used roads under the condition that traffic on the other, relatively small, roads is strongly reduced, or that small roads are closed or removed altogether (cf. Bagley, 1998; Walder & Bagley, 1999). Although elevated or underground roads may confront us with new problems (e.g., hydrology), they would eliminate negative interactions of different species that use the relatively few and narrow passages. In case of the hedgehog narrow pipes may not be used in areas where badgers (*Meles meles*) are also present and leave their scent in the tunnels (Doncaster, 1999). Badgers are a potential predator of hedgehogs, and hedgehogs have been shown to avoid sites tainted with badger odour (Ward et al., 1997). It is likely that many other inter-species interactions exist (e.g., Clevenger & Waltho, 1999; 2000), but very few have yet been identified.

A final consideration is that wildlife passages and physical barriers require regular checking and maintenance. To prevent gradual neglect, these activities should be fully integrated into road- and road side verge maintenance schedules.

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CHAPTER 8

GENERAL DISCUSSION

GENERAL DISCUSSION

1. Introduction

In The Netherlands, traffic intensity and road density have shown a strong and consistent increase over the past decades (chapter 1, fig. 2). The construction, presence and use of roads and other infrastructure has many negative impacts on ecosystems and individual species (see reviews by Forman & Alexander, 1998; Van der Grift, 1999; Trombulak & Frisell, 2000). Apart from human safety and property damage issues (e.g., Groot Bruinderink & Hazebroek, 1996; Wu 1998), animal traffic victims are the most visible and direct effect and they result in demands for measures that reduce this mortality. However, when wildlife traffic mortality is addressed it is important to specify what effect one wishes to avoid, mitigate or compensate for (see Cuperus et al., 1999). This study focused on the hedgehog (*Erinaceus europaeus*), the most frequently recorded mammal species in traffic victim surveys throughout western Europe (e.g., Holsbeek et al., 1999; Smit & Meijer, 1999), and determined the effects on three different levels: individuals, populations, and the species.

2. Effects on individuals

Observations from volunteers and road maintenance crews showed that hedgehog traffic deaths occur throughout The Netherlands (Huijser & Bergers, 1998). According to the literature, the number of recorded hedgehog victims per km road length per year varies between 0.3 and 2.9 (chapter 1, table 1). Huijser and Bergers (1998) estimated that 113,000-340,000 hedgehogs fall victim to traffic on the Dutch roads each year. However, this study also concluded that their absolute number is easily underestimated since many of the carcasses disappear from the road surface within one day. Although the relation between traffic intensity and the number of victims is unclear (chapter 7, table 4), the continuing increase of traffic intensity, especially during the night (chapter 1, table 6), is likely to lead to either more victims or a stronger barrier effect (see discussion in chapter 7). Whichever it is, it will have a negative effect on the individuals concerned, and on the viability of the population (see later).

In The Netherlands and Belgium most hedgehogs are killed in the summer months (Huijser & Bergers, 1998; Holsbeek et al., 1999; Smit & Meijer, 1999). In this region, hibernation takes place from November/December until April/May (chapter 6; Reeve, 1994) and most of the mortality occurs during the peak of the mating season (June - August) (see Reeve, 1994; Huijser, 1997). Adult males were more abundant among the traffic victims than young and females (chapter 2; 3). The sex ratio in wild populations is about equal for all age categories (Kristiansson, 1984; Reeve, 1994; Huijser, 1997) and the predominance of adult males among the victims is largely based on the fact that they have relatively high activity levels. Adult males have far greater home ranges than females and also travel much greater distances per night, especially during the mating season (see review by Reeve, 1994). As a consequence, male hedgehogs encounter more roads, cross them more frequently than females do, and spend more time on roads. Therefore they run a greater risk of ending up as a traffic victim (chapter 2; 3).

When traffic approaches, hedgehogs vary greatly in their reaction. Some individuals freeze, crouch or roll up completely, while others turn around and run away (Bontadina et al., 1993; Mulder, 1996b). Walking hedgehogs are taller than those that freeze and crouch (chapter 5). Although hedgehogs that run may get out of the way of an approaching car, they are relatively vulnerable to cars with low clearance. The clearance of 26% of all passenger cars on the Dutch roads was insufficient to have them pass over a walking (or running) subadult or adult of average size (chapter 5). Hedgehogs that sit still and crouch run much less risk of being hit by the underside of a car. However, since these animals remain on the road they can also be hit by the tyres. Thus the behaviour of an individual hedgehog is likely to influence its survival probability on a road, but the trade off between crouching and running away is unknown. Nevertheless, it is likely that if many vehicles travel close together, a crouched hedgehog may never get off the road, and that it will eventually be run over. Thus, with the continuing growth in traffic intensity the survival chance for a running hedgehog will increase.

3. Effects on populations

Data from wildlife rescue centres suggest that humans are an important death factor for hedgehogs. Over 40% of all deaths recorded in three centres was related to humans, their activities or man-made objects (chapter 2). This included mortality due to traffic (9% of all deaths), drowning in waterbodies with steep banks, disturbance of nests with young, wounds inflicted by dogs and cats, poison, and other unnatural injuries. Most hedgehogs that are hit by a car die instantly and are never brought to a wildlife rescue centre. Therefore 9% is likely to be an underestimation of the relative importance of this death factor, despite other biases in samples from rescue centres.

A capture-mark-recapture study in a small scale agricultural landscape was combined with an intensive search for traffic victims in the same area to estimate the relative importance of this mortality factor (chapter 3). Traffic mortality was 12% of the total losses (deaths and dispersal) of the hedgehog population, excluding the young of the year. Over two successive seasons 6% and 9% of the animals in the study population fell victim to traffic. These figures fall within the wide range of estimates found in other studies (see review by Huijser et al., 1998). However, such figures are heavily influenced by local population density, road density, and possibly also by traffic intensity.

Another way to estimate the relative importance of traffic mortality is through combining the estimates of the total population size (N = 430,000, see chapter 1, fig. 4) and traffic mortality (N = 113,000-340,000, see Huijser & Bergers, 1998) for the whole country. However, the population estimate is based on densities in various habitats (see chapter 1, table 2) and these usually apply to subadults and adults during the summer months only. Apart from the animals that died during hibernation and early spring, the total number of animals needs to be corrected for the young born in summer and autumn. Given an equal sex ratio (see earlier) and assuming that all females will reproduce from their second summer onwards (see e.g., Reeve, 1994), there are 215,000 females who will produce 4 young on average (see Huijser, 1997). This amounts to 860,000 young in addition to the 430,000 hedgehogs that have survived at least one winter, which then totals to 1,290,000 individuals. Since the young are mostly born in late summer and autumn, they are only exposed to traffic mortality and other possible death causes for part of the year. In this calculation the individuals that died during hibernation and early spring are ignored to somewhat compensate for this. Thus, 113,000-340,000 traffic victims on a total of 1,290,000 hedgehogs amounts to 9-26% of the population size.

Percentages like those given above provide insight into the relative importance of traffic mortality in a population, but they do not tell whether hedgehog populations really suffer from it through, for example, low population density or reduced survival probability. Therefore a pairwise comparison was made of relative hedgehog densities in areas close to roads with those in areas that were at least 400 m away from roads (chapter 4). The results suggest that roads and traffic may reduce population density by about 30%, which may affect the survival probability of local populations. It is important to note that this reduction in density may not be caused by traffic mortality alone, but could also be influenced by other road and traffic related factors (for example, a reduction in habitat quality). In addition, an effect may not remain constant over the years through a lag in response (cf. Findlay & Bourdages, 2000), or the continuing increase in road density and traffic intensity (see chapter 1, fig. 2). Moreover, the presence or density of hedgehog populations close to roads may already depend on immigration from areas that lie at a greater distance from roads. These 'source' areas may decrease or vanish as road density continues to increase.

Finally, traffic mortality is likely to have an effect on the population structure. Since adult males have a relatively high chance of becoming a traffic victim, populations close to roads may consist of relatively young individuals and have a female biased sex ratio. Since hedgehogs do not form pairs and do not have territories, the remaining females are likely to reproduce, even though only a few males may be around. Nevertheless, apart from reducing the absolute number of males, the high death rate of males probably also results in a selection of individuals that are less active. Under natural circumstances such males would have been outcompeted by more active males and would have had limited access to females. Thus the predominance of adult males among the traffic victims could eventually lead to reduced fitness of individuals and negative effects on population viability.

4. Effects on the species

In order to understand the possible effects of traffic mortality on the species level, a broad view is needed on how vulnerable the hedgehog is to habitat fragmentation and how the hedgehog has responded to human induced changes in the landscape from their first influences onwards.

In The Netherlands hedgehogs are common and occur throughout the country (Hoekstra, 1992; Thissen & Hollander, 1996; Lapini, 1999). However, various studies have shown that they have relatively low population densities in some habitats (forests, large scale agricultural areas and urban centres), that their home range is relatively large (several tens of hectares) and that local population density may fluctuate considerably from one year to the next (see review in chapter 1, table 4). These characteristics make the species relatively vulnerable to infrastructure and other habitat fragmentation processes which may cause the local or regional disappearance of the species. In areas that are characterized by large scale agricultural lands or urban areas with little vegetation cover, high road density and high traffic intensity, this could well be the case already. However, other aspects lead to the overall conclusion that the hedgehog, as a species, is not very vulnerable to habitat fragmentation in general, or to traffic mortality in particular. Non-territoriality and relatively great dispersal distances facilitate recolonization, and the hedgehog's ability to exploit a broad range of habitat and food types enables it to cope with considerable changes in the landscape and the availability of certain prey species (chapter 1, table 4). Furthermore, reproduction is high enough to suggest that hedgehogs can withstand considerable mortality. Extensive habitat fragmentation through road infrastructure is a relatively new phenomenon, but the animals tend to avoid asphalt with its apparent hazards (chapter 1, table 4). Although hedgehogs are fast enough to get out of the way of an approaching car if they choose to, many of them may respond by sitting still (chapter 5). This may be why so many get killed after all (see earlier). Although most of the species' characteristics indicate that the hedgehog is unlikely to disappear completely from a region, extreme habitat fragmentation may cause extinction. This point may well have been reached in some regions in The Netherlands (see earlier).

When the relationship between human land use and hedgehogs is put in historical perspective, two major processes can be distinguished: agricultural development and urbanization. Several stages of the two processes were distinguished, ranked with respect to increasing human impact, and then linked to hedgehog population densities in the appropriate land use categories (chapter 1, fig. 1; 3). Hedgehogs have relatively high population densities in small scale agricultural landscapes with abundant edge habitat which is characterized by a transition of trees and shrubs to open areas such as grasslands. Urban areas with many parks and gardens have higher population densities than any other habitat, while relatively few hedgehogs are found in large scale agricultural areas, forests, and urban centres. The initial impact of humans on north-western Europe's natural forests must have led to an increase in edge habitat through fires, the grazing of livestock and the clearance of areas for agriculture. Since hedgehogs have high population densities in areas with abundant edge habitat, the species is likely to have benefited from these human activities (chapter 1, fig. 1). The later removal of hedgerows and small woodland fragments for more intensive agricultural use has probably caused hedgehogs to decline locally or perhaps even regionally. There is also an optimum for hedgehogs with respect to urbanization. Only few hedgehogs are found in urban centres as parks and gardens are rare and isolated through fences, walls, buildings and roads (chapter 1, fig. 3).

Forests, the natural habitat of the hedgehog, now cover about 10% of the terrestrial part of The Netherlands (Anonymous, 2000). Since forests have low hedgehog population densities, this area alone may not be enough to ensure the long term survival of the species. Therefore the future of the hedgehog may also depend on how well it does in other landscapes with much stronger human influence. Agriculture is the most important land use category in The Netherlands (69% of the terrestrial area) and developments within this habitat are likely to have a great effect on hedgehogs. Although hedgehogs do well in small scale agricultural areas, most of the present day agricultural lands lack sufficient edge habitat and may even be considered a barrier to this species (see chapter 6; 7). Also, the habitat in which most hedgehogs are found, urban areas with abundant green, only covers 9% of the land surface (93% of all urban areas, see chapter 1). The relatively small urban areas are often surrounded by large scale agricultural lands and may, like many forests, also be too small to sustain populations on the long term.

Apart from the loss of edge habitat and increase of barriers in both agricultural areas and urban centres over the past decades, the hedgehog seems to have benefited from human induced changes in the landscape. The species has much higher densities in anthropogenic landscapes with abundant edge habitat than in its natural habitat. The fact that this is still the case with the present road density and traffic intensity suggests that the species is not under direct threat from infrastructure in these habitats. However, in areas with low population density such as large scale agricultural landscapes, urban centres and forests, traffic mortality may already have led to its local or regional extinction. Ironically, the natural habitat of hedgehogs is one of the places where the hedgehog seems to be relatively vulnerable to traffic mortality. Fortunately road densities tend to be relatively low in forested areas (see Bergers & Nieuwenhuizen, 1999). Nevertheless, the long term future of the hedgehog will primarily depend on how well it does in areas with moderate to strong human influence. This is especially true for agricultural landscapes. The way these areas are managed seems to be more important to the species' survival than the present road density and traffic intensity (chapter 1). In addition, it is important to monitor whether hedgehogs continue to do well in urban habitats as parks and gardens tend to become smaller and more isolated in both existing and new town sections, and the species may also continue to be faced with new unnatural causes of death.

5. Passages for hedgehogs

It is clear that traffic mortality can be avoided or much reduced if impermeable barriers are placed along all major roads. This would solve most of the problems resulting from direct traffic mortality, especially at the individual level. However, fences or other structures (see e.g., chapter 7, fig. 2b) also strengthen the barrier effect of roads and traffic. Populations that become smaller and more isolated have lower survival probability (see e.g., Hanski, 1999; Debinski & Holt, 2000) and this also applies to hedgehogs with respect to major roads (Bergers & Nieuwenhuizen, 1999). Thus barriers should not be put into place unless connectivity between populations on either side is also provided for. However, even if no absolute barriers are present, the movements of hedgehogs are still clearly disturbed by roads and traffic. Wide roads have fewer hedgehog victims than narrow roads (chapter 7, table 4), which suggests that the animals are less likely to cross this potentially hostile habitat when it is wide. This is confirmed by Bontadina (1991) and Zingg (1994) who showed that roads are usually avoided and that hedgehogs cross wide roads at a greater speed than narrow ones. Street lights also contribute to the barrier effect of roads (chapter 7, table 6).

In The Netherlands, the barrier effect of infrastructure is usually reduced through wildlife passages that range from narrow tunnels with 30-150 cm diameter (for amphibians, badgers (*Meles meles*), otters (*Lutra lutra*) etc.), to tunnels or ecoducts that are at least several metres or several tens of metres wide. The latter are also suitable for relatively large species such as roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*) and red deer (*Cervus elaphus*) (Oord, 1995). Hedgehogs use narrow as well as wide passages (see review by De Vries, 1999), but negative interactions with other species such as badgers suggest that wide passages are probably more effective than narrow ones (chapter 7; Doncaster, 1999). Streetlights, or any other lights, should preferably be absent or turned off in the direct vicinity of a passage (chapter 7).

Passages for hedgehogs that are located close to or in areas with urban green, forests, forest edges, hedgerows or lines of trees have greatest chance of being used. It is important that such passages lie in the path of a hedgerow, forest edge or grass verge, since these linear elements guide hedgehogs in their movements through the landscape (chapter 6; 7). Existing or new wildlife passages can also be made more effective by changing the landscape in a zone adjacent to a road (chapter 6; 7). Newly planted hedgerows, forest edges or grass verges can guide hedgehogs towards a passage, while other landscape features such as arable land, heathland, and possibly also large scale short grasslands will help to keep hedgehogs away from the road at sections between passages. However, such changes in the landscape should be carefully considered before they are carried out (see discussion chapter 7, and see below) and additional physical barriers between the road and the surrounding landscape will probably remain necessary to obtain a major reduction in traffic mortality.

6. Road-side verges: habitat or effect zone?

An unattractive zone for hedgehogs at road sections between wildlife passages involves habitat loss and a decrease in habitat quality. Furthermore, these changes in the landscape may also have negative effects on other species that are, or have become, dependent on road side verges for at least part of their life cycle. This presents us with a difficult choice: reducing traffic mortality for the hedgehog may also be a threat to its own survival or to that of other species, despite possible compensation efforts elsewhere (cf. Cuperus et al., 1999). However, in cases like this it may help to note that the ecological role of road-side verges is related to the level of human impact on the surrounding countryside (see also chapter 7).

When a road is constructed in a landscape that has received very little human impact until then, the verges can be considered a disturbance factor. The verges, and of course the road itself, are a disruption of the natural vegetation and physical characteristics of the landscape. Verges are often dominated by grasses and herbs and may form a barrier for some species that, for example, need cover or trees for their movements (e.g., Oxley et al., 1974; Mader, 1984; Bright, 1998) or those that avoid roads in general (e.g., Rost & Bailey, 1979; Brody & Pelton, 1989; Thurber et al., 1994; Lovallo & Anderson, 1996). On the other hand, the grassland vegetation in the verges may be attractive to certain herbivores at certain times of the year because of the abundance of food in an otherwise wooded environment (e.g., Carbaugh et al., 1975). Predators may scavenge on road-kills and are at particular risk of being hit themselves (e.g., Wells et al., 1999). In forests, the verges may also be attractive to species that select edge habitat. Although the edge habitat in the verges is unnatural, it may resemble the early stages of secondary succession in natural landscapes. Such verges may be particularly attractive if the influence of natural dynamics (fire, flooding) in the surrounding landscape is suppressed. However, the animals in the verges may be faced with very high mortality rates due to traffic. Since the areas close to roads will continue to attract new immigrants, they can end up functioning as population sinks. This phenomenon has been demonstrated for the threatened Florida scrub-jay (*Aphelocoma coerulescens*) (Mumme et al., 1999), and it may also apply to the hedgehog in extensive forests that have little edge habitat. In other cases (rail-)road verges serve as a corridor for resident individuals or invading species (e.g., Getz et al., 1978; Gundersen & Andreassen, 1998). An invading species may be native to the region, but water or other barriers may have prevented earlier colonization of that particular area (e.g., Bekker & Mostert, 1998). More severe effects on the ecosystem can result from the invasion of truly exotic species (e.g., Wilcox, 1989; Tyser & Worley, 1992; Lonsdale & Lane, 1994; Seabrook & Dettmann, 1996; Stiles & Jones, 1998; Parendes & Jones, 2000).

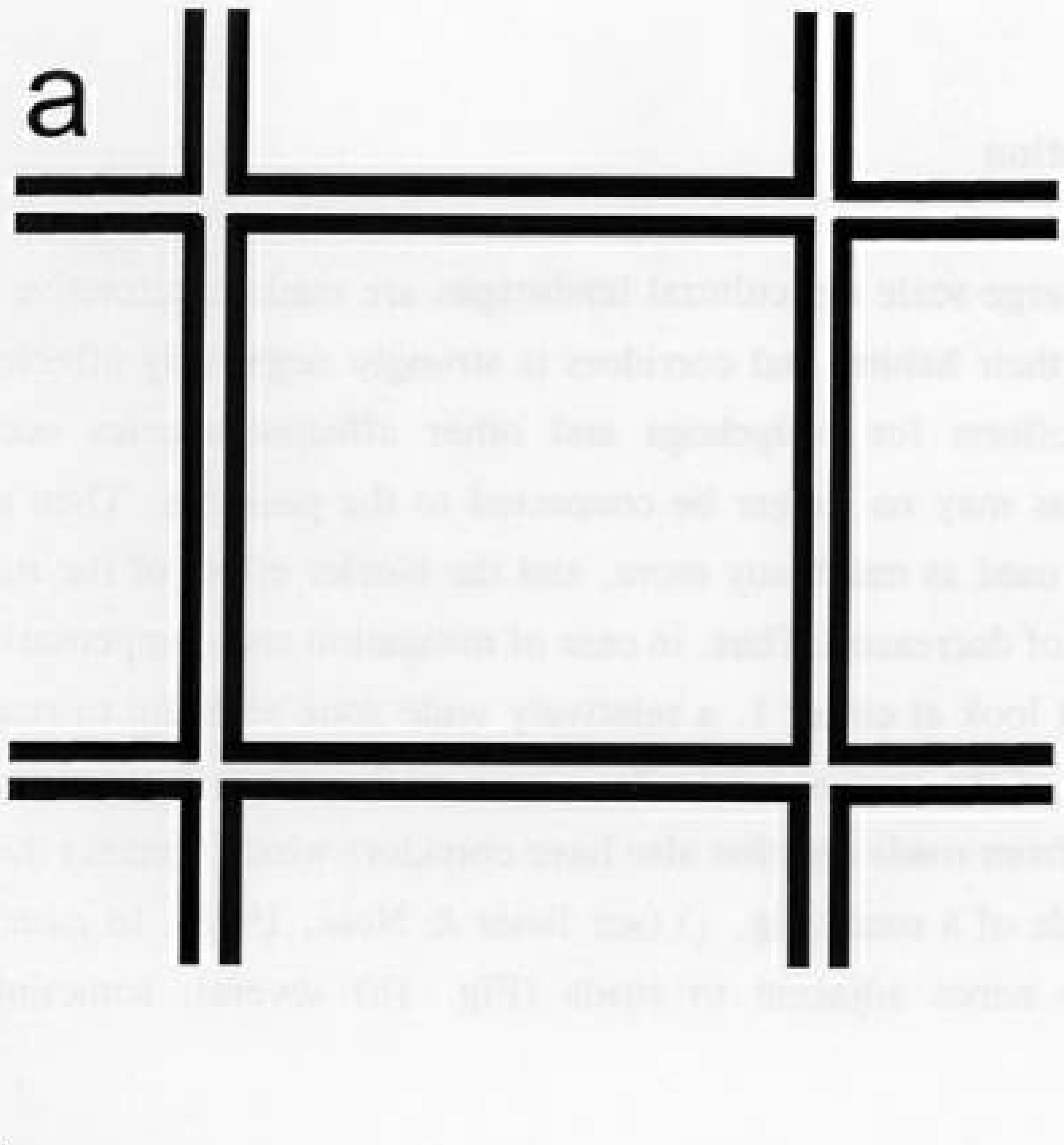
Further human impact on the landscape results in a mosaic of natural, semi-natural, and intensively managed vegetation. Road-side verges may be classified as any of these three, depending on the local situation. While such a diverse landscape with many transition zones may have a high biodiversity, the ecological integrity of the original ecosystem has much declined. When human impact increases even more, most of the remaining patches of semi-natural and natural vegetation will be lost. Road-side verges may then become habitat relicts for some species in an otherwise hostile environment. In some cases, these species are 'refugees' from the original ecosystem (e.g., Warner, 1992; Straker, 1998), while others did well with low to moderate human impact in the landscape, but now also face a decline (e.g., Munguira & Thomas, 1992; Sýkora et al., 1993; De Bruijn, 1994; Vermeulen, 1994; Meunier et al., 1998a; 1998b; 1999). Hedgehogs fall in the latter group. In large scale agricultural landscapes they may use verges with trees, shrubs and edge habitat for shelter and foraging. However, hedgehogs are unlikely to forage on the road surface (see chapter 5). Nevertheless, they sometimes use side walks, cycle paths or the road surface to swiftly cover relatively great distances within their home ranges (Bontadina et al., 1993; Zingg, 1994; Mulder, 1996b). These positive roles of the road-side verges should always be seen in relation to the condition of the surrounding landscape, and it does not eliminate the negative effects that are associated with infrastructure. For hedgehogs these may not only include traffic deaths and a barrier effect, but also a reduction of habitat quality through, for example, noise and light disturbance (cf. Reijnen et al., 1995; De Molenaar et al., 1997; chapter 7), pollutants (cf. Liem et al., 1985; Benfenati et al., 1992; Shore et al., 1996) and death resulting from management activities in the verges (see chapter 6, introduction).

In landscapes that still are largely unaffected by humans, the road disturbance zone should be kept as narrow as possible. It is only in very specific and alarming situations that a further degradation of the natural habitat through changes of the landscape should be considered. If a road is to remain in such an area, and if tunnels or the elevation of the road over long distances are not an option, then the mitigation measures will have to focus on physical barriers in combination with conventional wildlife passages. In mosaic landscapes changes in the vegetation adjacent to roads may be an option. These landscapes are much influenced by humans already, and the road-side verges are merely one of the elements in a relatively robust and extensive network of corridors and habitat patches. This does not necessarily imply that the road-side verges are not important, but if the habitat loss and the decrease in habitat quality are compensated for elsewhere, it may not lead to severe negative side effects for the plant and animal species in the region.

In landscapes that have lost most of the patches and corridors with semi-natural or natural vegetation, landscape changes adjacent to roads are risky. In such landscapes most of the road-side verges can be classified as semi-natural habitat relicts in areas with cultivated grasslands, crops or buildings. The verges themselves are home to a variety of plant and animal species and have become an important habitat and a corridor in addition to an effect zone (Fig. 1a). For some species the verges may be critical to their local or regional survival. This also applies to the hedgehog, especially when shrubs or trees are present in verges that run through large scale agricultural landscapes. Thus, in landscapes with high human impact, landscape changes should be very carefully considered. If they are carried out, they should be gradual and they may have to be combined with the capture and release of animals or the transplantation of plants that have low dispersal rates.

7. Integrated land defragmentation

If zones adjacent to roads in large scale agricultural landscapes are made unattractive to hedgehogs, an important part of their habitat and corridors is strongly negatively affected. Furthermore, if compensation efforts for hedgehogs and other affected species occur elsewhere, the compensation areas may no longer be connected to the passages. Then the under- or overpasses may not be used as much any more, and the barrier effect of the road may have been increased in stead of decreased. Thus, in case of mitigation and compensation efforts for the hedgehog we must look at either 1. a relatively wide zone adjacent to roads that will extent the width of most of the current road-side verges, or 2. sites that are at least several hundreds of metres away from roads and that also have corridors which connect them to habitat patches on the other side of a road (Fig. 1) (see Beier & Noss, 1998). In case of scenario 1 with relatively wide zones adjacent to roads (Fig. 1b) several, sometimes contrasting, objectives will have to be met in a transect that is only as wide as the zone concerned. Both habitat and corridors will have to be provided, as well as an unattractive zone which is located between the habitat and corridors on one side, and the road surface on the other. Data on the habitat use of hedgehogs in edge habitat (chapter 6, fig. 1) show that, in addition to a hedgerow (for example width 5 m) or a forest, at least 15-20 m of edge habitat is needed. This is then followed by an unattractive zone which extends to the pavement. The unattractive habitat can consist of arable land or heathland (chapter 7, table 6), but short grassland may have a similar effect and would be more applicable in most situations. There are no data available on how wide such an unattractive zone should be, but a width of 10-15 m seems reasonable. All in all a zone of at least 30-40 m wide would be needed. If the unattractive zone is replaced by physical barriers (e.g., chapter 7, fig. 2b), the width of this zone may be reduced to 20-25 m. However, in both variants the width of the zone extends further than that of most road-side verges and puts a claim on the adjacent agricultural lands. Finally, the habitat and corridors in these zones continue to be exposed to at least some of the negative effects of roads and traffic such as disturbance and pollution (see reviews by Forman & Alexander, 1998; Trombulak & Frisell, 2000), and the spatial



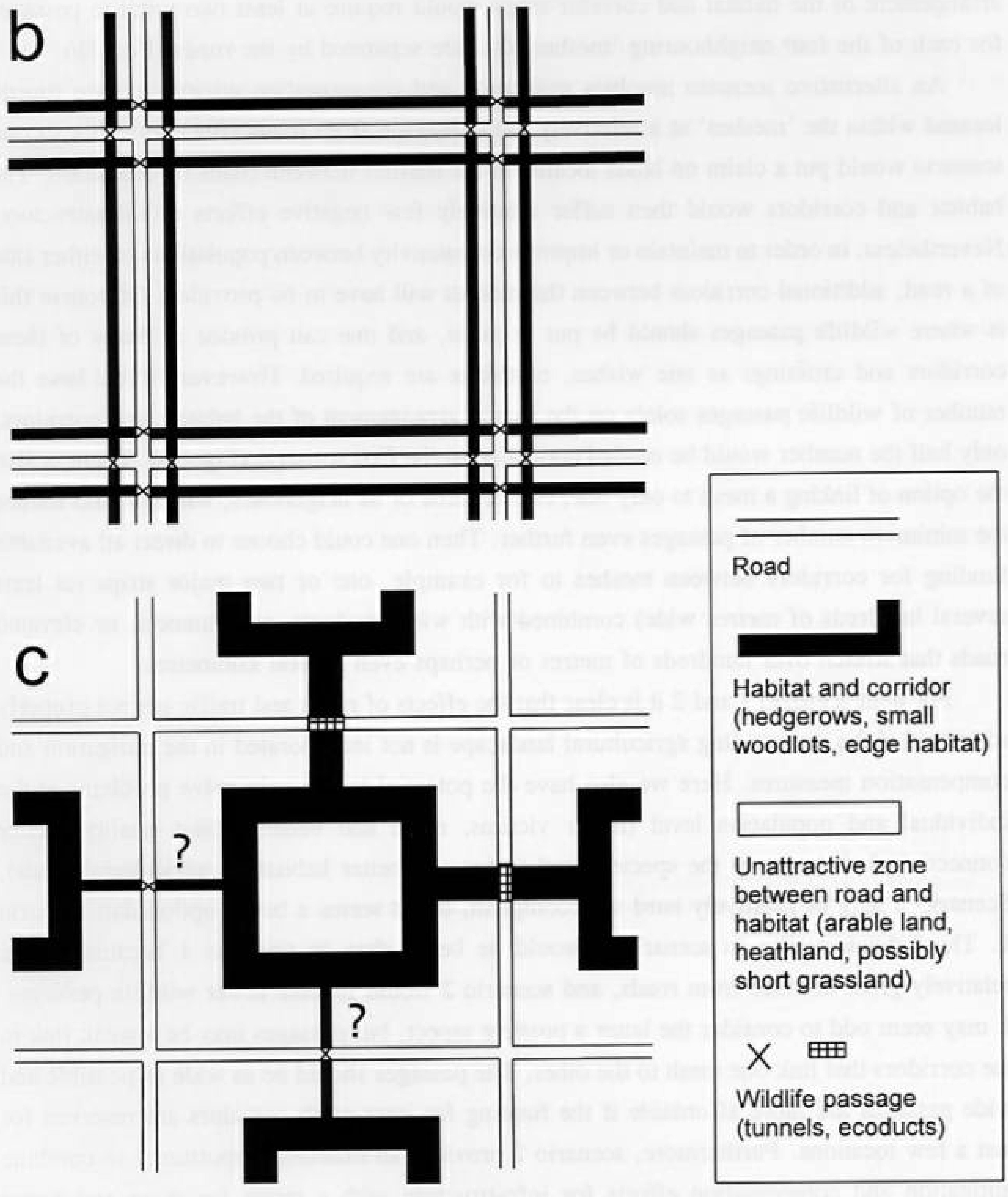


Fig. 1. Schematic arrangement of roads and habitat, corridors and wildlife passages for hedgehogs in an agricultural landscape. a. Present situation: habitat and corridors in road-side verges. b. Future situation 1: habitat, corridors and unattractive zones in road-side verges and wildlife passages. c. Future situation 2: habitat and corridors at a relatively great distance from roads, some wide corridors and wildlife passages provide a link to the adjacent meshes.

arrangement of the habitat and corridor strips would require at least two wildlife passages for each of the four neighbouring 'meshes' that are separated by the roads (Fig. 1b).

An alternative scenario involves mitigation and compensation efforts that are mostly located within the 'meshes' at a relatively great distance from roads (Fig. 1c). This second scenario would put a claim on lands located in the meshes between roads by definition. The habitat and corridors would then suffer relatively few negative effects of infrastructure. Nevertheless, in order to maintain or improve connectivity between populations on either side of a road, additional corridors between the meshes will have to be provided. Of course this is where wildlife passages should be put in place, and one can provide as many of these corridors and crossings as one wishes, or thinks are required. However, if we base the number of wildlife passages solely on the spatial arrangement of the habitats and corridors, only half the number would be needed compared to the first scenario (Fig. 1b). There is also the option of linking a mesh to only one, two or three of its neighbours, which would reduce the minimum number of passages even further. Then one could choose to direct all available funding for corridors between meshes to for example, one or two major strips (at least several hundreds of metres wide) combined with wide ecoducts, road tunnels, or elevated roads that stretch over hundreds of metres or perhaps even several kilometres.

For both scenario 1 and 2 it is clear that the effects of roads and traffic are not properly addressed if the surrounding agricultural landscape is not incorporated in the mitigation and compensation measures. Here we also have the potential to not only solve problems at the individual and population level (fewer victims, more and better habitat quality, better connectivity), but also at the species level (more and better habitat on agricultural lands). Scenario 2 may be relatively hard to accomplish, but it seems a better option dan scenario 1. The habitat quality in scenario 2 would be better than in scenario 1 because of the relatively great distance from roads, and scenario 2 would involve fewer wildlife passages. It may seem odd to consider the latter a positive aspect, but passages may be a weak link in the corridors that link one mesh to the other. The passages should be as wide as possible and wide passages are more affordable if the funding for inter-mesh corridors are reserved for just a few locations. Furthermore, scenario 2 provides an excellent opportunity to combine mitigation and compensation efforts for infrastructure with a strive for more and better natural values, increased recreational opportunities and more sustainable water quality-, and water quantity management on agricultural lands (e.g., Van Buuren, 1991; Bueno et al., 1995; McGuckin & Brown, 1995; Fry & Sarlöv-Herlin, 1997; Bouma et al., 1998; Opdam et al., 2000). In The Netherlands there is a great urgency to hold water in small ditches and streams for a longer time before it flows into large canals, rivers, lakes or the sea. Some lands will also be temporarily flooded since the dimensions of the waterways and technical facilities are unable to deal with the present and future peaks in precipitation and water discharge. Thus, the dimensions of many small ditches, ponds and streams will increase. Such changes can be combined with more natural values and increased recreation opportunities. The same accounts for buffer zones along streams and ditches on agricultural lands which reduce the high nutrient and pollution levels in the water. In addition, other human values and uses of agricultural lands that have a aesthetic, historical or cultural base may increase (e.g., Burel & Baudry, 1995; Fry & Sarlöv-Herlin, 1997; Shoard, 1999; Arler, 2000). The particular strength of integrating all these issues is that all the main habitat fragmentation problems and solutions would be identified at a regional or landscape level (see Hobbs, 1997). Apart from infrastructure, integrated land defragmentation plans would also focus on agriculture and urbanization (e.g., Mader, 1984; Searns, 1995).

Integrated land defragmentation plans could give several options for changes in land use that, according to calculations, allow for viable populations of selected plant- and animal species. This may not only involve the dimensions of the habitat network, but also the minimum size of the meshes between roads (see Jaeger, 2000). The latter could lead to road closure and road removal (cf. Bagley, 1998; Walder & Bagley, 1999) and may also have economic benefits (Swanson & Loomis, 1998). A network of both narrow and wide greenways would provide both habitat and connectivity for species that can cope with relatively high human impact in the surrounding areas (e.g., Burel & Baudry, 1995; Linehan et al., 1995). To meet the present needs of human society, some of the greenways would also receive relatively high human use themselves. However, it is important to note that many animal and plant species are adversely affected by human presence and activities (e.g., Pedevillano & Wright, 1987; Clevenger & Waltho, 2000), and that some of the habitat patches, corridors and passages will have to be exclusively reserved for natural values.

8. Conclusion

The hedgehog illustrates that the effects of roads and traffic may affect a species on different levels. In case of the hedgehog the negative effects are particularly clear at the level of individuals, and one can consider this reason enough to take action. In addition, hedgehogs are also likely to be affected at the population level. Mitigation measures that are entirely focused on reducing or preventing traffic victims through barriers along roads decrease connectivity between populations, reduce population viability, and are therefore inadvisable. On the other hand, many traffic victims would also be unacceptable, regardless of whether mitigation or compensation measures would ensure the long term survival of hedgehog populations and the species. Thus, mitigation and compensation measures have to take their possible effect at all levels into account.

At the species level, the hedgehog has mostly benefited from human-induced changes in the landscape as people increased the amount of edge habitat. Massive traffic mortality is a relatively recent negative aspect in the hedgehog's relationship with humans, but infrastructure alone is unlikely to be the main reason for hedgehogs to disappear completely. The long term future of the species primarily depends on how people manage the landscape, and agricultural areas in particular. Over the last decades the habitat quality of agricultural lands has much decreased through the removal of small woodlots, hedgerows and other edge habitat. This has led to low population densities in these areas and since agricultural lands cover nearly 70% of the terrestrial part of The Netherlands, it makes the hedgehog relatively vulnerable to widespread regional extinction. The future of many other plant and animal species now also depends on the availability of suitable habitat and corridors in agricultural areas. Therefore mitigation and compensation efforts for infrastructure should be integrated in regional plans that address all major habitat fragmentation problems including those resulting from agriculture and urbanization. Naturally, these plans should have a multi-species or ecosystem approach.

People will always have different views on how varied and sometimes contrasting values and uses of the land should be achieved. Finding ways in which the values and uses concerned will strengthen each other rather than compete will be the key to success for such multi-functional anthropogenic landscapes.

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CURRICULUM VITAE

Marcel Pieter Huijser was born on January 22nd 1968 in Soest, The Netherlands. He studied biology (population/ecosystems) at Wageningen University (Wageningen, The Netherlands) between 1986 and 1992. His two M.Sc. theses focused on 1. food availability for roe deer, red deer and wild boar in the Veluwe area, and 2. the habitat use of ungulates and geese in the Oostvaardersplassen wetland. These studies were conducted in cooperation with 1. the department of Animal Ecology of the Institute for Forestry and Nature Research[1] and the former department of Nature Management[2] at Wageningen University and 2. the section Landscape Ecology of the Directorate-General for Public Works and Water Management Flevoland[3], and the department of Animal Ecology[4] of the University of Groningen. Further practical experience was gained at the Wyoming Cooperative Fish and Wildlife Research Unit (Laramie, Wyoming, USA) through participating in a habitat use study of elk (red deer) in the Big Horn Mountains, and a similar study with respect to white-tailed deer and mule deer on Devils Tower National Monument in the Black Hills.

Between 1992 and 1995 Marcel studied interactions between vegetation development, abiotic conditions, grazing by large and small herbivores and other management practices in several freshwater and desalinating wetlands, including the Lauwersmeer and the Oostvaardersplassen. From 1995 until 1999 he was employed by the Dutch-Belgian Mammal Society[5], where he conducted a study on hedgehogs, roads and traffic. This study was financed by the Directorate-General for Public Works and Water Management[6] and resulted in this dissertation. For several months in 1998 and 1999 he was hired by the Dutch Ministry of Agriculture, Nature Management and Fisheries to assist with the completion of a database on the Dutch areas that qualify for protection under the Habitat- and Bird Directive of the European Union. He started working at the Research Institute for Animal Husbandry[7] in 1999. Here he focuses on transforming agricultural areas into landscapes in which the present need for more, better and sustainable nature values, recreation opportunities and water management are integrated.

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