

**DISTURBANCE BY CAR TRAFFIC AS A THREAT  
TO BREEDING BIRDS IN THE NETHERLANDS**

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# **DISTURBANCE BY CAR TRAFFIC AS A THREAT TO BREEDING BIRDS IN THE NETHERLANDS**

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## **GENERAL INTRODUCTION**

## **ROADS AS AN ENVIRONMENTAL PROBLEM**

Roads have long been used by man for the movement by foot and by animal-drawn vehicles. The introduction of motorized vehicles in the beginning of this century, however, has changed this transport system dramatically. The enormous increase of motorized traffic and the greater scale of movements, resulted in a strong expansion of networks of main roads with high traffic densities. In The Netherlands, the length of highways has extended from 87 km in 1938 to 2600 km in 1991 (CBS 1980; Anonymous 1993a). At present traffic densities on these roads vary from 10 000 to more than 100 000 cars per day (Anonymous 1992).

These developments have caused growing environmental problems. Main roads make great demands on the available land area and enlarge the degree of fragmentation of the landscape (e.g. Nijland *et al.* 1982). The dense car traffic is a major source of air and noise pollution. It is well known that emitted gases contribute significantly to the phenomenon of 'acid rain' (RIVM 1989), which causes a widespread deterioration of habitats (Bink *et al.* 1994). Noise pollution is restricted to zones adjacent to roads. However, the total area that has a significantly increased noise level due to car traffic can be very large. In The Netherlands, for example, the area that has a noise load of more than 50 dB(A), which is used as a threshold for man, covers about 8% of the total land area (Anonymous 1991). Furthermore, car traffic kills enormous numbers of animals annually (Jonkers & De Vries 1977; Van den Tempel 1993). As a result, there is now much attention on and concern with the effects of traffic and roads on the natural environment (Nijland *et al.* 1982; Leedy & Adams 1982; Bernard *et al.* 1987; Ellenberg *et al.* 1982; Bennett 1991).

This study meets the requirements for further research on the fauna near roads. Breeding birds were chosen because there are several indications of significant effects.

## **ROADS AND BREEDING BIRDS**

To discuss the impact of road systems on breeding birds it is useful to distinguish between effects related to habitat transformation caused by imposing roads on the landscape and effects related to the human activities upon the road.

### **Habitat transformation**

The direct effect of the construction of roads is loss of habitat. In particular, when roads have been constructed through areas that are important breeding sites, this may cause a major impact on local population size. For example, Ferris (1979) estimated that each

kilometre of a four-lane section of a highway in Maine, USA, destroyed an area that would support 130 pairs of breeding forest birds. Moreover, a reduction of the population size may increase the risk of extinction. This effect might be reinforced by habitat fragmentation and lead to regional extinctions (Opdam *et al.* 1993).

However, because roads change the landscape structure, one can also expect some secondary negative as well as positive effects. When woodland is crossed by roads, increase of edge habitat will on the one hand cause a decrease of interior species but on the other an increase of edge species (Ferris 1979). Furthermore, road side habitat might favour movements of species along the direction of the road. If such corridors connect different habitat patches or feeding and breeding sites, this could have a positive effect on several species. Also, it could lead to local or geographical range expansion. Although both corridor effects have been observed in some species (see review of Bennett 1991), their dimensions greatly depend on the existence of suitable habitat in the road side. In The Netherlands, if one restricts oneself to the system of main roads, these effects will not be important in breeding birds. Most of the road sides are rather narrow and consist of grassland, which is a habitat type poor in species and which will not likely give cues for home range movements and dispersal. However, because of the relative large numbers of voles and mice (Van der Reest 1992), the road sides provide suitable feeding grounds for predators, such as kestrel *Falco tinnunculus* L. and owls.

The road *per se* can also act as a barrier for animal movements. In breeding birds, however, this effect is probably not important, because of the relative mobility and the spatial scale of the movements (see e.g. Bennett 1991).

### Road use

The most eye-catching effect of road use is death of birds due to collisions by cars. Owing to the strong increase of the traffic density, this has become an important phenomenon. At present, enormous numbers of birds are killed in this way (e.g. Hodson & Snow 1965; Bergmann 1974; Adams & Geis 1981; Füllhaas *et al.* 1989; Van den Tempel 1993). A total estimation for The Netherlands points to a number of two millions of killed birds annually (Van den Tempel 1993). However, it has been concluded repeatedly that road kills do not exert a significant pressure on the population size (e.g. Leedy & Adams 1982; Ellenberg *et al.* 1981; Bennett 1991). Only for some large species that frequently contact roads and roadsides, such as the barn owl *Tyto alba*, road kills were claimed to have a significant effect on the population size (Braaksma & De Bruyn 1976; Illner 1992b; Van den Tempel 1993).

On the other hand, there are some reports indicating that several breeding bird species in woodland as well as in open field habitat can have strongly depressed densities in broad zones adjacent to busy roads (Räty 1979; Clark & Karr 1979; Van der Zande



*et al.* 1980; Reijnen & Thissen 1987). Disturbance distances appear to range to 500 m in woodland and more than 1000 m in open field habitat. Estimated reductions of the density over these distances reach to 60%. Since an important role of road mortality is not likely over this range, it is assumed that this effect is related to emissions of matter and energy, such as pollution, noise and visual stimuli, called disturbance (Van der Zande *et al.* 1980; Reijnen & Thissen 1987). For woodland it is argued that noise, in particular, might play an important role (Reijnen & Thissen 1987).

For the few species studied, the effects of disturbance appear to be much more important than those of habitat transformation. If disturbance would indeed be a common phenomenon in breeding birds, this should receive much attention.

## RESEARCH QUESTIONS AND STUDY DESIGN

This study focusses on the poorly understood but potentially important effect of disturbance by car traffic on the density of breeding birds. The main objective was to obtain knowledge that can be used in spatial planning procedures related to main roads, such as EIA, and in road management practice. To carry out such a study one is confronted with the following research questions:

1. How many and which type of species are affected and what is the quantitative relationship between disturbance and breeding density?
2. Which factors related to car traffic cause the effect?
3. To which extent is density a good indicator for the decline of the habitat quality?

An optimal design in impact assessment studies requires that data collection has taken place in (Green 1979; James & McCulloch 1985; Kamil 1988):

- areas before and after the intervention has occurred;
- areas not subjected to the intervention (control areas).

Such an approach, also called BACI-design (Before-After-Control-Impact, e.g. Stewart-Outen 1986), was not practicable in this study. It takes many years to collect data and one is dependent on plans for the building of new roads. Therefore, the impact had to be inferred from spatial patterns alone. As a consequence, one has to take into account other factors that can determine densities of breeding birds and that will vary between different areas. In general, this has been achieved through randomization (see e.g. Kamil 1988). This means that the other factors (secondary variables), are allowed to take different values but that these values are random with respect to the levels of the traffic related factors (independent variables). A practical advantage of this approach is that the number of sampling units can be kept at a rather low level.

To investigate the mechanisms causing the effects an experimental approach would have been required. Such an approach is very labour-intensive and would take many years to carry out. Within the framework of the study this was not possible. To obtain an indication for causal factors, it was examined whether there are study sites in which an effect on the density can be explained the most likely by one of the potential causal factors.

A reduction of the density in areas adjacent to roads points to a decreased habitat quality. This is important because there are many indications that the size and persistence of breeding populations mainly depend on areas with a high quality (Wiens & Rotenberry 1981; Bernstein *et al.* 1991). On the other hand it is known that density is not always a good indicator of habitat quality and might be even misleading (Fretwell 1972; Van Horne 1983). In several bird species it has been shown that, when overall density is high, less-preferred habitat is more strongly occupied than when overall density is low (Kluyver & Tinbergen 1953; Glas 1962; O'Connor & Fuller 1985). This means that a decrease in density can underestimate the decrease of the habitat quality adjacent to roads. It might even be possible that a reduced habitat quality is not reflected at all in a reduced density. To account for this phenomenon the effect of car traffic on the density of breeding birds was measured during several years in the same study area and related to the overall population size in these years. Furthermore, a detailed population study was carried out to obtain evidence for a decreased habitat quality close to the road and to determine which processes play a role in allocating individuals between habitat categories.

## OUTLINE OF THE THESIS

Chapter 2 deals with the dimensions of the problem: the number of bird species which are affected and the degree to which the breeding density is reduced in relation to the traffic load and to the distance to the road. For practical reasons the study was restricted to woodland (par. 2.1) and moist and wet open agricultural grassland (par. 2.2). The study on woodland birds, in particular, suggests that the noise emission by car traffic is the causal factor reducing breeding densities.

In Chapter 3 the disturbance by car traffic is treated as a reduction of the habitat quality next to the highway. In the first paragraph (3.1) the assumption was tested whether in years with a high overall population size, the use of density as a response variable underestimates the reduction of habitat quality close to roads. Again, this was only carried out for woodland birds. The next two paragraphs deal with a study of a colour-ringed population of willow warblers *Phylloscopus trochilus* adjacent to a busy

highway. By comparing demographic parameters in habitat close to the road with those in similar habitat further away, the effect on the habitat quality was measured (par. 3.2). Furthermore, it was examined how the presumed preference for areas further away from the road is expressed in the dispersal processes, and how this affects population dynamics in relation to the distance to the road (par. 3.3).

In chapter 4 the results of the previous two chapters are summarized and discussed and methods are developed to implement these results in planning and managing road systems (a manual for practical use is published elsewhere: Reijnen *et al.* 1992). An example of application explores the dimensions of the problem in The Netherlands.

**2**

## **THE EFFECTS ON DENSITY**

## 2.1 REDUCTION OF DENSITY OF BREEDING BIRDS IN WOODLAND

### SUMMARY

1. This study investigated the effect of car traffic on the breeding density of birds in deciduous and coniferous woodland and the importance of noise and visibility of cars as possible factors affecting density.
2. Of the 43 species analyzed in both woodland types, 26 species (60%) showed evidence of reduced density adjacent to roads (based on analysis with Wilcoxon signed-ranks test and regression).
3. Regression models with noise load as the only independent variable gave the best overall results. Calculated 'effect distances' (the distance from the road up to where a reduced density was present) based on these regressions varied between species from 40-1500 m for a road with 10 000 cars/day to 70-2800 m for a road with 60 000 cars/day (120 km/hour and 70% amount of woodland along the road). For a zone of 250 m from the road the reduction of the density varied from 20 to 98%.
4. When visibility of cars was controlled for, the number of species showing density reductions was much higher on plots with a high noise load than on ones with a low noise load. When noise conditions were held constant, however, there was no difference in bird densities between plots with high and low visibility of cars.
5. It is argued that noise load is probably the most important cause of the reduced densities. Visibility of cars, direct mortality and pollution are considered unimportant.
6. The results of this study stress the importance of considering the effect of car traffic on the breeding density of birds in planning and constructing main roads.

*With Ruud Foppen, Cajo ter Braak and Johan Thissen*

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## INTRODUCTION

The effect of car traffic on birds has received much attention, but most of the studies are focused on road victims (e.g. Hodson & Snow 1965; Bergmann 1974; Füllhaas *et al.* 1989; van den Tempel 1993). However, from a conservation point of view, it is much more interesting to know the consequences at the population level. This has been poorly investigated. The few available studies (woodland and open field) point out that several territorial species show a lower breeding density in areas adjacent to roads than in control areas further away (e.g. Clark & Karr 1979; Råty 1979; Ferris 1979; van der Zande *et al.* 1980; Adams & Geis 1981; Reijnen & Thissen 1987; Illner 1992a). In some species higher densities were found adjacent to roads (Ferris 1979; Clark & Karr 1979; Adams & Geis 1981), but there is evidence that this was due to different conditions of the vegetation structure close to the road.

Estimated effect distances (the distance from the road up to where a lower density can be observed) in open field habitat extend to more than 1000 m (van der Zande *et al.* 1980), in woodland up to several hundred meters (Reijnen & Thissen 1987; Råty 1979). Since there are indications that the reduction of the density in the disturbed zone can be rather large (van der Zande *et al.* 1980; Råty 1979; Reijnen & Thissen 1987), this might point to an important effect on breeding bird populations.

How car traffic causes densities to be reduced, is still unknown. It has been generally assumed that the increase of the mortality due to road traffic will be too small to cause a significant decrease of the density or the population size (e.g. van der Zande *et al.* 1980; Leedy & Adams 1982; Ellenberg *et al.* 1981). This implies that possible causes are probably more related to emission of matter and energy by road traffic, such as pollution, visual stimuli and noise (van der Zande *et al.* 1980; Reijnen & Thissen 1987). For woodland it is assumed that noise load, in particular, might play an important role (Reijnen & Thissen 1987; Reijnen & Foppen 1994).

The objective of this study is to determine which woodland species show lower breeding densities next to roads, over which distances such an effect occurred and to which degree the densities were lower. Furthermore the assumption was tested that noise is the most critical cause of the effect.

## METHODS

### Study areas and site selection

The study was carried out in areas with deciduous woodland and coniferous woodland crossed by main roads, scattered over The Netherlands. The traffic density of roads

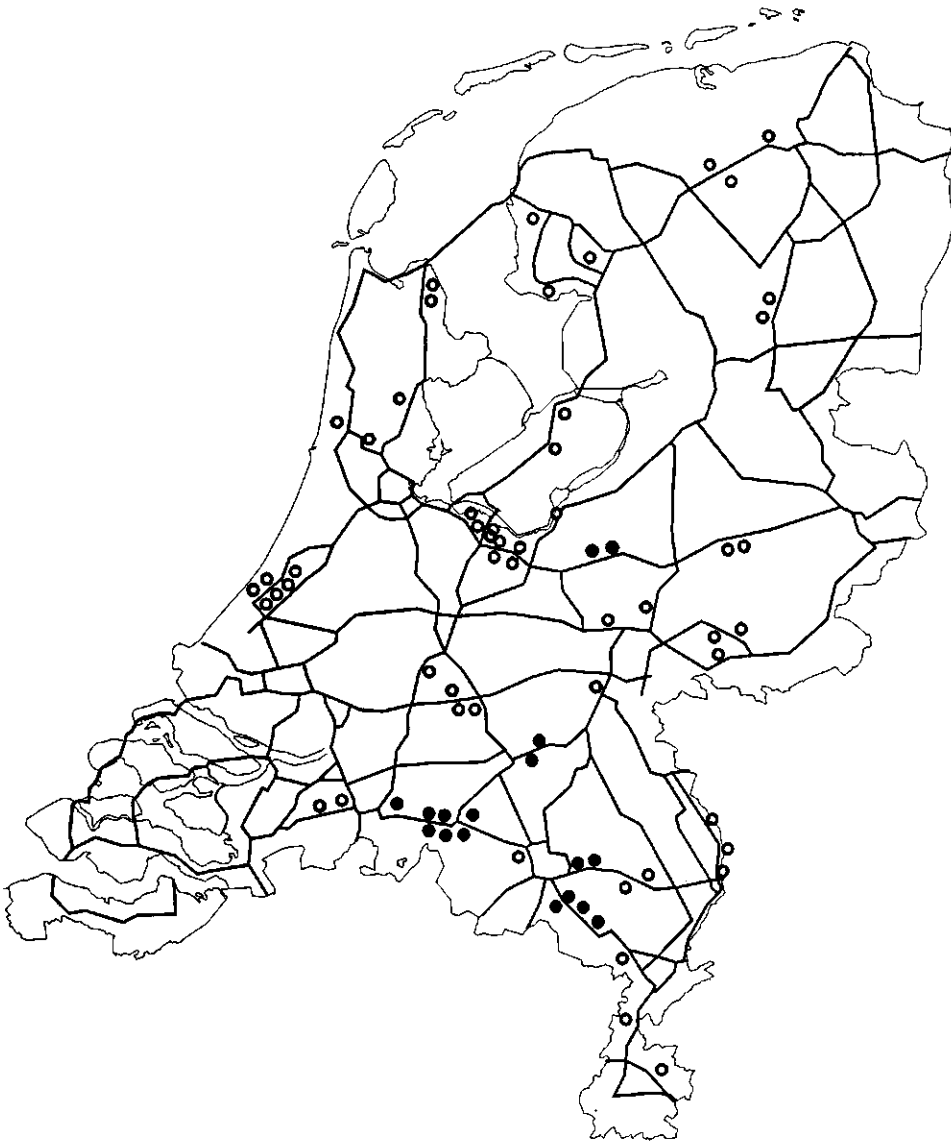
in areas with deciduous woodland was 8000-61 000 (mean 30 334) cars a day and in areas with coniferous woodland 29 000-69 000 (mean 45 319) cars a day. In deciduous woodland 38 paired plots and in coniferous woodland 17 paired plots were selected (Fig. 1). One plot of a pair was situated adjacent to the road (road plot) and one plot at a distance of on average 400 m (control plot). Within each pair of plots habitat differences were controlled for (see section of methods 'Control of other factors that influence breeding density'). Because available studies in woodland indicate that effect distances can be rather large (Räty 1979; Reijnen & Thissen 1987), some or part of the control plots might still be influenced by car traffic. For practical reasons these control plots were not located farther away from the road. To obtain reliable bird densities a minimum plot area of 1.5 ha was taken for deciduous woodland and 5 ha for coniferous woodland (based on Hustings *et al.* 1985, see Table 1 for mean size of plots). Investigations were carried out in 1987 (deciduous woodland) and 1988 (coniferous woodland).

Oak (*Quercus robur* L.) was the dominant tree species in 30 of the 38 paired plots of deciduous woodland, poplar (*Populus spec.*) in five, beech (*Fagus sylvatica* L.) in three, and alder (*Alnus glutinosa* L.) in two. The development and floristic composition of shrub and herbaceous layers also varied between the paired plots. In all coniferous woodland plots, pine (most *Pinus sylvestris* L.) was the dominant tree species and a shrub layer was almost absent. The herbaceous layer was characterized by species of poor soil conditions, of which *Deschampsia flexuosa* (L.) Trin. was most abundant.

### Breeding density

Breeding bird densities were measured as the number of territories per area unit using the mapping method according to Hustings *et al.* (1985). In the mapping method the number of territories of a species in an area is derived from all individual registrations of territorial behaviour made on several visits in the field. However, because of the rather small size of the plots, for some species that have large territories, the number of registrations was used to calculate densities. To calculate the total density of all species combined, the densities of species which were based on registrations were divided by two.

Every plot of a pair was visited 12 times from the beginning of March till the end of June. The distance of 50 m at which an observer should approach to all parts of the plot (Hustings *et al.* 1985) was reduced to 25 m in order to minimize the masking effect of traffic noise on bird song. For territories which overlapped the boundaries of a plot, only the proportion of the territory within the plot (based on percentage of registrations) was included in the calculation of density.



**Figure 1.** Main roads in The Netherlands (bold lines) and location of paired plots in deciduous woodland (open dots) and coniferous woodland (black dots).



## Traffic load

To measure the traffic load of plots or part of plots (see analysis) we used parameters for the noise load and for the visibility of cars. Other possible causes, such as pollution and road mortality, could not be measured quantitatively.

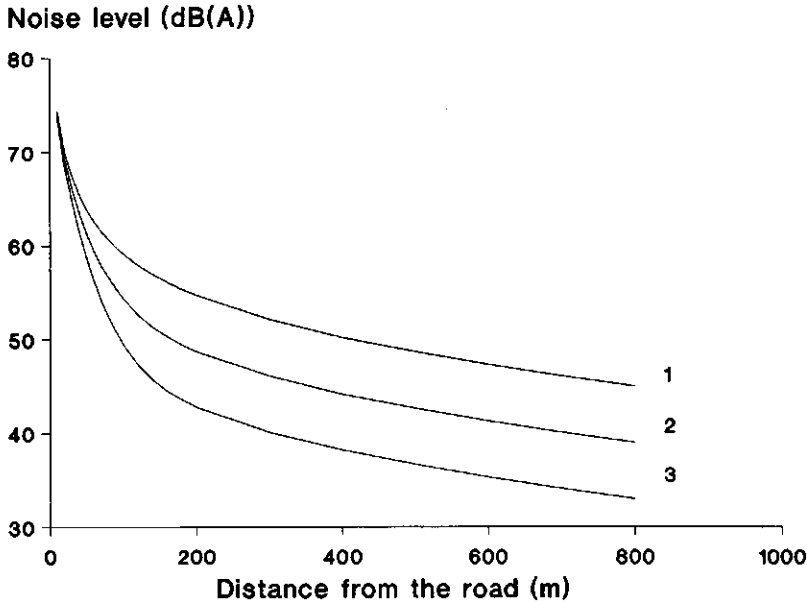
The noise load was estimated using an existing mathematical model, which expresses the noise level in dB(A) as the 24-hour value of the equivalent noise level (Moerkerken & Middendorp 1981). Calculated noise levels refer to points and the most relevant parameters in our study were: traffic density, speed and type of cars, shortest distance from the receiver point to the road and height of road above ground level. Other parameters such as road surface and ground surface did not vary and for the receiver height, 1 m was taken (other heights were investigated, but the calculated values were all strongly correlated with the 1 m data,  $r = > 0.90$ ).

Because the model does not take into account the noise reducing effect of woodland, which can be very important (Huisman 1990; Huisman & Attenborough 1991), the calculated noise levels were adapted by using a 'woodland effect term' according to Huisman (1990). This 'woodland effect term' is a function of woodland type, the shortest distance between road and receiver point, the receiver height and the proportion of woodland between receiver point and the road (PW). It is specific for road traffic noise and ranges from 0 to 12 dB(A) for most woodland types (deciduous and pine) and from 0 to 16 dB(A) for dense coniferous woodland. The maximum reduction is reached at 200 m from the road (see Fig. 2). Because changes in noise transmission between the road and the receiver point are most important in a sight angle from the receiver point to the road (Moerkerken & Middendorp 1981), assessing of PW was restricted to this sight angle (set at 143 degrees).

To obtain a mean noise level for a plot or part of a plot, the value of one representative point was taken. This point was situated in the middle of the line parallel to the road at a distance of  $10^{(\log DL - \log DS)/2}$  (log distance is chosen, because noise levels in dB(A) have a logarithmic scale), in which DL is the largest distance and DS the smallest distance of the plot from the road. Traffic data were available in reports of the Ministry of Traffic, Public Works and Water Management (traffic density, speed of cars, type of cars). The distance from the representative point to the road and PW were derived from cartographic maps. The height of the road above ground level and the woodland type were estimated in the field.

To measure the visibility of cars of plots or part of plots, a simple method was developed. The distance from the road where the traffic could not be seen any more, was the basic estimate. This was measured in early spring (leaves absent) and in late spring (leaves present). Assuming that the visibility of cars decreases with the distance to the road, the relative value for a plot (between 0 = no visibility and 1 = visibility

in the verge of the road) was calculated as the proportion of the plot influenced by visibility multiplied by the mean level of the visibility in the influenced part of the plot (see Fig. 3). Differences in traffic density and type of cars were not considered. It was assumed that when traffic is more or less continuous (> 10 000-20 000 cars a day), the visual experience of traffic remains constant.



**Figure 2.** Estimation of the noise load of car traffic along a highway with 50 000 cars a day and a speed of cars of 120 km/hour based on Moerkerken & Middendorp (1981) and Huisman (1990)(see Methods for further explanation). 1 = open field; 2 = proportion of woodland along the road 0.5; 3 = proportion of woodland along the road 1.0.

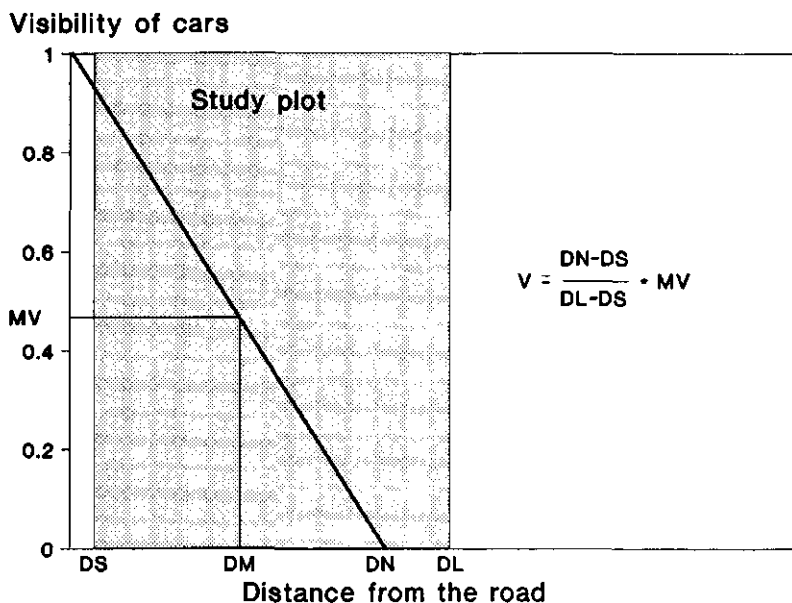
### Control of other factors that influence breeding density

To identify the effect of road traffic, we chose plots that were as similar as possible in other variables that influence breeding density. Because of the paired design, the similarity was only required for the plots of one pair. Variables taken into account were area of plots, vegetation structure, surrounding landscape and management. Only plots along roads used by traffic for more than five years were considered.

To assess the similarity of vegetation structure between the road and control plots of each pair the following measurements were made. The vegetation structure was

measured along randomly chosen transects with a length of 100 m. To obtain values for the vegetation cover, every 5 m the presence of vegetation was scored at eight height classes. Also the distance to the nearest tree from these points and the height and circumference of this tree were established. The proportion of the boundary of the plot bordering open field was used to characterize the edge.

Since species were not always present in all the paired plots of a series, additional tests were carried out on subsets of paired plots. The results were similar as compared with the whole dataset. Significant differences between road and control plots were only present in deciduous woodland and restricted to the cover of the layer > 20 m.



**Figure 3.** Estimation of a relative value for the visibility of cars (V) in woodland (see also Methods). DS = mean smallest distance of plot to the road, DL = mean largest distance of plot to the road, DN = mean distance from the road where traffic can no longer be seen any more, DM = mean distance from the road of the part of the plot that is influenced by visibility of cars, MV = mean value for the visibility in the influenced part of the plot (is value at DM). Because DS was always very close to the road, differences in the visibility of cars in the zone between the roadside and DS were neglected with respect to the visibility parameter.

**Table 1.** Habitat characteristics of road and control plots in deciduous and coniferous woodland (mean values). Statistical significance is based on Wilcoxon signed-ranks test.

Estimate	Deciduous woodland <i>n</i> =38			Coniferous woodland <i>n</i> =17		
	Road	Control	Sign.	Road	Control	Sign.
<i>Cover of vegetation layers (%)</i>						
< 25 cm	59	55	NS	72	75	NS
25-50 cm	31	35	NS	63	65	NS
50-100 cm	30	28	NS	33	33	NS
1-2 m	19	21	NS	3	8	NS
2-5 m	42	41	NS	25	27	NS
5-10 m	55	51	NS	56	49	NS
10-20 m	49	53	NS	37	33	NS
> 20 m	14	20	**			
<i>Tree characteristics</i>						
Circumference (cm)	87	86	NS	63	63	NS
In between distance (m)	3.1	2.8	NS	18.8	20.4	NS
Height (m)	16.4	17.0	NS	12.5	12.6	NS
<i>Size and edge</i>						
Size (ha)	4.04	4.24	NS	7.20	8.20	NS
Borderline with open area (%)	53	53	NS	55	46	NS

NS,  $P > 0.10$ ; \*\*  $P < 0.01$

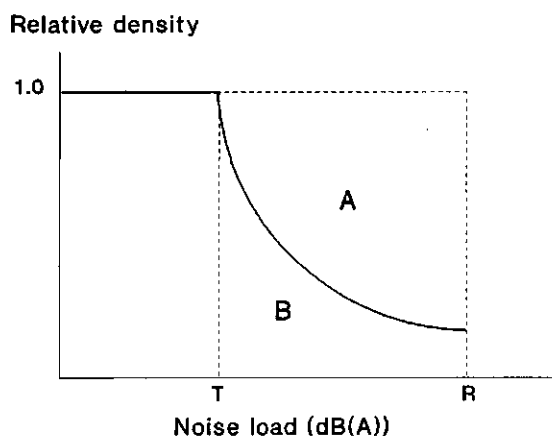
In deciduous woodland only one characteristic of the vegetation structure, the cover of the layer > 20 m, showed a significant difference between road and control plots (Table 1). However, it is not likely that this caused significant differences in breeding densities between road and control plots. The cover of the layer > 20 m was of minor importance for the structure of the deciduous woodlands and the difference between road and control plots was not supported by a difference in the height of the trees. There were no differences of vegetation structure between road and control plots in coniferous woodland plots.

## Analysis

In accordance with the study design (paired plots), the data were analyzed at first with the Wilcoxon signed-ranks test. A non-parametric test was chosen for robustness. The basic analysis was a comparison of densities between road and control plots. Moreover, to detect possible effects on the density at a very short distance from the road, large road plots (at least twice the required minimum size) were divided into two parts that were near to and far from the road. This was only done for road plots that had a very homogeneous vegetation structure. Because we expected lower densities close to the road, differences in density were tested one-sided. Deciduous woodland and coniferous woodland were treated as separate series of paired plots and an analysis for individual species was carried out if the number of territories was  $> 10$  or the number of registrations  $> 20$ .

In order to obtain information about the size of the effect on the density and to determine the relative importance of noise load and visibility of cars, a supplementary analysis was carried out using a regression model with noise load and visibility of cars as independent variables. Since both measurements of visibility of cars were strongly correlated with each other ( $r=0.95$ ), only visibility of cars in early spring (without leaves) was used in the regression analysis. Although the correlation between noise load and visibility of cars was also rather high ( $r=0.63$ ), using both explanatory variables in the regression models was considered acceptable. For a more precise measurement of the effect distance, large homogeneous plots were split in two or sometimes more subplots (depending on the size). As dependent variable the number of territories or registrations was taken and to model densities, the logarithm of the area of the (sub)plots was included in the model as an offset. Because counts tend to follow a Poisson-like distribution in which the variance is proportional to the mean, the numbers of territories were modelled by Poisson regression with correction for possible overdispersion (Jongman *et al.* 1987; see *F*-test below). Including a factor for pairs in the model accounted for differences between pairs of plots (which may be due to differences in vegetation structure, etc.). If the level of sensitivity of birds to traffic load follows a Gaussian distribution, the relation between numbers and traffic load is sigmoidal. However, theoretically the most ideal combination of fitting a sigmoidal relation with a Poisson regression and a factor for pairs was very difficult to compute. Instead, a threshold model was used: below the threshold there is no change in bird density; above the threshold an equal percentage of the number of territories disappears per unit of noise load. The threshold value and the decrease factor were estimated by loglinear Poisson regression with a numerical search procedure for the best-fitting threshold value. For the estimation of the decrease factor see Fig. 4. The significance of the effect of the noise level was tested with the *F*-test (Jorgensen 1989)

with two degrees of freedom (one for the threshold value and one for the slope) in the numerator and, therefore, had to be two-sided. However, in the absence of a threshold the test was one-sided. Over-dispersion was indicated if the mean deviance was larger than 1. In such cases the mean deviance was used as denominator of the  $F$ -statistic, otherwise the value 1 was used. An approximate 90% confidence interval for the threshold value was constructed as a sideproduct of our numerical search procedure for the best-fitting threshold value. The interval contains the threshold values which yielded deviance values that exceeded the minimum residual deviance by no more than  $sF$ , where  $s$  is the mean deviance (set to 1 if  $s$  was smaller than 1) at the best-fitting threshold value and  $F$  is the 90% point of an  $F$ -distribution with one degree of freedom in the numerator and the degrees of freedom of the residual in the denominator. Because some plots were split into subplots, some dependence between data was introduced. As a result, the confidence interval for the threshold value may be somewhat too narrow. We did not succeed in obtaining a simultaneous confidence region for the threshold and the decrease factor.



**Figure 4.** Estimation of the decrease factor of the density based on loglinear Poisson regression using a threshold model (see Methods).  $T$  = threshold value in  $\text{dB(A)}$ ,  $R$  = noise load in  $\text{dB(A)}$  in the verge of the road. The decrease factor = area of  $A$ /(area of  $A+B$ ).

To get a further indication of the importance of noise load and visibility of cars, subsets of paired plots were created in which the road plots differed in one explanatory variable but not in the other (see Table 2). This was only possible for deciduous woodland. If noise load is the most important cause of reduced densities one would

expect that the effect on the density in the subset with a high noise load is much larger than in the subset with a low noise load. Between the subsets that differed in visibility of cars, differences in the effect on the density should then be much smaller or absent. The analysis was done with the Wilcoxon signed-ranks test and regression.

Because of the small size of the data set, besides a significance level of  $P < 0.05$ , a significance level of  $P < 0.10$  was also considered. We used a comparison-wise significance level, to avoid loss of power and thereby accept that we are likely to mark too many species as showing a significance change.

**Table 2.** Traffic load of road plots for subsets of paired plots in deciduous woodland (mean values). Statistical significance is based on Wilcoxon signed ranks test.

Subset of plots	<i>n</i>	Cars per day	Noise load	Visibility of cars
Noise load				
High	19	33 179	58	0.46
Low	19	27 488	48	0.35
			***	NS
Visibility of cars				
High	19	30 562	53	0.61
Low	19	30 106	52	0.21
			NS	***

NS,  $P > 0.10$ ; \*\*\*  $P < 0.001$

## RESULTS

### Density in deciduous woodland

Of the 50 species present in the 38 paired plots, 41 (see Table 3) were sufficiently numerous to allow analysis. By using the Wilcoxon signed-ranks test, the density of 12 of the 41 species was reduced close to the road (at  $P < 0.10$ , 6 species at  $P < 0.05$ , Table 3). For three of these 12 species there was only an effect on the density when comparing parts of the road plots that were near to and far from the road (at  $P < 0.10$ , 1 species at  $P < 0.05$ , Table 3). Despite the negative effect on several species, the density of all species combined was not significant reduced close to the road (Table 3).

**Table 3.** Density of breeding birds in road (R) and control (C) plots of deciduous woodland. Species for which a comparison of densities within road plots was carried out are marked with parentheses and results are only shown if they were significant<sup>1</sup>.

Species	NP	NT	R	C	Sign.
<i>Anas platyrhynchos</i>	10	16	0.10	0.05	NS
<b><i>Buteo buteo</i></b> ( )	18	64	0.16	0.21	NS
<i>Phasianus colchicus</i>	13	60	0.13	0.22	*
<b><i>Cuculus canorus</i></b>	13	35	0.04	0.16	*
<i>Scolopax rusticola</i>	11	42	0.11	0.09	NS
<i>Columba oenas</i> ( )	14	37	0.08	0.12	NS
<i>Columba palumbus</i> ( )	30	186	0.59	0.54	NS
<b><i>Picus viridis</i></b>	7	27	0.05	0.12	NS
<i>Dendrocopos minor</i>	10	11	0.02	0.05	*
<i>Dendrocopos major</i> ( )	28	85	0.25	0.25	NS <sup>1</sup>
<i>Anthus trivialis</i>	8	33	0.09	0.08	NS
<i>Troglodytes troglodytes</i> ( )	34	289	0.91	0.96	NS
<i>Prunella modularis</i> ( )	16	41	0.16	0.14	NS
<i>Erithacus rubecula</i> ( )	34	357	1.09	1.00	NS
<i>Phoenicurus phoenicurus</i>	10	17	0.05	0.06	NS
<i>Turdus merula</i> ( )	38	350	1.15	1.04	NS
<i>Turdus philomelos</i> ( )	24	112	0.29	0.32	NS
<i>Acrocephalus palustris</i>	5	11	0.04	0.15	+
<i>Hippolais icterina</i>	7	16	0.11	0.15	*
<i>Sylvia borin</i> ( )	28	175	0.70	0.82	NS
<i>Sylvia atricapilla</i> ( )	35	172	0.56	0.62	NS
<i>Phylloscopus sibilatrix</i>	10	22	0.04	0.10	NS
<i>Phylloscopus collybita</i> ( )	35	222	0.87	0.90	NS
<i>Phylloscopus trochilus</i> ( )	26	264	0.70	0.98	**
<i>Regulus regulus</i>	7	23	0.05	0.07	+
<i>Muscicapa striata</i> ( )	26	85	0.27	0.24	NS
<i>Ficedula hypoleuca</i> ( )	13	27	0.09	0.06	NS
<i>Aegithalos caudata</i> ( )	25	39	0.17	0.13	NS
<i>Parus montanus</i>	18	31	0.09	0.19	NS
<i>Parus palustris</i> ( )	23	65	0.17	0.20	NS
<i>Parus caeruleus</i> ( )	33	252	0.79	0.75	NS
<i>Parus major</i> ( )	37	504	1.63	1.45	NS
<i>Sitta europea</i> ( )	18	65	0.22	0.17	NS
<i>Certhia brachydactyla</i> ( )	30	142	0.44	0.44	NS <sup>1</sup>
<i>Oriolus oriolus</i>	10	33	0.04	0.20	+
<i>Garrulus glandarius</i> ( )	29	146	0.50	0.40	NS
<i>Pica pica</i> ( )	17	66	0.20	0.23	NS <sup>1</sup>
<i>Corvus corone</i> ( )	29	185	0.83	0.71	NS
<i>Sturnus vulgaris</i>	20	121	0.41	0.45	NS
<i>Coccothraustes coccothraustes</i>	10	18	0.03	0.06	+
<i>Fringilla coelebs</i> ( )	32	238	0.72	0.85	NS
All species combined( )	38	4493	14.76	15.53	NS

<sup>1</sup>Significant lower density in part of road plots near to the road (N) than in part of road plots further away from the road (F). *Dendrocopos major*  $P < 0.01$  ( $N = 0.21$ ,  $F = 0.41$ ), *Certhia brachydactyla*  $P < 0.10$  ( $N = 0.50$ ,  $F = 0.66$ ), *Pica pica*  $P < 0.10$  ( $N = 0.33$ ,  $F = 0.56$ ).

NP, number of paired plots involved; NT, total number of territories or registrations. For species in bold the data are based on number of registrations. Statistical significance is based on Wilcoxon signed-ranks test. NS,  $P > 0.10$ ; +  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ .



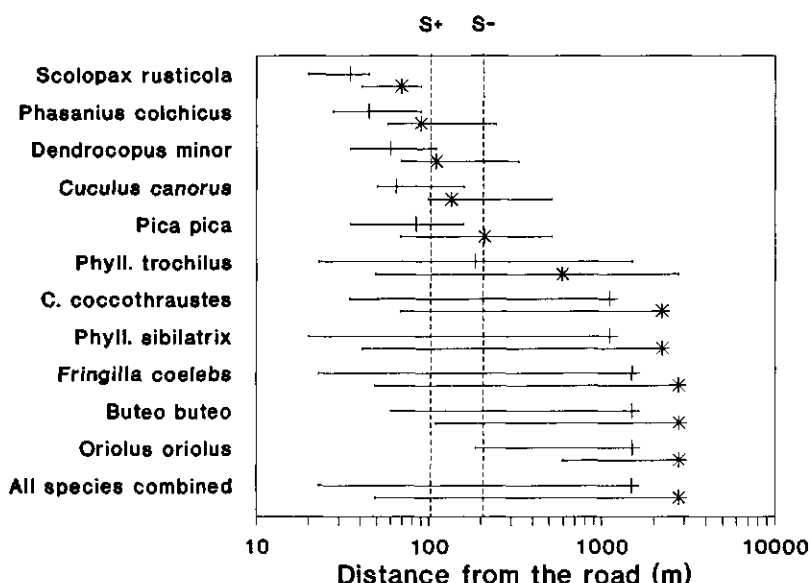
With regression the model with only noise load resulted in a significant reduction of the density for seven of the 12 species (at  $P < 0.10$ , 5 species at  $P < 0.05$ , Table 4) which showed an effect with the paired test and also for four additional species (at  $P < 0.10$ , 2 species at  $P < 0.05$ , Table 4). Moreover, there was an effect on the density of all species combined (at  $P < 0.10$ , Table 4). Adding visibility of cars to the model and assuming interaction between noise load and visibility of cars, did not improve these models. If noise load was replaced by visibility of cars, only five species with significant regressions remained (at  $P < 0.05$ , Table 4) and the effect on the density of all species combined disappeared. So the model with only noise load gives the best overall results. For the five species showing an effect with noise load and visibility of cars, the fit of the regression models was similar. This means that, in these species, the effect can either be explained by noise load or visibility of cars.

**Table 4.** Significant regressions of breeding density on noise load (N) or visibility of cars (V) in deciduous woodland using a threshold model (see Methods). For species in bold the data are based on number of registrations.

Species	N/V	df	F	T(CFL)	C	Sign.
<b><i>Buteo buteo</i></b>	N	1/45	2.88	$\leq 23(?-50)$	-0.050	*
<i>Phasianus colchicus</i>	N	2/28	5.15	53(45-58)	-0.253	*
	V	1/29	2.92	0(?-7)	-0.009	*
<b><i>Scolopax rusticola</i></b>	N	2/28	2.53	56(53-62)	-2.191	+
<b><i>Cuculus canorus</i></b>	N	2/31	8.28	49(40-52)	-1.143	**
	V	1/32	18.60	0(?-24)	-0.064	***
<i>Dendrocopus minor</i>	N	2/23	2.84	50(43-56)	-3.207	+
	V	2/23	3.81	46(33-59)	-1.191	*
<i>Phylloscopus sibilatrix</i>	N	1/24	5.41	$\leq 26(?-62)$	-0.052	*
<i>Phylloscopus trochilus</i>	N	2/61	4.30	39(?-60)	-0.034	*
	V	2/61	4.30	62(44-81)	-0.077	*
<i>Oriolus oriolus</i>	N	1/27	14.00	$\leq 23(?-39)$	-0.121	***
	V	1/27	13.00	0(?-57)	-0.038	***
<b><i>Pica pica</i></b>	N	2/43	2.95	46(40-56)	-0.086	+
<i>Coccothraustes coccothraustes</i>	N	1/30	3.30	$\leq 26(?-56)$	-0.067	*
<i>Fringilla coelebs</i>	N	1/66	2.51	$\leq 23(?-60)$	-0.013	+
All species combined	N	1/81	1.98	$\leq 23(?-60)$	-0.004	+

df, degrees of freedom; F, change in  $F$ -statistic (see Methods) after adding noise load or visibility of cars; T(CFL), threshold value in dB(A) and 90% confidence limits (? means that a lower limit could not be calculated); C, regression coefficient. NS,  $P > 0.10$ ; +  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

Effect distances (threshold value in m) were estimated for noise load only. Two traffic intensities were chosen that covered the whole range of intensities present in the data set: 10 000 and 60 000 cars a day. Other variables which influenced the effect distance were kept constant, such as car speed (120 km/hour) and amount of woodland along the road (70% = mean value for the plots). For 10 000 cars a day the effect distances of species varied from 40 to 1500 m, and for 60 000 cars a day from 70 to 2800 m (Fig. 5). However, the confidence limits were very large, especially for the large effect distances. The density decrease factor in the zone between the road and the threshold value was in most species very high (median 0.69) (Table 5). Calculated for a fixed zone of 250 m adjacent to the road, the decrease factor was still significant (10 000 cars/day, median 0.33; 60 000 cars/day, median 0.49)(Table 5).



**Figure 5.** Effect distances with confidence limits in m in deciduous woodland for 10 000 cars/day (---|---) and 60 000 cars/day (---\*---). The car speed was fixed at 120 km/hour and the amount of woodland along the road at 70%. Effect distances were derived from the regression with noise load as explanatory variable and a conversion of noise load to distance in m (see Methods). S = mean range of visibility of cars with leaves (+) or without leaves (-).

**Table 5.** Decrease factor (see Methods) of the breeding density for species and all species combined in deciduous woodland in the zone between the road and the threshold value and in a fixed zone of 250 m from the road. Based on regressions with noise load as explanatory variable. For species in bold the data are based on number of registrations.

Species	Decrease factor up to threshold	Decrease factor up to 250 m	
		10 000 cars a day	60 000 cars a day
<b><i>Buteo buteo</i></b>	0.62	0.76	0.81
<i>Phasianus colchicus</i>	0.77	0.14	0.28
<b><i>Scolopax rusticola</i></b>	0.97	0.14	0.27
<b><i>Cuculus canorus</i></b>	0.96	0.25	0.52
<i>Dendrocopus minor</i>	0.98	0.24	0.43
<i>Phylloscopus sibilatrix</i>	0.61	0.73	0.79
<i>Phylloscopus trochilus</i>	0.38	0.28	0.45
<i>Oriolus oriolus</i>	0.82	0.95	0.98
<b><i>Pica pica</i></b>	0.58	0.20	0.49
<i>Coccothraustes coccothraustes</i>	0.68	0.81	0.86
<i>Fringilla coelebs</i>	0.25	0.32	0.36
All species combined	0.09	0.11	0.13

### Density in coniferous woodland

Of the 28 species occurring in the 17 paired plots, 18 species (see Table 6) were sufficiently numerous to allow an analysis. By using the Wilcoxon signed-ranks test, only four species showed a reduced density close to the road (at  $P < 0.10$ , 3 species at  $P < 0.05$ , Table 6), but there was a clear effect on the density of all species combined (at  $P < 0.05$ , Table 6).

Because there was a strong correlation between noise load and visibility of cars ( $r = > 0.90$ ), the regression was carried out with noise load only. Of the five species which showed an effect (at  $P < 0.10$ , 2 species at  $P < 0.05$ , Table 7), two also had an effect with the paired test. Again there was also a clear effect on the density of all species combined (at  $P < 0.05$ , Table 7).

Effect distances and decrease factors were calculated using the same traffic data and amount of woodland along the road as for deciduous woodland. The effect distances of species varied from 50 to 790 m for 10 000 cars a day and from 100 to 1750 m for 60 000 cars a day (Fig. 6). The decrease factor of the density in the disturbed zone value was in most species very high (median 0.61) and remained

important if calculated for a fixed zone of 250 m (10 000 cars/day: median 0.23; 60 000 cars/day: median 0.60) (Table 8).

**Table 6.** Density of breeding birds in road (R) and control (C) plots of coniferous woodland. Species for which a comparison of densities within road plots was carried out are marked with parentheses and results are only shown if they were significant<sup>1</sup>.

Species	NP	NT	R	C	Sign.
<i>Columba palumbus</i> ()	11	48	0.32	0.63	*
<i>Anthus trivialis</i> ()	10	30	0.13	0.23	NS
<i>Troglodytes troglodytes</i> ()	14	37	0.16	0.22	NS
<i>Erithacus rubecula</i> ()	16	55	0.32	0.26	NS
<i>Turdus merula</i>	13	25	0.09	0.15	NS
<i>Sylvia atricapilla</i>	5	11	0.04	0.05	NS
<i>Phylloscopus collybita</i> ()	8	23	0.10	0.11	NS
<i>Phylloscopus trochilus</i>	8	24	0.11	0.25	*
<i>Regulus regulus</i> ()	14	41	0.22	0.36	* <sup>1</sup>
<i>Parus montanus</i>	12	19	0.06	0.11	NS
<i>Parus cristatus</i> ()	16	48	0.29	0.33	NS
<i>Parus ater</i> ()	15	29	0.17	0.29	+
<i>Parus caeruleus</i>	8	12	0.05	0.09	NS
<i>Parus major</i> ()	17	49	0.26	0.27	NS
<i>Garrulus glandarius</i>	13	39	0.12	0.32	NS
<i>Pica pica</i> ()	10	59	0.31	0.26	NS
<i>Corvus corone</i> ()	11	108	0.42	0.38	NS
<i>Fringilla coelebs</i> ()	13	77	0.45	0.52	NS
All species combined()	17	256	2.35	3.39	*

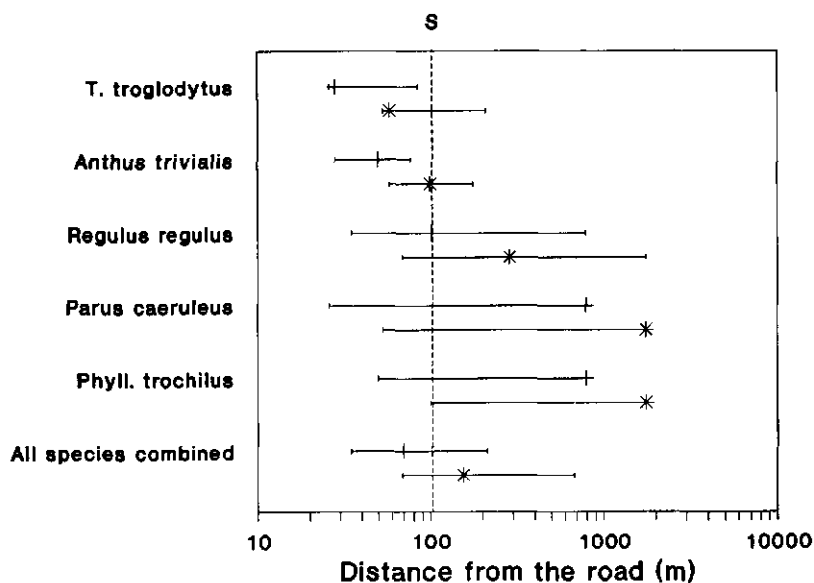
<sup>1</sup>Also significant lower density in part of road plots near to the road (N) than in part of road plots further away from the road (F). *Regulus regulus*  $P < 0.01$  ( $N = 0.04$ ,  $F = 0.22$ ).

NP, number of paired plots involved; NT, total number of territories or registrations. For species in bold the data are based on number of registrations. Statistical significance is based on Wilcoxon signed-ranks test. NS,  $P > 0.10$ ; +  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ .

**Table 7.** Significant regressions of breeding density on noise load in coniferous woodland using a threshold model (see Methods).

Species	df	F	T(CFL)	C	Sign.
<i>Anthus trivialis</i>	2/23	4.12	52(47-58)	-2.618	*
<i>Troglodytes troglodytes</i>	2/25	2.72	58(46-59)	-6.846	+
<i>Phylloscopus trochilus</i>	1/17	3.00	≤ 29(?-52)	-0.043	*
<i>Regulus regulus</i>	2/28	3.54	44(?-56)	-0.080	+
<i>Parus caeruleus</i>	1/19	2.46	≤ 29(?-59)	-0.057	+
All species combined	2/30	5.84	8(38-56)	-0.042	**

df, degrees of freedom; F, change in *F*-statistic (see Methods) after adding noise load; T(CFL), threshold value in dB(A) and 90% confidence limits (? means that a lower limit could not be calculated); C, regression coefficient. +  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ .



**Figure 6.** Effect distances with confidence limits in m in coniferous woodland for 10 000 cars/day (—|—) and 60 000 cars/day (---\*---). The car speed was fixed at 120 km/hour and the amount of woodland along the road at 70%. Effect distances were derived from the regression with noise load as explanatory variable and a conversion of noise load to distance in m (see Methods). S = mean range of visibility of cars.

**Table 8.** Decrease factor (see Methods) of the breeding density for species and all species combined in coniferous woodland in the zone between the road and the threshold value and in a fixed zone of 250 from the road. Based on regressions with noise load as explanatory variable.

Species	Decrease factor up to threshold	Decrease factor up to 250 m	
		10 000 cars a day	60 000 cars a day
<i>Anthus trivialis</i>	0.98	0.20	0.39
<i>Troglodytes troglodytes</i>	0.99	0.11	0.23
<i>Phylloscopus trochilus</i>	0.53	0.62	0.69
<i>Regulus regulus</i>	0.58	0.61	0.74
<i>Parus caeruleus</i>	0.61	0.23	0.78
All species combined	0.35	0.10	0.22

#### Comparison of densities in subsets of paired plots differing in noise load or visibility of cars

In the two subsets of paired plots that differed in noise load but not in visibility of cars, 28 species could be compared. With the Wilcoxon signed-ranks test nine species showed a lower density close to the road in the subset with a high noise load (at  $P < 0.10$ , 4 at  $P < 0.05$ , Table 9) and only two in the subset with a low noise load (at  $P < 0.05$ , Table 9). Moreover, in the subset with a low noise load all species had an effect at a very short distance (comparison of densities within road plots), while in the subset with a high noise load this was only the case in three of the nine species (Table 9). With regression, using noise load as the explanatory variable, negative effects on the density were only found in the subset of paired plots with a high noise load (7 species at  $P < 0.05$ , Table 10). This supports the results obtained with the Wilcoxon signed-ranks test. Furthermore, for the density of all species combined, there was only a negative effect in the subset of paired plots with a high noise load (at  $P < 0.05$ , Tables 9 and 10).

For the two subsets of paired plots that differed in visibility of cars but not in noise load, no clear pattern arose. Here, 26 species could be compared. With the Wilcoxon signed-ranks test, only three species showed a lowered density close to the road with a high visibility of cars (at  $P < 0.10$ , 1 species at  $P < 0.05$ , Table 11) and three with a low visibility of cars (at  $P < 0.10$ , 2 at  $P < 0.05$ , Table 11). In the regression analysis, with visibility of cars as the explanatory variable, the number of species that showed a negative effect on the density was two in plots with high visibility (at  $P < 0.10$ , 1 species at  $P < 0.05$ , Table 12) and one in low visibility plots (at  $P < 0.10$ , Table 12). In none of these cases was an effect on the density of all species found.

**Table 9.** Density of breeding birds in road (R) and control (C) plots of deciduous woodland with high and low noise load. Species for which a comparison of densities within road plots was carried out are marked with parentheses and results are only shown if they were significant<sup>1</sup>. NP, number of paired plots involved. For species in bold the data are based on number of registrations. Statistical significance is based on Wilcoxon signed-ranks test.

Species	Noise load high				Noise load low			
	NP	R	C	Sign.	NP	R	C	Sign.
<i>Phasianus colchicus</i>	9	0.07	0.28	**	5	0.19	0.17	NS
<i>Buteo buteo</i>	9	0.15	0.12	NS	8	0.17	0.29	NS
<i>Scolopax rusticola</i>	6	0.12	0.07	NS	5	0.11	0.11	NS
<i>Colomba oenas</i>	8	0.09	0.08	NS	6	0.06	0.15	NS
<i>Columba palumbus</i> ()	14	0.53	0.49	NS	16	0.62	0.55	NS
<i>Dendrocopus major</i> ()	11	0.22	0.25	NS <sup>1</sup>	17	0.28	0.25	NS <sup>1</sup>
<i>Troglodytes trogl.</i> ()	17	0.70	0.78	NS	17	1.11	1.14	NS
<i>Prunella modularis</i>	9	0.19	0.18	NS	7	0.12	0.10	NS
<i>Erithacus rubecula</i> ()	16	1.15	1.11	NS	18	1.00	0.90	NS
<i>Turdus merula</i> ()	19	1.07	0.99	NS	19	1.24	1.10	NS
<i>Turdus philomelos</i> ()	13	0.40	0.41	NS <sup>1</sup>	10	0.20	0.25	NS
<i>Sylvia borin</i> ()	14	0.62	1.13	*	14	0.78	0.51	NS
<i>Sylvia atricapilla</i> ()	17	0.48	0.72	+	17	0.65	0.57	NS
<i>Phylloscopus collybita</i> ()	18	0.78	0.94	+	17	0.96	0.86	NS
<i>Phylloscopus trochilus</i> ()	13	0.69	1.12	**	13	0.72	0.83	NS
<i>Muscicapa striata</i> ()	13	0.26	0.24	NS	13	0.28	0.25	NS
<i>Aegithalos caudata</i>	12	0.14	0.16	NS	13	0.19	0.10	NS
<i>Parus montanus</i>	8	0.10	0.14	NS	10	0.08	0.23	NS
<i>Parus palustris</i>	11	0.20	0.25	+	12	0.14	0.15	NS
<i>Parus caeruleus</i> ()	17	0.78	0.74	NS	16	0.79	0.75	NS
<i>Parus major</i> ()	19	1.58	1.54	NS	18	1.67	1.36	NS
<i>Sitta europaea</i>	9	0.21	0.18	NS	9	0.23	0.16	NS
<i>Certhia brachydactyla</i> ()	15	0.42	0.44	NS <sup>1</sup>	15	0.46	0.44	NS <sup>1</sup>
<i>Garrulus glandarius</i> ()	15	0.53	0.42	NS	14	0.47	0.38	NS
<i>Pica pica</i> ()	8	0.15	0.16	NS	9	0.24	0.30	NS
<i>Corvus corone</i> ()	14	0.82	0.46	NS	15	0.84	0.97	NS
<i>Sturnus vulgaris</i>	10	0.45	0.59	NS	10	0.36	0.31	NS
<i>Fringilla coelebs</i> ()	16	0.61	0.87	NS	16	0.82	0.83	NS
All species combined()	19	13.30	15.80	*	19	14.10	13.30	NS

<sup>1</sup> Significant lower density in part of road plots near to the road (N) than in part of road plots further away from the road (F). *Dendrocopus major*  $P < 0.05$  (noise load high,  $N = 0.10$ ,  $F = 0.25$ ) and  $P < 0.01$  (noise load low,  $N = 0.17$ ,  $F = 0.45$ ), *Turdus philomelos*  $P < 0.10$  ( $N = 0.49$ ,  $F = 0.79$ ), *Certhia brachydactyla*  $P < 0.10$  (noise load high,  $N = 0.44$ ,  $F = 0.64$ ) and  $P < 0.05$  (noise load low,  $N = 0.57$ ,  $F = 0.83$ ).

NS,  $P > 0.10$ ; +  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ .

**Table 10.** Significant regressions of breeding density on noise load in deciduous woodland with high noise load using a threshold model (see Methods). For species in bold the data are based on number of registrations.

Species	df	F	T(CFL)	C	Sign.
<i>Phasianus colchicus</i>	2/15	5.28	40(?-58)	-0.099	*
<i>Scolopax rusticola</i>	2/11	3.99	56(55-61)	-2.515	*
<i>Sylvia borin</i>	1/27	3.24	≤23(?-54)	-0.024	*
<i>Sylvia atricapilla</i>	1/37	4.20	≤23(?-48)	-0.036	*
<i>Phylloscopus trochilus</i>	2/29	5.73	38(?-50)	-0.046	**
<i>Pica pica</i>	2/22	3.45	46(33-56)	-0.092	*
<i>Fringilla coelebs</i>	1/33	3.39	≤23(?-56)	-0.019	*
All species combined	1/38	5.30	≤23(?-48)	-0.008	*

df, degrees of freedom; F, change in *F*-statistic (see methods) after adding noise load; T(CFL), threshold value in dB(A) and 90% confidence limits (? means that a lower limit could not be calculated); C, regression coefficient. \*  $P < 0.05$ ; \*\*  $P < 0.01$ .

## DISCUSSION

### Reduction of densities

Of the 43 species that could be analyzed in the paired plots of deciduous and coniferous woodland, 26 species (60%) showed evidence of a reduced density (Wilcoxon signed-ranks test and regression). Although one can argue that there is some uncertainty for species that had a weakly significant effect (only  $P < 0.10$ ), there still remain 18 species with a significant effect at  $P < 0.05$  (= 42%). This is considerably more than the few available studies indicate (Reijnen & Thissen 1987; Adams & Geis 1981; Ferris 1979). Nine of the 10 species which showed an effect in the study of Reijnen & Thissen (1987), also did so in this study. So, the results indicate that along busy roads, car traffic causing reduced densities of breeding birds in woodland, is a rather general phenomenon. This is reinforced by the fact that species of very different taxonomic groups were affected.

Of the few available studies that give rough estimates of the effect distance and the size of the effect on the density, only the study of Reijnen & Thissen (1987) allows an appropriate comparison with our results of deciduous woodland. They investigated similar species along a highway with 45 000 cars/day and estimated a mean effect distance of about 500 m and a decrease factor of the density for all species combined of 0.15. Although the decrease factor for all species combined is



**Table 11.** Density of breeding birds in road (R) and control (C) plots of deciduous woodland with high and low visibility of cars. Species for which a comparison of densities within road plots was carried out are marked with parentheses and results are only shown if they were significant<sup>1</sup>.

Species	Visibility of cars high				Visibility of cars low			
	NP	R	C	Sign.	NP	R	C	Sign.
<i>Phasianus colchicus</i>	5	0.21	0.24	NS	8	0.05	0.20	**
<i>Buteo buteo</i>	9	0.18	0.25	NS	8	0.13	0.16	NS
<i>Columba palumbus</i> ()	15	0.55	0.59	NS	15	0.63	0.49	NS
<i>Dendrocopus major</i> ()	16	0.32	0.28	NS	12	0.17	0.21	NS <sup>1</sup>
<i>Troglodytes troglod.</i> ()	17	0.92	0.96	NS	17	0.89	0.90	NS
<i>Prunella modularis</i>	8	0.16	0.13	NS	8	0.15	0.16	NS
<i>Erethacus rubecula</i> ()	20	1.21	1.26	NS	15	0.76	0.81	NS
<i>Turdus merula</i> ()	19	1.36	1.10	NS	19	0.94	0.98	NS
<i>Turdus philomelos</i> ()	15	0.26	0.33	NS	9	0.33	0.32	NS
<i>Sylvia borin</i> ()	13	0.54	0.48	NS	15	0.86	1.16	NS
<i>Sylvia atricapilla</i> ()	18	0.50	0.61	+ <sup>1</sup>	16	0.63	0.67	NS
<i>Phylloscopus collybita</i> ()	17	0.74	0.85	NS	18	1.00	0.96	NS
<i>Phylloscopus trochilus</i> ()	12	0.26	0.66	** <sup>1</sup>	14	1.14	1.40	+
<i>Muscicapa striata</i> ()	14	0.35	0.28	NS	13	0.41	0.41	NS
<i>Aegithalos caudata</i>	13	0.18	0.14	NS	12	0.15	0.12	NS
<i>Parus palustris</i>	15	0.25	0.32	NS	8	0.10	0.08	NS
<i>Parus montanus</i>	7	0.08	0.13	NS	11	0.10	0.25	NS
<i>Parus caeruleus</i> ()	18	0.94	0.86	NS	15	0.63	0.64	NS
<i>Parus major</i> ()	19	1.83	1.58	NS	19	1.28	1.28	NS
<i>Sitta europaea</i>	11	0.35	0.22	NS	7	0.09	0.12	NS
<i>Certhia brachydactyla</i> ()	18	0.53	0.62	NS <sup>1</sup>	12	0.35	0.26	NS
<i>Garrulus glandarius</i> ()	15	0.51	0.42	NS	14	0.50	0.38	NS
<i>Pica pica</i> ()	7	0.16	0.15	NS	10	0.23	0.31	NS
<i>Corvus corone</i> ()	14	0.54	0.59	NS	15	1.07	0.83	NS
<i>Sturnus vulgaris</i>	14	0.68	0.67	NS	6	0.14	0.22	NS
<i>Fringilla coelebs</i> ()	17	0.82	0.97	NS	15	0.61	0.73	NS
All species combined()	15	13.00	13.70	NS	16	11.70	12.50	NS

<sup>1</sup> Significant lower density in part of road plots near to the road (N) than in part of road plots further away from the road (F). *Dendrocopus major*  $P < 0.01$  ( $N = 0.18$ ,  $F = 0.45$ ), *Sylvia atricapilla*  $P < 0.10$  ( $N = 0.45$ ,  $F = 0.63$ ), *Phylloscopus trochilus*  $P < 0.05$  ( $N = 0.17$ ,  $F = 0.84$ ), *Certhia brachydactyla*  $P < 0.10$  ( $N = 0.41$ ,  $F = 0.64$ ).

NP, number of paired plots involved. For species in bold the data are based on number of registrations. Statistical significance is based on Wilcoxon signed-ranks test. NS,  $P > 0.10$ ; +  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ .

**Table 12.** Significant regressions of breeding density on visibility of cars in deciduous woodland with high (H) and low (L) visibility of cars using a threshold model (see Methods).

Species	H/L	df	F	T(CFL)	C	Sign.
<i>Phasianus colchicus</i>	H	2/7	3.38	50(11-71)	-0.058	+
<i>Phylloscopus trochilus</i>	H	1/27	12.16	0(?-41)	-0.017	**
<i>Fringilla coelebs</i>	L	1/33	2.74	0(?-57)	-0.010	+

df, degrees of freedom; F, change in *F*-statistic (see methods) after adding visibility of cars; T(CFL), threshold value in dB(A) and 90% confidence limits (? means that a lower limit could not be calculated); C, regression coefficient. +  $P < 0.10$ ; \*\*  $P < 0.01$ .

somewhat higher than in this study, the effect distance is much lower. These differences could be due to the rough and descriptive method used by Reijnen & Thissen (1987)(comparison of densities in plots at different distances from the road). However, the difference in the effect distance is not necessarily significant, since the value of Reijnen & Thissen (1987) remains within our confidence limits (see Fig. 5). Moreover, our largest effect distances might be overestimated, because they were obtained from regressions in which a threshold was absent. The absence of a threshold could be due to the relative small numbers of sub plots at a greater distance from the road.

#### Possible causes of reduced densities

The fact that significant relations were found between traffic related factors and breeding density suggest that car traffic and not the presence of a road *per se*, is the main cause of the observed effects (see also Van der Zande *et al.* 1980; Illner 1992a). This is supported by the relatively small numbers of reduced densities in the subset of paired plots with a low noise load.

This study suggests that the effect of car traffic on breeding bird densities in woodland can be largely explained by noise load. For subsets of paired plots which differed in noise load but not in visibility of cars, a larger number of species had a reduced density with a high noise load than with a low noise load. On the other hand, there were no clear differences between subsets of paired plots which differed in visibility of cars but not in noise load. Furthermore, the few significant relationships with visibility, when noise load is held constant, are all for species in which noise levels produce models which are at least as good. Although the absolute numbers of species involved are actually not very great, the noise load hypothesis is in particular supported by the fact that effects on the density of all species combined were only found in the subset of paired plots with a high noise load. Moreover, of all (sub)sets of paired plots, the number of species that had reduced densities was highest in this

subset. One can point out that the measurement of visibility of cars might give some uncertainty, because differences in traffic density were not taken into account. However, it is unlikely that this would be very important, since traffic densities were rather high and quite similar in all subsets of paired plots in deciduous woodland (Table 2).

Because other possible causes such as collisions and pollution (e.g. van der Zande *et al.* 1980; Reijnen & Thissen 1987) were not considered in our analysis, the noise load is not necessarily the only cause of the reduced densities. However, there is some evidence that these other factors are not very important. It is assumed that an increase of mortality due to road traffic is not very important in causing reduced densities near the road (e.g. Leedy & Adams 1982; Ellenberg *et al.* 1981). This is plausible for species which have small territories and that are less likely to fly across roads ( $\pm 60\%$  of the studied species), which is supported by a study of Reijnen & Foppen (1994). They observed equal survival rates of male willow warblers *Phylloscopus trochilus* (which showed a clear decreased density near the road in our plot series) close to a highway and in areas at a distance of several hundred meters. On the other hand, a study by Sargeant (1981) indicates that also in species with large territories (ducks), road mortality (0.2% of breeding populations) cannot be very important in reducing densities. Only for owls, in particular barn owl *Tyto alba*, there is some indication that road mortality might influence population levels (van den Tempel 1993; Illner 1992b). However, owls were not present in our data set.

Pollution caused by road traffic can affect abundance and size of insects adjacent to roads (Przybylski 1979; Bolsinger & Flückinger 1989) and therefore might have an effect on densities of breeding birds by reducing the availability of insects as a food source. However, the reported range of the effect is very small (up to 50 m from the road in rather open area). Moreover, of the 27 insectivorous species investigated in this study, only 16 species showed a reduced density of which 13 had a maximum effect distance between 100 and 1500 m.

Pollution can also cause increased levels of toxic substances in birds. This has been shown for lead, but the levels were far below the toxic level (Grue *et al.* 1986; Lowell *et al.* 1977) and an effect on reproduction and mortality could not be established (Lowell *et al.* 1977).

There is also a more general indication that pollution by car traffic is not very important as a cause of reduced densities. P. Kuggeleijn (pers. comm.) estimated that in woodland concentrations of exhaust gases and other pollutants reaches background levels within 50 m from a highway with dense traffic (40-50 000 cars a day). The majority of the species in this study (75%), however, showed maximum effect distances between 100 and 1500 m (see Fig. 5 and 6).

Very little is known about how noise load could cause reduced densities of breeding birds. An obvious explanation would be disturbance of the communication pattern between birds (see also Martens *et al.* 1985). Reijnen & Foppen (1994) found that male willow warblers *Phylloscopus trochilus* close to a highway experienced difficulties in attracting or keeping a female and moved away from the road in the following year. It was argued that distortion of the song might be a possible cause of this effect. In the hazelhen *Bonasia bonasia* it was assumed that the decrease of the breeding density in partly urbanized areas was due too a more permanent increase of the noise level, which increases predation by hampering hearing alarm calls (Scherzinger 1973). However, there are some indications that disturbance of the communication pattern is not a general mechanism in causing reduced densities. Traffic noise in woodland has a wide frequency band of at least 100 Hz to about 10 kHz with the highest sound pressure levels between 100-200 Hz and 0.5-4 kHz (Huisman & Attenborough 1992). So, if disturbance of communication is an important mechanism, those species producing song and calls with a frequency band similar to these highest sound pressure levels of traffic noise would be expected to be more vulnerable. Frequency bands of song and calls of birds were taken from Bergmann & Helb (1982). However, there was not a clear pattern (chi-squared test, 2 df,  $P > 0.10$ , Table 13), but the numbers are low and hardly allow statistical testing. Because there are indications that noise load due to car traffic can cause stress in birds (Helb & Hüppop 1991), an alternative, or more likely, a supplementary explanation could be that birds avoid road habitats because of this aspect (cf. Reijnen & Foppen 1994).

**Table 13.** Reduction of density of species related to coverage of the frequency spectrum of song and calls by the frequency spectrum of traffic noise (see also Discussion).

Frequency spectrum of traffic noise, and of song and calls of the studied bird species	Number of species with	
	Reduced density	No effect on density
Similar	9	6
Partly similar	7	7
Not similar	10	4

### Population consequences and practical implications

Because the analysis was based on the hypothesis that there is a negative relationship between car traffic and breeding density, possible positive relations could not be detected. One might argue that species which are not affected by road traffic can reach higher densities if related species are affected (due to competition). The presence of road victims could also favour feeding conditions of carrion eaters, such as many corvid species (e.g. Ellenberg *et al.* 1981). This would diminish the overall effect on the breeding density. However, such patterns could not be detected in our data. One corvid species, the magpie *Pica pica*, even showed a negative effect on the breeding density. Moreover, in both woodland types the total density of all species combined was reduced close to the road. The fact that in deciduous woodland only a weak significance was found, could be due to the large number of paired plots with a low noise load close to the road. For the subset of paired plots with a high noise load the density of all species combined was clearly reduced (Tables 9 and 10).

The available studies also do not indicate positive effects of car traffic. Although higher densities close to roads were found in some studies (Ferris 1979; Clark & Karr 1979; Adams & Geis 1981), in the first two studies this was explained by differences in the vegetation structure. For the study of Adams & Geis (1981) this was shown by a rough recalculation of the data. They investigated breeding densities of species in transects perpendicular to roads and observed lower densities close to the road in seven species and higher densities in nine species. Excluding the part of the transects close to the road (which had different habitat features), six species had reduced densities towards the road and higher densities towards the road were no longer observed.

Since road traffic affects a large proportion of breeding bird species in woodland and causes significant reductions of the density up to large distances from the road, the effect is probably important in affecting breeding bird populations in larger areas. This is reinforced by the assumption that lower densities indicate a lower habitat quality (van der Zande *et al.* 1980; Reijnen & Thissen 1987), which was verified for the willow warbler (Reijnen & Foppen 1994). Because differences in density will not always equally reflect differences in quality (e.g. Van Horne 1983; Bernstein *et al.* 1991), the reduction of the habitat quality along roads might be underestimated.

The results of this study stress the importance of considering the effect of car traffic on the breeding density of birds in designing new and modifying existing major roads. If noise load is the most important cause of reduced densities, it is possible to reduce these effects by constructing noise muffling devices along roads. However, to justify such expenditure it is necessary to provide further evidence that noise load is the main cause of the reduced densities of many bird species adjacent to busy roads.

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## 2.2 REDUCTION OF DENSITY OF BREEDING BIRDS IN AGRICULTURAL GRASSLANDS

### ABSTRACT

The effect of car traffic on the breeding density of grassland birds was studied in 1989 in 15 transects along main roads in The Netherlands. Out of 12 species that could be analyzed, seven showed a reduced density adjacent to the road. There was also a strong effect on the summed densities of all species. Disturbance distances varied between species, ranging from 20 to 1700 m from the road at 5000 cars a day and from 65 to 3530 m at 50 000 cars a day (car speed 120 km per hour). At 5000 cars a day most species had an estimated population loss of 12-56% within 100 m of roads, but beyond 100 m >10% loss only occurred in black-tailed godwit (22% for 0-500 m zone) and oystercatcher (44% up to 500 m and 36% for 0-1500 m zone). At 50 000 cars a day all species had estimated losses of 12-52% up to 500 m while lapwing, shoveler, skylark, black-tailed godwit and oystercatcher populations were reduced by 14-44% up to 1500 m. In The Netherlands, with a dense network of extremely crowded motorways, car traffic should be considered a serious threat to breeding bird populations in grasslands. Greater care should be taken in planning new roads, and it is important to explore how the present effects can be reduced.

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## INTRODUCTION

In The Netherlands, there is much interest in the effects of disturbance from roads on breeding bird populations in agricultural grasslands. This was initiated by a preliminary study by Veen (1973), who found that the summed densities of five wader species (lapwing *Vanellus vanellus* L., black-tailed godwit *Limosa limosa* L., oystercatcher *Haematopus ostralegus* L., redshank *Tringa totanus* L. and ruff *Philomachus pugnax* L.) were depressed over surprisingly large 'disturbance distances' from roads (from 500-600 m for a quiet rural road to 1600-1800 m for a busy highway). Van der Zande *et al.* (1980) reanalyzed the data of Veen (1973) by separating the influences of roads and agricultural practice, and came to similar conclusions for black-tailed godwit and lapwing estimating a total breeding population loss of 60% in the disturbed zone. Numbers of redshank and ruff were too small to be analysed separately, while there was no effect on oystercatcher. However, the number of sampling units (transects perpendicular to the road) was very low in both studies and no quantitative statistical analyses were carried out. Results of some other preliminary studies (discussed in Reijnen & Foppen 1991) also indicate a possible effect of roads on oystercatchers.

These waders represent only a part of the bird community in agricultural grasslands and there is some circumstantial evidence for effects of roads on other species (see review in Reijnen & Foppen 1991). Furthermore, a few studies in other open habitat types show that species from several other taxa can have depressed densities adjacent to main roads (Clark & Karr 1979; Illner 1992). The density depressing effect of roads has also been found in a wide variety of breeding bird species in woodland (Reijnen *et al.* 1995).

The aim of this study was (1) to obtain more accurate information on the disturbance distances and density reductions in these waders by collecting fresh data and applying quantitative statistical techniques, and (2) to test the hypothesis that other bird species are also affected by car traffic.

## METHODS

### Study areas and site selection

The study was carried out in 1989 in open moist grassland in the north and west of The Netherlands. To obtain sufficient data of many species, areas which had a total density of more than 50 territories per 100 ha were considered. In these areas 15 transects perpendicular to main roads were established (Fig. 1). The traffic density



varied from 3000 to 52 000 cars a day (mean 29 685 cars) and all roads had been used by traffic for more than 15 years.



**Figure 1.** Main roads in The Netherlands (bold lines) and location of study sites (open dots).

The open grassland was divided by a fine maze of ditches. Power lines, hedge-rows, wooded banks and farm houses, which can depress grassland bird densities over considerable distances (Van der Zande *et al.* 1980), did not occur within 250 m of the transects.

The transects started at the road side and were 634-2626 m (mean 1318 m) long. The mean width was 950 m and the areas varied from 70 to 297 ha (mean 149 ha). Each transect was divided into 3-10 strips (mean 5) parallel to the road. To obtain reliable bird densities, strips were at least 200 m broad and 20-25 ha (based on Hustings *et al.* 1985).

Strips within a transect were similar in abiotic conditions and the presence of small roads and ditches. Where more than one soil type or ground water level occurred they were equally distributed over the strips and there was no indication that roads influenced the hydrology of the transects. Owing to agricultural activities there was also very little variation in the floristic composition of the grasslands. In 11 transects intensively used for dairy farming, *Lolium perenne* L. was the dominant plant species, and in four transects situated in nature reserves for grassland birds the vegetation was characterized by *Poa trivialis* L., *Alopecurus geniculatus* L., *A. pratensis* L. and *Rumex acetosa* L.

### **Breeding density**

Breeding bird densities were measured from all individual registrations of territorial behaviour made on several field visits (Hustings *et al.* 1985). Each plot was visited seven times between 1 April and 15 June. For territories which overlapped the boundaries of a strip, the proportion of the territory within each strip (based on % of registrations) was used in the calculation of the densities.

### **Traffic load**

All traffic-related factors, such as pollution, visual stimuli and noise, become less important at an increasing distance from the road. Therefore, it was assumed that measuring one factor would be sufficient to determine the traffic load on transect strips. Noise was used, because it carries a long way and takes account of many characteristics of traffic that might be important in relation to road distance e.g. number, size and speed of vehicles. There is also evidence that noise is the most critical factor in reducing densities of breeding birds in woodland adjacent to roads (Reijnen *et al.* 1995).

The 'noise load' was estimated using an existing mathematical model, which expresses the noise level in dB(A) as the 24-hour value of the equivalent noise level (Moerkerken & Middendorp 1981). Calculated noise levels refer to points at a height

of 0.5 m above the ground surface. Other heights were investigated, but the calculated values were all strongly correlated ( $r = > 0.95$ ). Traffic data were obtained from the Ministry of Traffic, Public Works and Water Management (Anon. 1990).

To obtain the mean noise level of a strip, a reading was taken at a point situated in the middle of the line parallel to the road at a distance of  $10^{(\log DL - \log DS)/2}$ , where DL is the largest distance and DS the smallest distance of the strip from the road (and dB(A) is measured on a log scale). The noise load in the transects from road traffic, varied from  $59 \pm 6$  dB(A) in the strips adjacent to the road to  $38 \pm 5$  dB(A) in the most remote strips.

### Agricultural activities

To obtain a measure of the variation in habitat quality that was due to agricultural activities we used the simulation program MEADOSIM version 1.3 (Spaak, 1988), which is mainly based on the model of Beintema and Müskens (1987). The program predicts the 'quality' of a management unit of agricultural grassland for a given bird species based on a detailed agricultural management scheme which is composed of data on numbers and grazing systems (during day or during day and night) of dairy, young cattle and sheep, and of dates of egalizing the surface of the grassland and of fertilizing and cutting operations. The quality measure estimates the probability of achieving hatching success (value between 0 and 1).

In each transect, management units were determined by taking fields enclosed by ditches and fences. The size of these units varied from 0.5 to 5 ha. Agricultural management schemes were estimated by carrying out a field survey twice a week. The 'quality' of each transect strip was taken to be the mean of the management unit values weighted by area.

The program only estimates 'quality' values for black-tailed godwit, lapwing, oystercatcher, redshank and ruff. For other species which also nested within a management unit, an extrapolation was made. This was based on the assumption that species which are exposed to the same agricultural measurements because of a similar timing of breeding, will suffer equally. Thus, for the yellow wagtail *Motacilla flava* L. the ruff data were used and for the shoveler *Anas clypeata* L. and the skylark *Alauda arvensis* L. the black-tailed godwit data. For coot *Fulica atra* L. and mute swan *Cygnus olor* (Gmelin) the influence of agricultural activities was considered not important because they nest in ditches and for mallard *Anas platyrhynchos* L., tufted duck *Aythya fuligula* L. and meadow pipit *Anthus pratensis* L. because suitable nest sites i.e. rough vegetations were only present on the slope of ditches and on the borderline of management units (Bauer and Glutz von Blotzheim 1968, 1969; Hötke and Sudfeld 1982). For the summed density of all species we used the black-tailed

godwit data, as this was the most abundant species. Uncertainty in these 'quality' extrapolations were considered to be not very important in influencing the outcome of the analysis. It appeared that there was very little variation in the 'quality' values of strips within transects.

### Analysis

Species were analyzed separately if the total number of territories was greater than 10 and the number of transects in which they were present was greater than four. The density of territories (number/area) was modelled using a threshold model in the variable noise load (Fig. 2); below the threshold value ( $T$ ) for noise load the density was constant, whereas, above the threshold, the density decreased exponentially with rate ( $r$ ). The parameters  $T$  and  $r$  were estimated by Poisson loglinear regression analysis, with a numerical search procedure for the best-fitting threshold value (Reijnen *et al.* 1995). There were two additional explanatory variables in the model, namely quality (so as to correct for between-strip differences in quality) and the factor transect (so as to account for all possible between-transect differences, e.g. in management regime). If the regression were a linear regression, then the logarithm of the density would have been the natural response variable. However, the logarithm of the density could not be calculated because the observed density was sometimes zero and the logarithm of zero is undefined. The modern standard solution to this problem is to carry out a Poisson loglinear regression with the number of territories as response variable and the logarithm of the area as an offset (i.e. an extra regressor with unit regression coefficient; see McCullagh & Nelder 1983). Standard errors and statistical tests were adjusted for overdispersion in the number of territories in the standard way (McCullagh & Nelder 1983; see also Reijnen *et al.* 1995). From the estimated values of  $T$  and  $r$ , a decrease factor was calculated (Fig. 2) as a measure for the effective reduction in number of territories in an area that borders the road side and extends up to a distance from the road where the noise load equals the threshold value.

The significance of the effect of noise load was tested using the F-test with two degrees of freedom (one for the threshold and one for the slope) in the numerator and therefore was two-tailed. However, if a threshold was absent the test was one-tailed. An approximate 90% confidence interval was constructed for the threshold value (see Reijnen *et al.* 1995).

For a given situation (traffic density, car speed, etc.) the disturbance distance was obtained by converting the threshold value in dB(A) to distances in m from the road using the mathematical model of Moerkerken & Middendorp (1981)(see above).

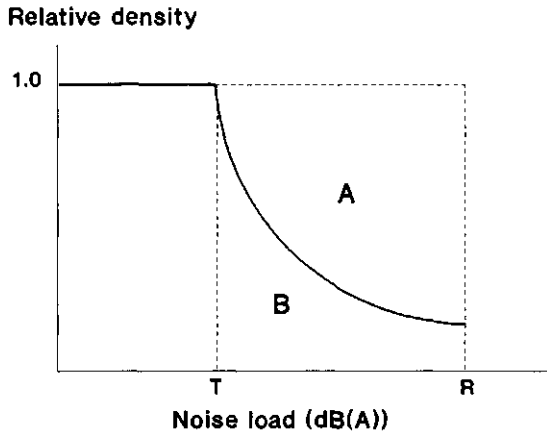


Fig. 2. Threshold model based on loglinear Poisson regression which allows estimation of the density decrease factor (see Methods) where T is the threshold value and R is the roadside. The decrease factor = area of A/(area of A + B).

## RESULTS

### Reduction of density in relation to noise level

Of the 19 species present in the 15 transects, 12 were sufficiently numerous to allow analysis (Table 1). Seven of the 12 species showed a significant negative relationship between noise level and density ( $P < 0.05$ , Table 1). There was also a strongly significant effect on the summed density of all species ( $P < 0.001$ , Table 1). The threshold value and the decrease factor for the density varied considerably between species (Tables 1 and 2). Fig. 3 shows the relationships for meadow pipit (high threshold value, high decrease factor), black-tailed godwit (low threshold value, average decrease factor) and for all species combined.

### Disturbance distance and population loss

Disturbance distances were determined for two traffic densities that cover the whole range of densities present in our study areas (5000 and 50 000 cars a day) and by taking a car speed of 120 km/hour (which is most common; Anon. 1990). With respect to species the estimated disturbance distance varied from 20 to 1700 m at 5000 cars a day and from 75 to 3530 m at 50 000 cars a day (Table 2). For the density of all species combined the disturbance distance was 120 and 560 m, respectively (Table 2).

**Table 1.** Regressions of noise load from car traffic on density of breeding birds using a threshold model (see methods)<sup>1</sup>

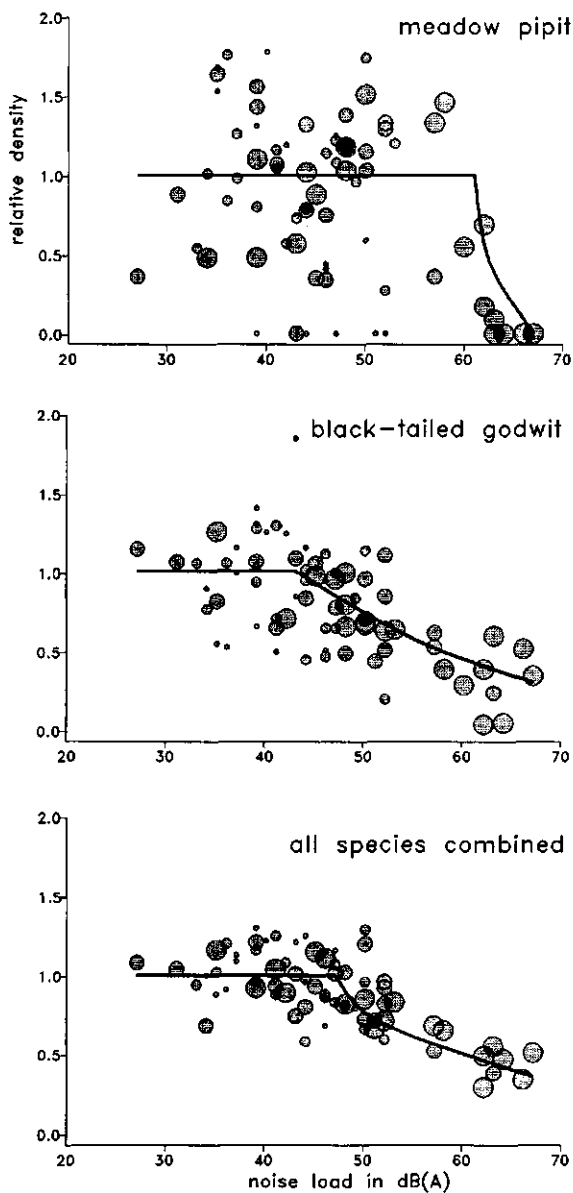
Species	NP/Z	NT	df	F	T(CFL)	C	Sign. <sup>2</sup>
Mute swan	6/40	17	2/32	0.37	36	-0.028	NS
Mallard	14/71	305	2/55	2.62	53(27-61)	-0.048	NS
Shoveler	12/58	77	2/43	3.23	51(42-59)	-0.093	*
Tufted duck	6/33	17	2/25	0.92	61	-5.106	NS
Coot	10/58	128	2/46	3.74	60(41-63)	-0.235	*
Oystercatcher	15/75	375	1/58	9.86	≤ 27(?-43)	-0.022	**
Lapwing	15/75	729	2/57	12.00	47(42-51)	-0.042	***
Black-tailed godwit	15/75	1208	2/57	23.20	43(37-48)	-0.053	***
Redshank	15/75	179	2/57	1.31	52	-0.038	NS
Skylark	14/72	519	2/55	14.40	48(46-56)	-0.079	***
Meadow pipit	15/75	159	2/57	6.38	59(56-62)	-0.509	*
Yellow wagtail	8/45	56	2/34	0.70	58	-0.157	NS
All species combined <sup>3</sup>	15/75	3818	2/57	34.60	47(42-49)	-0.047	***

<sup>1</sup>NP/Z, number of transects/number of strips; NT, total number of territories; df, degrees of freedom; F, change in *F*-statistics after adding noise load; T(CFL), threshold in dB(A) with confidence limits (? means that a lower limit could not be calculated); C, regression coefficient.

<sup>2</sup>NS,  $P > 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

<sup>3</sup>Summed density of all species present in the transects.

The potential % loss of population in an area, as measured by the estimated reduction in density, was calculated for three zones along the road: 0-100, 0-500 and 0-1500 m. At 5000 cars a day seven species (out of the 12 studied) had a population loss of more than 10% within 100 m of the road (12-56%), but further from the road such reduction only occurred in black-tailed godwit (22% at 0-500 m) and oystercatcher (44% at 0-500 m and 36% at 0-1500 m)(Fig. 4). At 50 000 cars a day all species breeding within 100 m of the road showed an estimated loss of 40-74% in population and >10% in a zone of 0-500 m from the road (Fig. 5). Lapwing, shoveler, skylark, black-tailed godwit and oystercatcher showed reductions of 14-44% up to 1500 m (Fig. 5).



**Fig. 3.** Relationship between relative density and mean noise load for black-tailed godwit, meadow pipit and all species combined based on loglinear Poisson regression using a threshold model. The size of the points (four classes) reflect their weight in the regression. The roadside noise load is 70 dB(A).

**Table 2.** Decrease factor (see Fig.2) and disturbance distances (m) of species and of all species combined for 5000 and 50 000 cars a day and a car speed of 120 km per hour

Species	Decrease factor	Disturbance distance	
		5000 cars/day	50 000 cars/day
Coot	0.62	20 (10-315) <sup>1</sup>	75 (50-1150)
Meadow pipit	0.82	25 (15-35)	90 (55-140)
Shoveler	0.53	65 (20-265)	320 (90-1030)
Skylark	0.53	100 (35-140)	490 (140-640)
Lapwing	0.36	120 (65-265)	560 (320-1030)
Black-tailed godwit	0.47	230 (100-560)	930 (490-1690)
Oystercatcher	0.38	1700 (230-?)	3530 (930-?)
All species combined	0.39	120 (90-315)	560 (425-1150)

<sup>1</sup>disturbance distances were derived from the regression with noise load as explanatory variable and a conversion of noise load to distance in m from the road; in parentheses the 90% confidence limits (? means that a upper limit could not be calculated).

## DISCUSSION

### Reduction of density

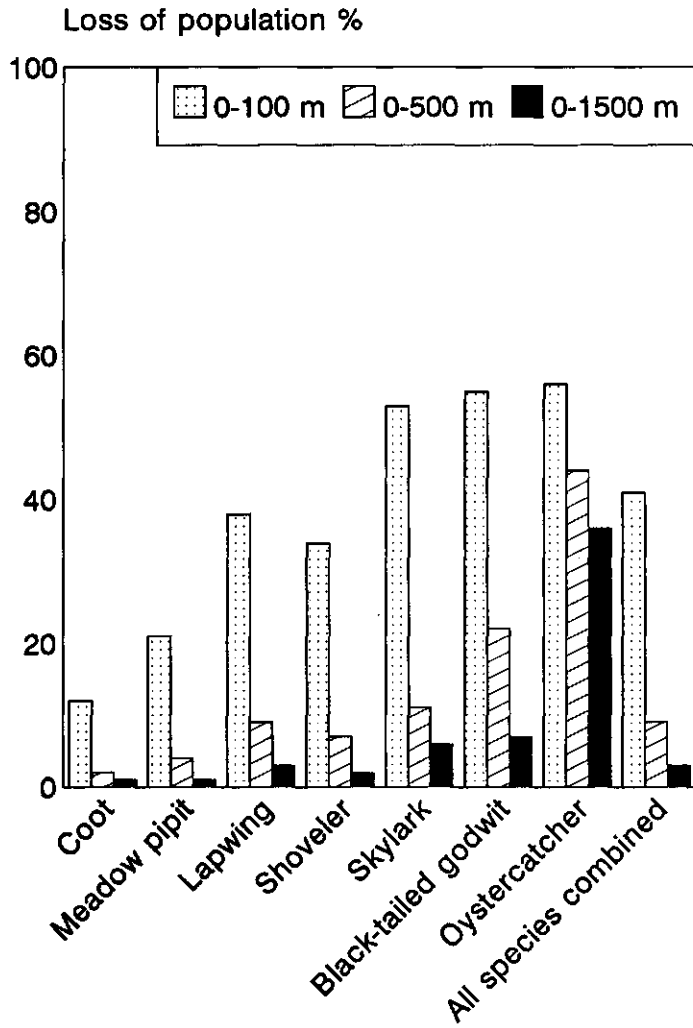
As in the study of Van der Zande *et al.* (1980), black-tailed godwit and lapwing were present in reduced densities near roads. The reduced densities of oystercatcher, shoveler and skylark agree with the findings of preliminary studies (see review in Reijnen & Foppen 1991), but a possible effect of roads on the redshank (Van der Zande *et al.* 1980) could not be confirmed.

Disturbance distances of black-tailed godwit and lapwing were much lower in this study than indicated by Van der Zande *et al.* (1980), even if we consider the upper confidence limits (Table 3). The same holds true for the decrease factor of the density (36-47% and 60% respectively). However, it is likely that van der Zande *et al.* (1980) overestimated the disturbance distances by taking the distance from the road at which the maximum breeding density is reached. Their study was also based on a much smaller number of transects.

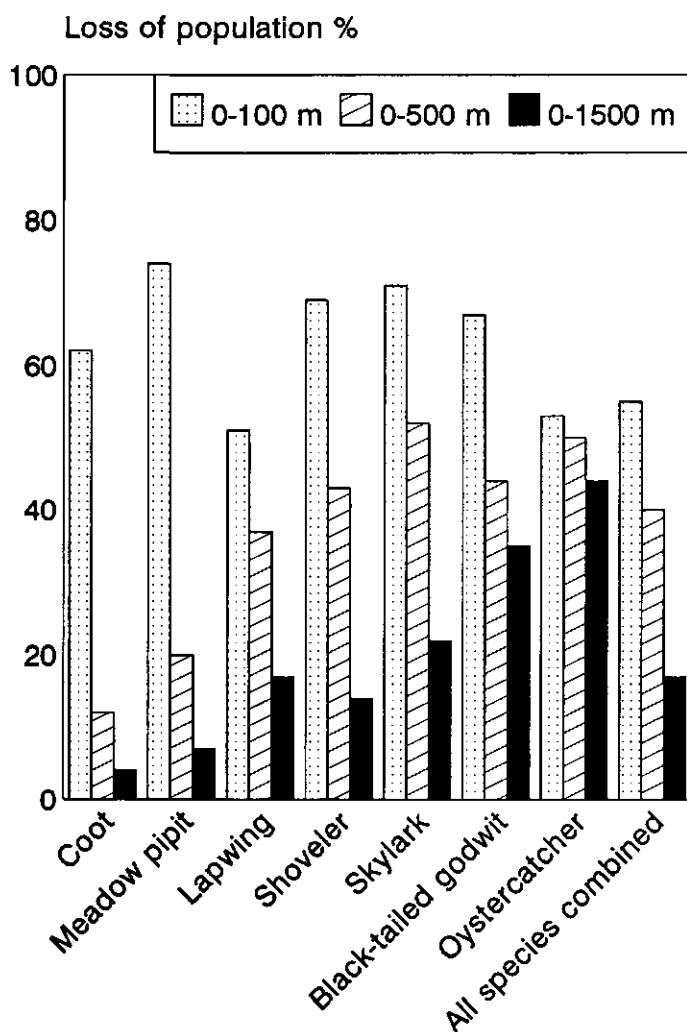
No threshold value was observed in the oystercatcher and consequently the disturbance distance was extremely large at high traffic densities (> 3000 m at 50 000 cars/day, Table 2). The absence of a threshold value may have been due to the relatively small number of sampling strips with a low noise load, so the disturbance distance was probably overestimated. Nevertheless, this result is in contrast with the



findings of van der Zande *et. al.* (1980), who did not establish any reduced density for the oystercatcher.



**Fig. 4.** Loss of population (based on density reduction) in different zones adjacent to a road with 5000 cars/day and a car speed of 120 km/hour.



**Fig. 5.** Loss of population (based on density reduction) in different zones adjacent to a road with 50 000 cars/day and a car speed of 120 km/hour.

### Possible causes of reduced density

Although the noise load accounted for the reduction in the density of breeding birds adjacent to roads very well, other traffic-related factors could exert direct effects (Van der Zande *et al.* 1980; Reijnen *et al.* 1995). Lead pollution by car traffic is probably not very important, because most of the accumulation of lead in soil and

plants occurs within 25 m of highways (Motto *et al.* 1970). Moreover, there is evidence that lead accumulation has little effect on roadside biota (Bennett 1991). Some evidence has shown that visual stimuli by car traffic also have only a limited effect. For birds breeding in woodland Reijnen *et al.* (1995) found that when noise conditions were held constant, there was no difference in bird densities between plots with high and low visibility of cars. In open landscape, visual stimuli reach much farther than in wooded areas and breeding birds might respond differently. A study by Illner (1992) sheds some light on this problem. He found that in open arable farmland grey partridge *Perdix perdix* L. density was also lowered along roads bordered by hedgerows which stopped visual stimuli. This points to noise as the critical factor, but does not exclude visual stimuli from having some effect.

Further research is still needed to determine how disturbance by car traffic could cause reduced densities of breeding birds in open areas.

**Table 3.** Disturbance distances (in m) of black-tailed godwit and lapwing in the study areas of Van der Zande *et al.* (1980).

Study area	Traffic density in cars per day	Species	Disturbance distance <sup>1</sup>	
			A	B
Rapijnen	54 000	Black-tailed godwit	2000	960 (51-1750)
		Lapwing	2000	590 (330-960)
Rijnenburg	7311	Black-tailed godwit	1125	180 (82-460)
		Lapwing	875	95 (53-210)
Nieuwkoop	4560	Black-tailed godwit	625	128 (60-340)
		Lapwing	625	70 (40-150)

<sup>1</sup>A = original values, B = estimated values based on the results of this study (in parentheses the 90% confidence limits).

### Population consequences and practical implications

In the north and west of The Netherlands, which inhabits most of the grassland bird populations, about 10% of the area has a traffic noise load of more than 50dB(A) and about 30% of more than 40dB(A)(Anon. 1988). Since the threshold value for the density of all species combined is 47 dB(A) and for the black-tailed godwit, the most characteristic species, 42 dB(A)(Table 1), significant population reductions can be expected. Because most grassland birds also suffer heavily from intensive agricultural management (Beintema, 1986), the cumulative effect of these threats might be very important. This reinforces the recommendations made by van der Zande *et al.* (1980)

that extra care should be taken in planning new roads in open grassland areas, in particular when high traffic densities are expected. From a conservation point of view, however, it is also very important to explore how the present effects can be reduced. Possibly, one can reduce the effects adjacent to roads by constructing noise muffling devices, which also will stop visual stimuli. However, such devices might also act as a source of disturbance themselves and will be only appropriate if very long disturbance distances occur. Probably, a better strategy is to improve habitat quality for grassland birds in areas further away from roads. This would involve extensification of agricultural management in these areas, but in exchange agricultural management close to roads could be intensified.

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**THE EFFECTS ON HABITAT QUALITY IN  
RELATION TO DENSITY**

### **3.1 INFLUENCE OF POPULATION SIZE ON THE REDUCTION OF DENSITY OF WOODLAND BREEDING BIRDS CLOSE TO A HIGHWAY**

#### **SUMMARY**

1. This study tested the assumption that in years with a low overall population size the density-depressing effect of roads on breeding birds will be more important than in years with a high overall population size.
2. The effect on the density was investigated in 1984, 1986 and 1988. Of the 23 species that could be analyzed each year, 17 species had a reduced density close to the road in at least one year. In 1984 and 1986 the number of affected species was much higher (10 and 14 respectively) than in 1988 (4).
3. The number of affected species, as well as the effect size for all species combined and for most individual species, was negatively correlated with the overall population size.
4. It is concluded that in years with a high-overall population size, the use of density as a response variable will cause a considerable underestimation of the reduction of the habitat quality close to roads. This has not been recognized well in impact studies concerning road traffic, nor in other impact studies.

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## INTRODUCTION

Several studies show that densities of woodland birds are lower adjacent to roads than in control areas further away (Ferris 1979, Rätty 1979, Adams & Geis 1981, Reijnen & Thissen 1987, Reijnen *et al.* 1995). This points to a reduced habitat quality near the road (cf. Reijnen *et al.* 1995), which is verified for the willow warbler *Phylloscopus trochilus* (Reijnen & Foppen 1994).

However, density is not always a good indicator of habitat quality and might even be misleading (Fretwell 1972; Van Horne 1983; Bernstein *et al.* 1991). In several territorial bird species it has been shown that when overall density is high, less-preferred habitat is more strongly occupied than when overall density is low (Kluyver & Tinbergen 1953; Glas 1962; O'Connor & Fuller 1985). This means that density would be a reasonably good measure of habitat quality only in years when overall density was low (Van Horne 1983).

So, when evaluating reduced densities of breeding birds close to roads, the effect in terms of reduced quality might be underestimated (cf. Reijnen *et al.* 1995). It would even be possible that a reduced habitat quality was not reflected by a reduced density at all. In this study these assumptions were tested by investigating the effect of road traffic on the density of breeding bird species in the same study area during several years and by relating these effects to the overall population size in the different years.

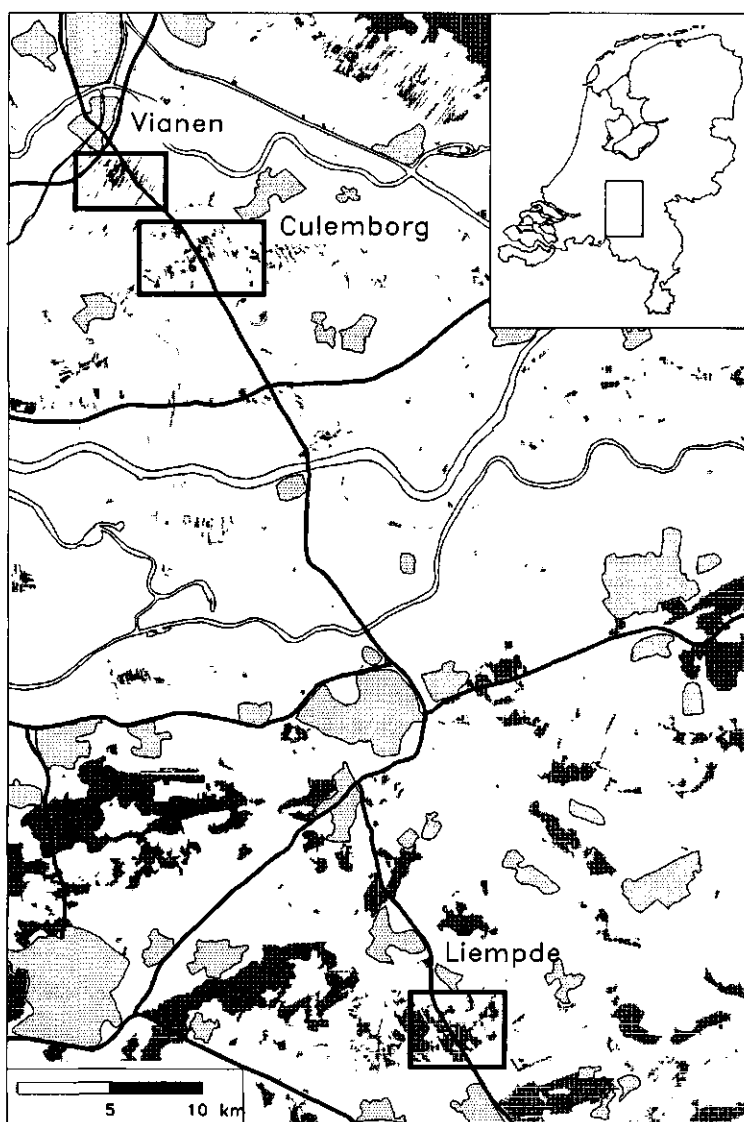
Nomenclature of birds follows Voous (1973,1977).

## METHODS

### Study areas and site selection

The study was carried out in three areas crossed by highway A2 (40 000 - 52 000 cars/day) between Utrecht and Eindhoven (Fig. 1). In the area near Liempde poplar *Populus* sp. woodland was the dominant woodland type, while the other areas near Vianen and Culemborg had a mixture of poplar woodland and willow *Salix* sp. coppice. The herbaceous and shrub layers in both woodland types were very well developed due to the relatively rich and moist soils. In the poplar woods *Urtica dioica* L., *Galeopsis tetrahit* L., *Holcus lanatus* L. and *Symphytum officinale* L. were the most abundant species in the herb layer and *Corylus avellana* L., *Prunus padus* L., *Rubus* sp. and *Sorbus aucuparia* L. in the shrub layer. For a more detailed description of the vegetation structure of the willow coppices see Reijnen & Foppen (1994).





**Figure 1.** Location of study areas in the Netherlands. Highways are shown as bold lines, rivers and canals as double lines; woodlands and urban areas are dotted (dense and sparse respectively).

To detect an effect of car traffic on the breeding density of birds, 16 to 18 paired plots were selected. One plot of a pair was situated adjacent to the road (road plot) and one plot at a distance ranging from 180 to 2500 m (on average 700 m, control plot). To

obtain reliable densities, the minimum plot size taken was 1.5 ha for poplar wood and 1.0 ha for willow coppice (based on Hustings *et al.* 1985, see table 2 for mean size of plots). Willow coppices in the first year after cutting were not included, because of low breeding densities (see also Reijnen & Foppen 1994). In consequence, a number of plots could not be used every year. Investigations were carried out in 1984 (16 paired plots), 1986 (18 paired plots) and 1988 (16 paired plots).

### **Breeding density**

Breeding bird densities were measured as the number of territories per unit area using the mapping method according to Hustings *et al.* (1985). In the mapping method the number of territories of a species in an area is derived from all individual registrations of territorial behaviour made on several visits in the field. However, because of the rather small size of the plots, for some species that have large territories, the number of registrations was used to calculate densities. To calculate the total density of all species combined, the densities of species which were based on registrations were divided by two.

Each plot was visited 12 times from the beginning of March till the end of June. The distance of 50 m at which an observer should approach to all parts of the plot (Hustings *et al.* 1985) was reduced to 25 m in order to minimize the masking effect of traffic noise on bird song. For territories which overlapped the boundaries of a plot, only the proportion of the territory within the plot (based on percentage of registrations) was included in the calculation of the density.

### **Traffic load**

To quantify differences in traffic load between plots the noise load was taken. Reijnen *et al.* (1995) show that this factor is probably the most important cause of reduced bird densities close to roads. The noise load of a plot was derived from traffic data by using a mathematical model, which expresses the noise level in dB(A) as the 24-hour value of the equivalent noise level for a point at a given distance from the road (Moerkerken & Middendorp 1981). The calculated noise levels were adapted according to Huisman (1990), in order to take the influence of woodland on noise transmission into account. For further details see Reijnen *et al.* (1995).

Although there was an increase of the traffic density from 1984 to 1988, the mean noise load of the study plots between the three years did not differ significantly (Table 1). This can be explained by the fact that part of the selected plots was different between years.

**Table 1.** Traffic density in the study areas and noise load of road and control plots. Statistical significance is based on ANOVA.

Year	Traffic density in cars per day	Noise load in dB(A)	
		Road plots	Control plots
1984	39 962	57 ± 4	35 ± 7
1986	46 755	58 ± 4	38 ± 6
1988	52 255	55 ± 4	36 ± 7
Sign.		NS	NS

NS,  $P > 0.10$

**Table 2.** Habitat characteristics of road (R) and control (C) plots. Statistical significance (S) is based on Wilcoxon signed-ranks test.

Estimate	1984			1986			1988		
	R	C	S	R	C	S	R	C	S
<i>Poplar wood + willow coppice</i> <sup>1</sup>									
Herb layer: coverage (%)	86	84	NS	90	86	NS	89	83	NS
height (cm)	70	70	NS	65	65	NS	62	69	NS
Shrub layer: coverage (%)	62	68	NS	55	61	NS	62	69	NS
height (dm)	28	30	NS	27	29	NS	35	34	NS
Size of patch (ha)	3.7	3.8	NS	3.3	3.4	NS	2.9	3.3	NS
Proportion of patch perimeter bordered by grassland	0.65	0.64	NS	0.65	0.79	+	0.61	0.69	NS
<i>Poplar wood</i> <sup>2</sup>									
Tree layer: coverage (%)	68	70	NS	72	77	NS	59	64	NS
height (m)	19.8	17.0	NS	21.6	19.1	NS	19.2	17.1	NS
Circumference of trees (dm)	9.9	8.5	*	11.7	10.3	*	10.7	9.1	*
<i>Willow coppice</i> <sup>3</sup>									
Large willow stubs (ha <sup>-1</sup> )	4.3	5.1	NS	4.7	5.1	NS	3.4	4.1	NS
Hawthorns height > 2 m (ha <sup>-1</sup> )	3.8	3.3	NS	4.5	5.6	NS	5.0	6.1	NS

<sup>1</sup>number of paired plots: 1984=16, 1986=18, 1988=16

<sup>2</sup>number of paired plots: 1984=6, 1986=8, 1988=7

<sup>3</sup>number of paired plots: 1984=10, 1986=10, 1988=9

NS,  $P > 0.10$ ; +  $P < 0.10$ ; \*  $P < 0.05$

### **Control of other factors that influence breeding density**

To identify the effect of road traffic, we chose plots that were as similar as possible in other variables that influence breeding density. Because of the paired design, the similarity was only required for the plots of one pair. Variables taken into account were area of plots, vegetation structure, surrounding landscape and management. For vegetation structure this was rather easy because the poplar woods and willow coppices were very homogeneous.

The similarity of plots was tested for area and vegetation structure. The vegetation structure was measured at points selected by unaligned systematic sampling (Cochran 1977), because the woodland types showed regular patterns due to planting of trees and the presence of ditches. Only the circumference of trees (all years) significantly differed between road and control plots (Table 2). However, since the difference was very small, it is not likely that this caused significant differences in breeding densities between road and control plots.

Since species were not always present in all the paired plots of a year, additional tests were carried out on subsets of paired plots. The results were similar as compared with the whole dataset. Significant differences between road and control plots were restricted to the circumference of trees.

Also, there were no indications of changes in environmental factors during the study period that could have influenced breeding bird densities between the plots of one pair. Forestry did not affect the surroundings of our study plots and outdoor recreation was nearly absent in all years.

### **Population size**

To estimate changes in the population size of species present in our study area, the overall population indices of the breeding bird survey in The Netherlands were used (see Van Dijk 1990). Indices for deciduous woodland only were inappropriate, since many species, especially those in the willow coppices were not represented well in these data.

Although population indices for the study areas and the immediate surroundings would have been preferable, this was not possible because the number of survey plots in this part of the Netherlands was too small (see also Verstrael *et al.* 1990). Our own density data could also not be used. At first, there is the risk of circular reasoning, since the paired plots were situated along roads. Using the control plots only, which might reduce this risk, was not possible for practical reasons. In the willow coppices only a few control plots were investigated in all the three years. Moreover, for a number of species present in the willow coppices, the sample of measurements of density was not appropriate, because they were much more abundant in other habitat types.

Some evidence that changes in the national population indices reflect local changes

can be found in the fact that during the study period some strong winters were the main cause of changes in the population size. Furthermore, changes in the few control plots that were studied in all the three years were very similar to those of the national indices.

Table 3 shows the indices of the analyzed species for 1984, 1986 and 1988 (most recent values, pers. comm. T. Verstrael). The indices for all species combined were estimated by averaging the log of the species indices weighted for differences in absolute numbers.

### Analysis

In accordance with the study design (paired plots), at first the data were analyzed with the Wilcoxon signed-ranks test (one-sided). The basic analysis was a comparison of densities between road and control plots. Moreover, to detect possible effects on the density at a very short distance from the road, large road plots (at least twice the required minimum size) were divided into two parts that were near to and far from the road. This was only done for road plots that had a very homogeneous vegetation structure. The analysis was carried out for species if the number of territories was  $> 10$  or the number of registrations  $> 20$ .

In order to obtain information on the size of the effect on the density, a supplementary analysis was carried out by using a regression model with noise as the explanatory variable. For this, large homogeneous plots were split into two or sometimes more sub-plots (depending on the size). The numbers of territories or registrations were modelled by loglinear Poisson regression by using a threshold model and with correction for possible overdispersion (for further explanation see Reijnen *et al.* 1995). A factor for pairs of plots accounted for differences between pairs. The effect size was defined as the product of the decrease factor (relative decrease of the density between threshold and road side, see Reijnen *et al.* 1995) and the difference in noise between the road side and the threshold. The significance of the effect of noise was tested with the *F*-test with two degrees of freedom (one for the threshold and one for the slope) in the numerator and therefore was two-sided. However, in the absence of a threshold the test was one-sided. For the threshold value an approximate 90% confidence interval was constructed (see Reijnen *et al.* 1995).

Because of the small size of the data set, besides a significance level of  $P < 0.05$ , a significance level of  $P < 0.10$  was also considered. We used a comparison-wise significance level, to avoid loss of power and thereby accept that we are likely to mark too many species as showing a significant change.

**Table 3.** Overall population indices in The Netherlands (see van Dijk 1990) for species which could be analyzed each year. The monitoring program started in 1984.

Species	Population index		
	1984	1986	1988
<i>Anas platyrhynchos</i>	100	108	103
<i>Phasianus colchicus</i>	100	116	103
<i>Columba palumbus</i>	100	92	93
<i>Troglodytes troglodytes</i>	100	60	97
<i>Prunella modularis</i>	100	92	93
<i>Erithacus rubecula</i>	100	87	97
<i>Turdus merula</i>	100	94	107
<i>Turdus philomelos</i>	100	46	60
<i>Acrocephalus palustris</i>	100	112	118
<i>Sylvia communis</i>	100	164	196
<i>Sylvia borin</i>	100	101	111
<i>Sylvia atricapilla</i>	100	101	129
<i>Phylloscopus collybita</i>	100	102	135
<i>Phylloscopus trochilus</i>	100	100	109
<i>Muscicapa striata</i>	100	81	81
<i>Parus montanus</i>	100	112	119
<i>Parus caeruleus</i>	100	83	103
<i>Parus major</i>	100	91	93
<i>Garrulus glandarius</i>	100	87	86
<i>Pica pica</i>	100	121	132
<i>Corvus corone</i>	100	124	132
<i>Emberiza schoeniclus</i>	100	89	95
<i>Fringilla coelebs</i>	100	96	107
All species combined	100	95	106

## RESULTS

### Reduction of density

Of the 54 species that had territories in our plots in one or more years, 28 species were

sufficiently numerous to allow analysis (see Tables 4 and 5). With the Wilcoxon signed-ranks test 16 species showed a lower density close to the road in one or more years (at  $P < 0.10$ , 10 species at  $P < 0.05$ , Table 4). For four of these 16 species there was only an effect on the density when comparing parts of the road plots near to and far from the road (at  $P < 0.10$ , 2 at  $P < 0.05$ , Table 4). Significant regressions were found for 10 of the 16 species (at  $P < 0.10$ , 9 species at  $P < 0.05$ , Table 5) and also for three other species (at  $P < 0.010$ , 2 species at  $P < 0.05$ , Table 5).

Most of the species had a lower density close to the road in only one or two years. If we restrict ourselves to the 23 species that could be analyzed each year (see Table 3), the number of affected species (paired test and regression, see Tables 4 and 5) was highest in 1984 and 1986 (10 and 14 species respectively at  $P < 0.10$ , and 7 and 9 species respectively at  $P < 0.05$ ) and very low in 1988 (4 species at  $P < 0.10$  and 3 species at  $P < 0.05$ ). Because only two species had a significant regression in more than one year, differences in effect size were not considered.

In every year the density of all species combined was lower close to the road if analyzed with the Wilcoxon signed-ranks test (Table 4). With regression there was only an effect in 1984 and 1986 (Table 5). In 1986 the threshold value was much lower (= larger distance from the road) than in 1984, while the decrease factor of the density was similar (0.34 and 0.35 respectively, calculated with data from Table 5). This means that the effect size was higher in 1986 than in 1984:  $(70-42) \times 0.34 = 9.86$  and  $(70-52) \times 0.35 = 6.10$  respectively. However, the confidence limits of the threshold of especially 1984 were rather large (see Table 5). Fig. 2 shows the effect curves for all three years.

### **Correlation between population size and reduced densities**

For all species combined the effect size increased with decreasing values for the population index, which is concurrent with the clear negative relationship between the number of species that showed a reduced density and the population index (Fig. 3). In 1988, the year with the highest population index, the negative effect on the density was apparently so small (only four species), that an effect size could not be established.

To get an indication of the relationship between population index and effect size for species separately, we considered regression coefficients irrespective of their significance (see Table 5). This was only done for the 23 species that could be analyzed each year (Table 3). The relationship was estimated by the coefficient of linear regression of effect size on population index. Of all species 70% showed a negative relationship and for the species that had one or more significant effects with regression this was 82% (Fig. 4).

**Table 4.** Densities of breeding birds in road (R) and control (C) plots. For the comparison of densities within road plots only the statistical significance is shown (in parentheses, if absent comparison was not possible).

Species	Year	NT	NP	R	C	Sign.
<i>Anas platyrhynchos</i>	1984	89	15	1.00	1.18	NS(NS)
	1986	92	18	1.04	1.89	NS(NS)
	1988	31	13	0.31	0.54	NS
<i>Phasianus colchicus</i>	1984	15	14	0.05	0.25	**
	1986	33	17	0.24	0.37	NS(NS)
	1988	17	8	0.15	0.28	NS
<i>Scolopax rusticola</i>	1988	23	5	0.22	0.11	NS
<i>Columbus palumbus</i>	1984	101	16	0.78	1.23	*(NS)
	1986	75	15	0.48	1.18	** (NS)
	1988	46	11	0.37	0.59	NS(NS)
<i>Streptopelia turtur</i>	1984	18	7	0.03	0.18	**
<i>Cuculus canorus</i>	1984	35	12	0.12	0.40	**
	1986	34	12	0.12	0.58	**
<i>Dendrocopus major</i>	1984	13	7	0.09	0.09	NS
	1986	14	10	0.19	0.34	NS
<i>Troglodytes troglodytes</i>	1984	211	16	1.79	1.81	NS(*)
	1986	75	18	0.56	0.78	*(**)
	1988	122	16	1.28	1.48	NS(NS)
<i>Prunella modularis</i>	1984	53	15	0.45	0.51	NS(NS)
	1986	31	17	0.31	0.33	NS(NS)
	1988	18	13	0.31	0.25	NS(NS)
<i>Erithacus rubecula</i>	1984	92	15	0.59	0.63	NS(NS)
	1986	54	11	0.47	0.66	+(NS)
	1988	79	11	0.43	0.78	*(NS)
<i>Turdus merula</i>	1984	120	16	0.83	1.19	*(NS)
	1986	31	18	0.31	0.48	+(*)
	1988	73	16	0.62	0.85	NS(NS)
<i>Turdus philomelos</i>	1984	116	15	0.93	0.88	NS(NS)
	1986	32	15	0.25	0.33	NS(*)
	1988	44	16	0.47	0.45	NS(NS)
<i>Acrocephalus palustris</i>	1984	115	13	1.25	1.40	NS(+)
	1986	156	12	1.79	1.96	NS(NS)
	1988	67	10	0.83	1.05	NS(NS)
<i>Sylvia communis</i>	1984	29	12	0.24	0.46	+(NS)
	1986	36	14	0.36	0.50	+(NS)
	1988	15	7	0.58	0.26	NS
<i>Sylvia borin</i>	1984	140	14	1.71	1.41	NS(NS)
	1986	98	18	0.80	1.07	+(NS)
	1988	83	15	1.05	1.07	NS(NS)



Table 4. continued

Species	Year	NT	NP	R	C	Sign.
<i>Sylvia atricapilla</i>	1984	103	14	0.82	0.72	NS(NS)
	1986	60	14	0.58	0.61	NS(NS)
	1988	51	12	0.55	0.42	NS(NS)
<i>Phylloscopus collybita</i>	1984	151	16	1.26	1.23	NS(NS)
	1986	102	18	0.58	1.08	NS(+)
	1988	128	15	1.33	1.55	+(NS)
<i>Phylloscopus trochilus</i>	1984	172	15	1.40	2.12	*(+)
	1986	196	17	1.62	2.37	*(NS)
	1988	137	15	1.95	2.10	NS(NS)
<i>Muscicapa striata</i>	1984	32	6	0.26	0.38	NS
	1986	35	9	0.23	0.59	+
	1988	12	6	0.21	0.09	NS
<i>Parus montanus</i>	1984	56	15	0.49	0.60	NS(*)
	1986	67	17	0.59	0.67	NS(**)
	1988	51	16	0.57	0.70	NS(*)
<i>Parus caeruleus</i>	1984	28	14	0.21	0.24	NS(NS)
	1986	21	12	0.30	0.20	NS(NS)
	1988	21	10	0.20	0.23	NS
<i>Parus major</i>	1984	66	16	0.55	0.73	NS(NS)
	1986	51	16	0.43	0.44	NS(NS)
	1988	36	15	0.32	0.51	NS(NS)
<i>Garrulus glandarius</i>	1984	46	11	0.24	0.39	+
	1986	36	14	0.15	0.43	*
	1988	35	11	0.37	0.29	NS
<i>Pica pica</i>	1984	27	10	0.22	0.41	NS
	1986	26	11	0.18	0.46	NS
	1988	17	9	0.13	0.33	NS
<i>Corvus corone</i>	1984	26	9	0.21	0.17	NS
	1986	99	18	0.89	0.99	NS(NS)
	1988	32	10	0.41	0.32	NS
<i>Emberiza schoeniclus</i>	1984	36	7	0.39	0.46	NS
	1986	26	8	0.53	0.61	NS
	1988	27	6	0.42	0.34	NS
<i>Fringilla coelebs</i>	1984	51	12	0.36	0.29	NS(NS)
	1986	41	7	0.38	0.52	NS
	1988	30	9	0.22	0.24	NS(NS)
<i>Sturnus vulgaris</i>	1984	27	7	0.28	0.18	NS
	1986	37	6	0.49	0.44	NS(NS)
All species combined	1984	2060	16	16.30	19.40	+(+)
	1986	1685	18	11.40	14.60	***(**)
	1988	1362	16	12.50	14.50	*(NS)

NP, number of paired plots. NT, total number of territories. For species in bold the data are based on number of registrations. Statistical significance is shown for Wilcoxon signed-ranks test. NS,  $P > 0.10$ ; +  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

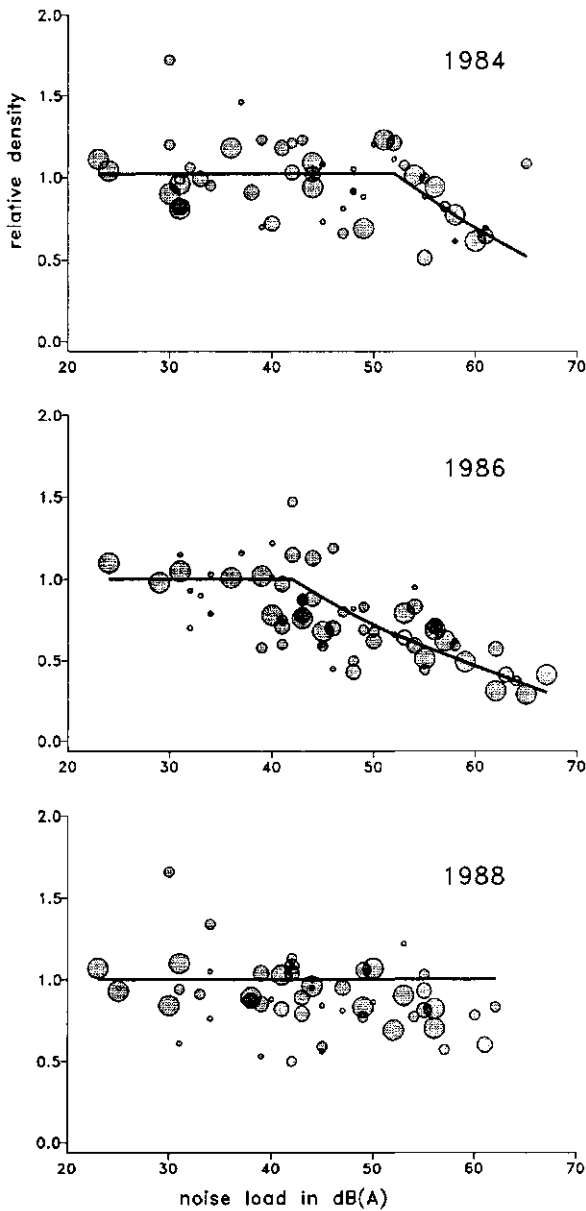
**Table 5.** Regressions of noise load on density using a threshold model (see Methods). For species in bold the data are based on number of registrations.

Species	Year	df	F	T(CFL)	C	Sign.
<i>Anas platyrhynchos</i>	1984	1/35	0.07	≤24	-0.003	NS
	1986	1/44	0.12	≤24	-0.005	NS
	1988	2/21	1.55	59	-6.046	NS
<i>Scolopax rusticola</i>	1988	2/17	1.14	≤29	+0.029	NS
<i>Phasianus colchicus</i>	1984	2/26	3.48	38(24-56)	-0.106	*
	1986	1/36	1.14	≤24	-0.024	NS
	1988	2/15	2.39	55	-7.538	NS
<i>Columbus palumbus</i>	1984	2/36	1.90	51	-0.086	NS
	1986	2/36	4.75	43(24-49)	-0.058	*
	1988	2/24	0.48	53	-0.102	NS
<i>Sireptopelia turtur</i>	1984	1/20	2.51	≤23(?-54)	-0.047	+
<i>Cuculus canorus</i>	1984	1/29	9.16	≤23(?-39)	-0.062	***
	1986	2/25	6.80	36(29-44)	-0.121	**
<i>Dendrocopus major</i>	1984	2/16	0.47	42	-0.045	NS
	1986	2/22	0.68	56	-0.314	NS
<i>Troglodytes troglodytes</i>	1984	2/36	0.15	42	-0.006	NS
	1986	2/43	3.24	47(31-57)	-0.087	*
	1988	1/33	0.46	≤23	-0.007	NS
<i>Prunella modularis</i>	1984	1/36	0.16	≤23	-0.006	NS
	1986	1/37	0.76	≤24	-0.020	NS
	1988	1/21	1.20	≤23	+0.280	NS
<i>Erithacus rubecula</i>	1984	1/30	0.20	≤23	+0.001	NS
	1986	2/26	1.00	37	-0.030	NS
	1988	2/25	1.04	38	-0.028	NS
<i>Turdus merula</i>	1984	1/36	2.80	≤23(?-61)	-0.016	+
	1986	1/43	2.16	≤24(?-65)	-0.026	+
	1988	1/33	4.26	≤23(?-46)	-0.030	*
<i>Turdus philomelos</i>	1984	2/36	0.51	54	-0.070	NS
	1986	1/41	2.22	≤24(?-64)	-0.034	+
	1988	1/33	0.72	≤23	-0.014	NS
<i>Acrocephalus palustris</i>	1984	2/26	1.69	45	-0.038	NS
	1986	2/20	0.54	45	-0.016	NS
	1988	2/14	1.16	55	-0.232	NS
<i>Sylvia communis</i>	1984	1/18	1.58	≤23	-0.024	NS
	1986	2/27	0.31	39	-0.017	NS
	1988	2/12	1.25	57	-2.128	NS
<i>Sylvia borin</i>	1984	2/27	0.51	55	-0.074	NS
	1986	2/43	0.83	53	-0.049	NS
	1988	1/26	0.58	≤23	+0.010	NS

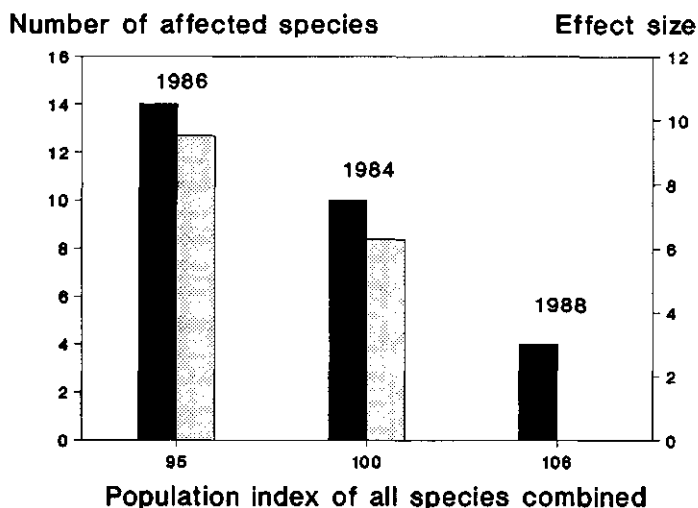
Table 5. continued

Species	Year	df	F	T(CFL)	C	Sign.
<i>Sylvia atricapilla</i>	1984	2/37	0.37	61	+0.265	NS
	1986	2/33	0.20	59	-0.082	NS
	1988	2/25	0.50	31	+0.017	NS
<i>Phylloscopus collybita</i>	1984	2/36	1.03	56	-0.112	NS
	1986	2/43	0.96	46	-0.027	NS
	1988	2/32	0.49	39	-0.014	NS
<i>Phylloscopus trochilus</i>	1984	2/29	4.03	40(24-52)	-0.034	*
	1986	2/28	6.79	31(29-43)	-0.340	**
	1988	2/26	0.18	42	-0.009	NS
<i>Muscicapa striata</i>	1984	1/9	1.04	≤23	-0.023	NS
	1986	1/13	4.26	≤24(?-53)	-0.055	*
	1988	1/10	1.32	≤23	+0.047	NS
<i>Parus montanus</i>	1984	2/36	2.40	51	-0.126	NS
	1986	2/43	1.50	49	-0.055	NS
	1988	2/33	0.51	50	-0.052	NS
<i>Parus caeruleus</i>	1984	2/31	0.28	59	-0.796	NS
	1986	2/27	0.06	59	+0.040	NS
	1988	2/25	0.04	38	-0.017	NS
<i>Parus major</i>	1984	1/36	1.40	≤23	-0.016	NS
	1986	2/42	0.18	56	+0.040	NS
	1988	2/30	0.28	34	-0.017	NS
<i>Garrulus glandarius</i>	1984	2/27	2.10	39	-0.052	NS
	1986	2/35	5.30	56(55-60)	-5.785	*
	1988	1/28	1.12	≤23	-0.022	NS
<i>Pica pica</i>	1984	2/27	5.20	52(44-56)	-4.260	*
	1986	2/20	2.32	53	-0.209	NS
	1988	2/16	0.75	56	+0.140	NS
<i>Corvus corone</i>	1984	1/19	0.74	≤23	-0.007	NS
	1986	2/43	1.80	56	-0.112	NS
	1988	2/24	0.43	53	-0.140	NS
<i>Fringilla coelebs</i>	1984	2/28	0.39	44	+0.025	NS
	1986	1/18	1.82	≤23	-0.027	+
	1988	2/21	0.14	52	+0.068	NS
<i>Emberiza schoeniclus</i>	1984	2/12	0.04	54	-0.027	NS
	1986	1/19	2.48	≤29(?-58)	-0.039	*
	1988	1/11	0.16	≤31	+0.001	NS
<i>Sturnus vulgaris</i>	1984	2/10	0.33	50	+0.048	NS
	1986	1/9	0.38	≤32	+0.016	NS
All species combined	1984	2/36	4.83	52(32-55)	-0.051	*
	1986	2/43	20.32	42(41-46)	-0.032	***
	1988	2/33	2.29	35	-0.009	NS

df, degrees of freedom; F, change in *F*-statistics after adding noise load; T(CFL), threshold in dB(A) with confidence limits; C, regression coefficient. NS,  $P > 0.10$ ; +  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .



**Figure 2.** Relation between relative density of all species combined (standardised within years) and mean noise load in 1984, 1986 and 1988 based on loglinear Poisson regression using a threshold model (see methods). Each data point is a plot or subplot. The size of the points (four classes) reflect their weight in the regression. The noise load in the verge of the road is 70 dB(A). In 1988 the effect was not significant ( $P > 0.10$ ).



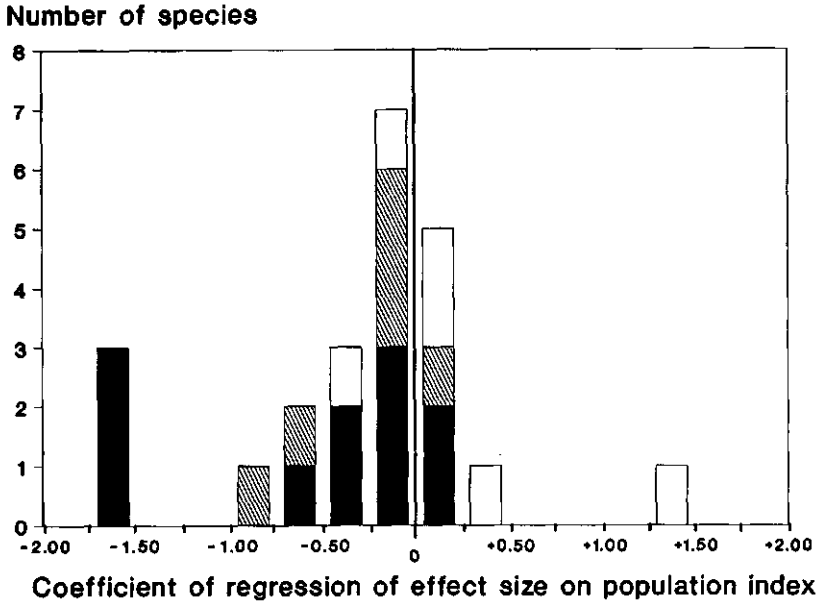
**Figure 3.** Relationship of the effect size for all species combined (dotted bars) and the number of affected species (black bars) with the population index.

## DISCUSSION

The results support the hypothesis that habitats close to roads are better filled when overall density is high than when it is low. Hence, this resembles relationships between high- and low-quality habitat (Fretwell 1972; Van Horne 1983; Bernstein *et al.* 1991). So, in years when overall density is high, density will underestimate the reduction of the habitat quality due to the traffic load along roads. The results point out that this underestimation can be substantial. When the overall densities were relatively high only very few species had lower densities near the road and for the density of all species combined an effect size could even not be established (Fig. 3). Moreover, it is possible that species which did not show a reduced density in the years of investigation, might do so in other years. Following this line, one should also be very careful in interpreting differences in response between species as differences in sensitivity for disturbance by road traffic, since the relative level of overall density of species might not be similar.

Because many species only showed a reduced density in one or two years, in the other year(s) they apparently occupied the zone with a lower quality close to the road to the same extent as farther from the road. This might indicate that the reduction of the quality in habitat close to the road in general was not extremely large, since other studies show that densities in low-quality habitats are always lower than in high-quality habitats

(Kluyver & Tinbergen 1953; Glas 1962; Krebs 1971; Wesolowski 1983; Gezelius *et al.* 1984). However, Reijnen & Foppen (1994) established for the willow warbler that the area close to the road had a 40% lower annual output of males than areas farther away and probably acted as a sink. This can be interpreted as a considerable reduction of the habitat quality, but for a more solid conclusion a comparison with appropriate demographic data of other low-quality habitats is needed. Such data could not be found.



**Figure 4.** Coefficient of regression of effect size (see methods) on population index for the 23 species that could be analyzed each year (1984, 1986 and 1988; see Table 3). Species are divided into three categories: no significant effect (open bars), significant effect with the paired test (hatched bars), significant effect with regression (black bars).

If areas close to roads can be considered sinks (which was shown for the willow warbler, Reijnen & Foppen 1994), the size and persistence of breeding populations will depend on areas with a high-quality nearby (e.g. Bernstein *et al.* 1991). Therefore, to understand the consequences of a reduction of the habitat quality near the road at the population level, one should consider the habitat quality pattern in a wider area. The largest reductions of the population size are expected to follow from major losses of source areas (cf. Bernstein *et al.* 1991; Howe *et al.* 1991). A further degradation of sink

areas can also have some effect, because they may contribute significantly to population size (Howe *et al.* 1991). This is supported by a study of Foppen & Reijnen (1994), who found that there is a quantitatively important breeding dispersal flow of male willow warblers from highway-induced low-quality habitat to high-quality habitat nearby.

The fact that density is not always a good indicator of a reduced habitat quality and even can give misleading results, has not been recognized well in available studies on the effect of car traffic on breeding bird populations. This might also be the case in many other studies concerning human effects on breeding bird populations, such as disturbance by outdoor recreation (e.g. Van der Zande 1984) and military training (Thissen 1983). Therefore, one should be very careful in interpreting the results of these studies, since there is a large probability that the consequences for breeding bird populations are underestimated considerably. An appropriate way to cope with this problem in future studies is to investigate the effect on the density during several years. The largest effect found then gives the best approximation for a reduction of the habitat quality. However, the effectiveness of this strategy depends on the occurrence of significant changes in the overall population size of species. Because of this and to support the results, it is always preferable to determine the habitat quality of one or some key species by measuring demographic parameters.

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### **3.2 EVIDENCE OF REDUCED HABITAT QUALITY FOR WILLOW WARBLERS (*PHYLLOSCOPUS TROCHILUS*) BREEDING CLOSE TO A HIGHWAY**

#### **SUMMARY**

1. This study investigated the effect of a highway with dense traffic on the quality of adjacent habitats for the willow warbler *Phylloscopus trochilus*.
2. In the zone of 0-200 m from the highway (road zone) the density of territorial males was much lower (2.1 ha<sup>-1</sup>) than in zones with a comparable habitat at a greater distance (3.3 ha<sup>-1</sup>).
3. The lower density in the road zone was due to a low presence of older males. As a consequence, the proportion of yearling males in the road zone was about 50% higher than in the other zones.
4. Yearling males occupied their territories in the road zone later than in the other zones.
5. In the road zone the proportion of successful yearling males was about 50% lower than in the other zones. No difference was observed in the number of nestlings per male.
6. In the road zone the total annual output of males per ha was about 40% lower than in the other zones. The road zone probably acts as a sink for males immigrating from the intermediate and control zones.
7. A possibly important cause of the reduced habitat quality is the noise.
8. There is much evidence that the highway reduced the population size of the whole study area (165 ha of which about 20% belonged to the road zone).

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## INTRODUCTION

Although the effects of roads on the distribution of birds have not been studied well, the few available studies suggest that several territorial species have lower breeding densities in areas adjacent to main roads than in control areas further away (e.g. R  ty 1979; van der Zande *et al.* 1980; Reijnen *et al.* 1987). It is suggested that this is caused by a reduction of the habitat quality (here defined as the product of density, mean individual survival probability and mean expectation of future offspring; cf. Van Horne 1983) due to disturbance by car traffic. However, circumstances might occur in which differences in density will not equally reflect differences in quality and might even be misleading (Fretwell 1972; Van Horne 1983; Bernstein *et al.* 1991). The verification of the assumption that road habitats have a reduced quality therefore needs a more accurate and reliable measurement of the habitat quality.

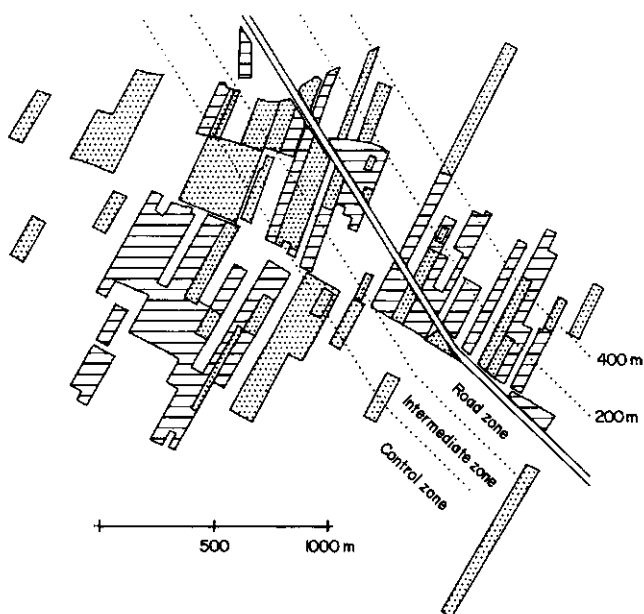
Indications for a reduced quality are delayed settlement of males (S  tther 1989; Brooke 1979; J  rvi 1983; Jakobsson 1988) and an increased proportion of yearlings (Greenwood and Harvey 1982; Gezelius *et al.* 1984; Lanyon and Thompson 1986; Labhardt 1988). For the most reliable information on habitat quality, however, the mean offspring production and survival characteristics should be considered. Differences in habitat quality then can be described as the difference between the total number of individuals (adults + offspring) surviving from year  $x$  to year  $x + 1$  per unit of area (cf. Van Horne 1983).

This paper focusses on the influence of a highway on the habitat quality of the willow warbler *Phylloscopus trochilus* L., a species showing a reduced density adjacent to roads (Reijnen *et al.* 1987).

## METHODS

### Study area

The study area was a nature reserve called 'Bolgerijen-Autena', situated in the centre of the Netherlands, south of Utrecht (51  75' N, 5  7' E) and crossed by highway A2 (about 50 000 cars per day). It consisted of willow *Salix sp.* coppices ( $\pm 150$  ha) and poplar *Populus sp.* plantations ( $\pm 15$  ha), which were separated by small patches of grassland. The study area was located in 76 ha of willow-coppice, a habitat type favoured by the willow warbler (Fig. 1). Poplar plantations were not involved, because the vegetation structure (mean height of trees about 10 m) was not suitable for the willow warbler (on average not more than 3 territories per year). Data were collected from 1988-1991.



**Figure 1.** The study area 'Bolgerijen-Autena' with the highway (double lined). The hatched parts indicate the selected willow-coppices, the dotted parts the other wooded vegetations (willow coppice and poplar wood). The remaining parts are meadows. The three zones are indicated by the dotted lines.

Because of the regular cutting of the willow-coppices (every 3 year), two habitat types were distinguished. Habitat type I represented the first year after cutting (which is done in winter), and habitat type II the two subsequent years. Both habitat types had a very uniform and homogeneous vegetation. Corresponding features were an almost full coverage (90-100%) by a tall (70-90 cm) luxurious herbaceous layer (mainly a mixture of *Symphytum officinale* L., *Holcus lanatus* L., *Alopecurus pratensis* L., *Urtica dioica* L., *Galeopsis tetrahit* L., *Rubus* sp. and large *Carex* species) and the presence of some scattered (about five per ha) old Hawthorns (*Crataegus monogyna* (Jacq.)). In habitat type II the willow-shrub layer had a coverage of 50-80% and a height of about 3-5 m, in habitat type I a willow-shrub layer only became important at the end of the breeding season.

To analyse the data the area was divided into three zones (corresponding zones on both sides of the highway were combined, Fig. 1): a 'road zone' up to 200 m from the

road (23 ha), an 'intermediate zone' from 200 to 400 m (12 ha) and a 'control zone' farther than 400 m from the road (41 ha). The distinction of these zones was based on earlier observations of the effect of road traffic on the distribution of the willow warbler in the same area, which showed that the density was affected up to several hundred meters from the road (Reijnen *et al.* 1987) and on a preliminary analysis of some demographic data of the first year of investigation (Reijnen & Foppen 1991). Differences in the structure of the habitat patches between the zones were of no importance, because the willow-coppice was very homogeneous throughout the whole study area and a comparison of 11 patches in the road/intermediate zone with 11 patches in the control zone did not show significant differences in a number of structural variables (Table 1).

The proportion of the study area which was cut every year (during 1988-91) varied from 25 to 33% (mean 30%). Per year the area cut was not equally distributed over the three zones, but the mean for all years was not very different (27% for the road zone, 33% for the intermediate part and 30% for the control zone).

**Table 1.** Vegetation structure of patches of habitat type I in different zones of the study area. The road/intermediate zone is 0-400 m and the control zone >400 m from the highway.

Estimate	Road + intermediate zone ( <i>n</i> =11)		Control zone ( <i>n</i> =11)		Sign.
	Mean	SD	Mean	SD	
1. Coverage of herb layer (%)	94	4.2	95	4.2	NS
2. Height of herb layer (cm)	76	13.0	80	11.8	NS
3. Coverage of shrub layer (%)	69	19.0	71	13.7	NS
4. Height of shrub layer (dm)	29.1	5.3	27.6	3.5	NS
5. Number of hawthorns (ha <sup>-1</sup> )	8.5	6.8	7.7	9.5	NS
6. Proportion of patch perimeter bordered by grassland	0.86	0.21	0.75	0.27	NS

Statistical significance is shown for single-factor ANOVA (estimates 1-5) or Mann-Whitney *U*-test (estimate 6), comparing the estimates in the road/intermediate zone and the control zone.

NS, *P* > 0.10.

### Catching and ageing males

Territorial males of the willow warbler were caught as soon as possible after territory establishment in spring, using a mistnet and playback song. Captured males received an unique combination of coloured rings, so they could be distinguished individually. Females

les were not included in the ringing efforts because they were relatively difficult to catch.

To determine the age of willow warblers in spring using biometrical and plumage characteristics, is very difficult. Although male yearlings on average have a smaller wing length than older birds (Hogstad 1985), this is not a reliable method. It is also possible to make use of the assumption that in a colour-ringed population the majority of the new unringed males are yearlings (immigration of older males is considered very low, see e.g. Radesäter *et al.* 1987; Jakobsson 1988; Bédard & La Pointe 1984). To achieve reliable results with this method the proportion of the population ringed should be very high. This could not be fully achieved, since the proportion of ringed males varied from 60%-80%.

However, yearlings could be identified because they had a consistently different response to song-recording than older males. The males which were easily caught showed strong agonistic behaviour and approached the 'intruder'. All 16 males which were known to be yearling (returned colour-ringed nestlings), without exception showed this behaviour and could be easily caught. The males that could not be caught only increased singing activity but did not approach the recorder. The same behaviour was shown by almost all 146 colour-ringed males that returned (which were at least 2 years old). Only one of these males behaved vigorously and hence was caught. Recatching of some other colour-ringed males occurred by accident, for example when they were approaching other males (see also Jakobsson 1988). Furthermore, there was no indication that males behaved differently in different zones of the study area. It is not very likely that yearlings were less agonistic close to the road as a consequence of traffic noise interfering with their detection of conspecific song, since in the road zone almost all unringed males behaved vigorously. Thus, unringed males which could not be caught were considered to be older than yearlings. The increase of the proportion of ringed birds during the study (from 60% in 1988 to 80% in 1991) is in agreement with this assumption.

So two age-groups were distinguished, yearlings (newly caught males) and older males (returning colour-ringed males and unringed males).

### Density

Territorial males were mapped six times or more from April till June. During each visit the whole area was thoroughly searched for males singing and showing other territorial behaviour. To distinguish territories, the criteria of the mapping method according to Hustings *et al.* (1985) were used. Since the mapping effort used in this study was much greater than Hustings *et al.* (1985) recommend in order to achieve an efficiency of 90% for the willow warbler (three visits in the most appropriate period), the number of observed territorial males will be very close to the number of territorial males actually present.

The density was calculated as the number of territories per ha. Territories that overlapped habitat and zone boundaries were allocated to the patch in which most of the observations were situated. The fact that this procedure can cause less accurate densities was negligible in our study area, because overlapping territories were very rare and only occurred in the case of zone boundaries. For the first year (1988) no reliable densities were available, because we searched only for the colour-ringed males.

### **Habitat occupancy**

To detect differences in habitat occupancy, the number of visits was increased to 12 in 1990. From the 22th of March, when the first willow warbler arrived, until the 16th of April, the study area was visited frequently (nine times). These visits each took 2-3 three days. The last three visits, each taking 5 days, were made in the second half of April (two) and in May (one).

### **Breeding performance**

In 1990 and 1991 the breeding performance was assessed for each territorial male by scores of mating and breeding success. A male was termed 'mated' when he was recorded with a female on at least two occasions. Although it is stated that females are inconspicuous (Tiainen 1983), it was easy to detect them with playback song, because they started producing typical calls (see also Järvi 1983; Schönfeld 1984). In many cases copulations were observed. Breeding success was recorded when a male succeeded in producing nestlings or fledglings (nest find or observed feeding behaviour). This was only done in a qualitative way (yes or no).

For an indication of the number of fledged young, the number of young in located nests was counted from 6 to 2 days prior to fledging. Nests were found in a systematic way by visiting all territories with feeding behaviour in a number of patches per zone.

### **Return rate**

To obtain values for the return rate of yearlings and older males (an indication of the survival rate) the whole nature reserve and a zone of 1 km around it were thoroughly searched for colour-ringed males.

The return rate of juveniles was measured by ringing 222 young birds in the nest in 1990. To detect the birds more easier, a colour-ring as well as the aluminium ring of the ringing station was used. In 1991 a zone of 5 km around the nature reserve was thoroughly searched. This field survey made it also possible to check whether the 1 km-zone used for the adult birds was sufficient.

## RESULTS

### Density

From 1989-1991 the total number of territories in the study area varied from 162 to 186 and most of them (85-96%) were situated in habitat type II (willow coppices 2-3 years after cutting). For all years combined the density in the road zone was in both habitat types (I and II) about 35% lower than in the intermediate and control zones (Tables 2 and 3). The densities for the years separately showed the same pattern, but the differences were not always significant or could not be tested.

Because the number of territorial males in habitat type I was very low, further analysis of the data is restricted to individuals occupying territories in habitat type II.

**Table 2.** Numbers (N) and densities (D) of willow warbler (territories ha<sup>-1</sup>) in habitat type I in the three zones of the study area. The road zone is 0-200 m, the intermediate zone 200-400 m and the control zone > 400 m from the highway.

Year	Road		Intermediate		Control		Sign.
	N	D	N	D	N	D	
1989	8	0.7	4	1.2	10	1.2	NS
1990	0	0.0	0	0.0	8	0.6	-
1991	1	0.3	12	1.7	11	0.7	-
Total	9	0.5	16	1.4	29	0.8	**

Statistical significance is shown for chi-square tests comparing the numbers in the three zones and taking account of differences in area. Tests have 2 degrees of freedom.

NS,  $P > 0.10$ ; \*\*  $P < 0.01$ .

### Proportion of yearlings

In habitat type II the proportion of yearlings in the road zone was 1.5 times higher than in the intermediate and control zone. In 1989 and for all years combined the difference was significant, in 1990 close to significant (Table 4). The effect is strongly influenced by the older males, because only these showed significant differences in the density between the three zones (Table 5).

**Table 3.** Numbers (N) and densities (D) of willow warbler (territories ha<sup>-1</sup>) in habitat type II in the three zones of the study area. The road zone is 0-200 m, the intermediate zone 200-400 m and the control zone > 400 m from the highway.

Year	Road		Intermediate		Control		Sign.
	N	D	N	D	N	D	
1989	26	2.3	25	3.3	99	3.0	NS
1990	44	2.2	32	3.4	102	3.7	*
1991	39	2.0	14	2.9	85	3.3	+
Total	109	2.1	71	3.3	286	3.3	***

Statistical significance is shown for chi-square tests comparing the numbers in the three zones and taking account of differences in area. Tests have 2 degrees of freedom.

NS,  $P > 0.10$ ; +  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*\*  $P < 0.001$ .

**Table 4.** Proportion of yearlings (PY) of the territorial male willow warblers in habitat type II in the three zones of the study area. The road zone is 0-200 m, the intermediate zone 200-400 m and the control zone > 400 m from the highway. Y is the number of yearlings, O is the number of older males.

Year	Road			Intermediate			Control			Sign.
	Y	O	PY	Y	O	PY	Y	O	PY	
1989	19	5	0.79	7	18	0.28	46	49	0.48	**
1990	30	15	0.67	16	15	0.52	46	55	0.46	+
1991	25	15	0.63	7	9	0.44	41	42	0.49	NS
Total	74	35	0.68	30	42	0.42	133	146	0.48	***

Statistical significance is shown for chi-square tests comparing the numbers in the three zones and taking account of differences in area. Tests have 2 degrees of freedom.

NS,  $P > 0.10$ ; +  $P < 0.10$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

### Habitat occupancy

In the control zone males (yearling and older) started to arrive 1 week earlier than in the road zone (22 March and 30 March, respectively). Nevertheless, the general pattern of settlement for the older males was not significantly different between the two zones (Mann-Whitney U-test,  $P > 0.10$ ). The yearlings, however, occupied their territories significantly later in the road zone (Mann-Whitney U-test,  $P < 0.05$ , Fig. 2).

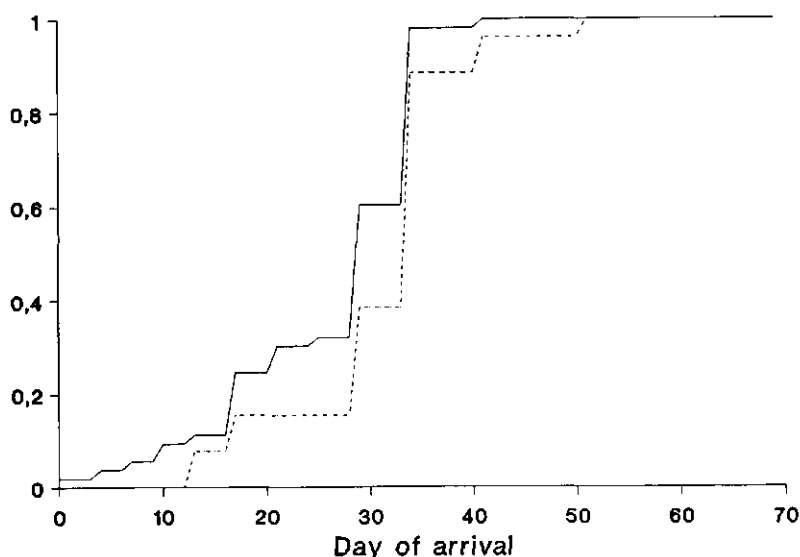
**Table 5.** Densities in territories per ha occupied by yearlings and older males of the willow warbler in habitat type II in the three zones of the study area. The road zone is 0-200 m, the intermediate zone 200-400 m and the control zone > 400 m from the highway.

Year	Yearlings				Older males			
	Road	Intermediate	Control	Sign.	Road	Intermediate	Control	Sign.
1989	1.7	0.9	1.4	NS	0.5	2.4	1.5	***
1990	1.5	1.7	1.7	NS	0.7	1.6	2.0	**
1991	1.4	1.5	1.9	NS	0.8	1.9	1.6	*
Total	1.5	1.4	1.5	NS	0.7	1.9	1.7	***

Statistical significance is shown for chi-square tests comparing the numbers in the three zones and taking account of differences in area. Tests have 2 degrees of freedom.

NS,  $P > 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

**Proportion arrived**



**Figure 2.** Settlement pattern of yearling males in the road zone (dotted) and the control zone (solid).



### Breeding performance

Since willow warblers produce one brood per year (Schönfeld 1984) and in only a few cases (<2%) bigamy was observed, the estimation of the number of nestlings of the males was based on one brood.

Older males in all zones and yearling males in the intermediate and control zone performed equally well. Only yearling males in the road zone were less successful (Table 6). In this zone the proportion of yearling males that succeeded in rearing young was about 40% lower than in the other zones. However, the yearlings who were successful in breeding, produced as many nestlings as the yearlings in the other zones and as all older males (Table 7).

Although the results indicate that the mating success was lower in the road zone, the differences between the zones were not significant. Within the road zone, however, yearling males had a significantly lower mating success (about 25%) than older males (chi-square test, 1 df,  $P < 0.05$ ).

**Table 6.** Mating and breeding success (proportion of total number of males being successful, see Tables 3 and 5) of yearlings and older males in habitat type II in the three zones of the study area in 1990-1991. The road zone is 0-200 m, the intermediate zone 200-400 m and the control zone > 400 m from the highway.

	Mating success				Breeding success			
	Road	Inter- mediate	Control	Sign.	Road	Inter- mediate	Control	Sign.
Yearlings	0.63	0.76	0.82	NS	0.40	0.60	0.69	*
Older males	0.85	0.88	0.89	NS	0.69	0.72	0.75	NS
Sign.	*	NS	NS		*	NS	NS	

Statistical significance is shown for chi-square tests comparing the mating and breeding success in the three zones. Tests between zones have 2 degrees of freedom, tests between age-classes 1 degree of freedom.

NS  $P > 0.10$ ; \*  $P < 0.05$ .

### Return rate

To achieve a sufficient number of returning adult males in the three zones, the observations were combined for all the years involved (1988-91).

Almost all males known to have survived returned to the study area and movements between successive breeding locations never exceeded 3 km (Foppen & Reijnen 1994). The return rate did not differ between the three zones, neither for yearling and older males, nor for both age groups combined (Table 8). There were also no significant dif-

ferences between the two age groups (chi-squared tests, 2 df,  $P > 0.10$ ). The overall return rate was 0.48.

Of the 222 nestlings ringed, 15 males returned to the study area or the 5 km zone around it. The return rate was not significantly different between the three zones (chi-squared test, 1 df,  $P > 0.10$ , Table 9), but the numbers are low and hardly allow statistical testing.

**Table 7.** Mean number of nestlings raised by pairs with yearling and older males of the willow warbler in habitat type II in the three zones of the study area. The road zone is 0-200 m, the intermediate zone 200-400 m and the control zone > 400 m from the highway. There were no differences between zones or age groups (ANOVA, 5 degrees of freedom,  $F = 0.53$ ,  $P = 0.76$ )

	Road zone			Intermediate zone			Control zone		
	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD
Yearlings	4	5.5	1.0	2	5.5	0.7	15	5.7	1.1
Older males	12	5.6	1.0	3	5.0	1.0	16	6.0	1.1

**Table 8.** Return rate (RR) of yearlings and older males during 1988-1991 in habitat type II in the three zones of the study area. N is the number of colour-ringed males, R the number of returned males. The road zone is 0-200 m, the intermediate zone 200-400 m and the control zone > 400 m from the highway.

	Road			Intermediate			Control			Sign.
	N	R	RR	N	R	RR	N	R	RR	
Yearlings	71	32	0.45	38	23	0.61	153	71	0.46	NS
Older males	20	12	0.60	28	12	0.43	61	25	0.40	NS
Total	91	44	0.48	66	35	0.53	214	96	0.45	NS

Statistical significance is shown for chi-square tests comparing the return rate (RR) in the three zones. Tests have 2 degrees of freedom.

NS,  $P > 0.10$ .

**Table 9.** Return rate (RR) of male nestlings ringed in 1990 for the three zones of the study area. N is the total number of ringed nestlings, N-males the number of ringed male nestlings (estimated by taking half of the total number N), R the number of returned birds. The road zone is 0-200 m, the intermediate zone 200-400 m and the control zone > 400 m from the highway.

	Road	Intermediate	Control	Total
N	47	40	135	222
N-males	23.5	20	67.5	111
R	3	2	11	16
RR	0.13	0.10	0.16	0.14

## DISCUSSION

### Evidence of reduced habitat quality near the highway

To detect a difference in habitat quality between the zones, the total annual output of males per ha was calculated (Table 10). This was done with the mean of the demographic data of all years combined to provide a more accurate assessment (Van Horne 1983). Because some demographic parameters were only measured in one year, an analysis of yearly patterns was not meaningful. Further, the intermediate and the control zones were combined, because differences in demographic data were very small and no significant patterns were established between them.

The much lower yearly output of males in the road zone compared with the intermediate/control zone (about 40% lower), points clearly to a decreased habitat quality adjacent to the road. The greater abundance and later arrival of yearling males in the road zone than in the control zone, support this result (see also Greenwood & Harvey 1982; Järvi 1983; Gezelius *et al.* 1984; Lanyon & Thompson 1986; Labhardt 1988; Jakobsson 1988).

The fact that in this study predominantly older males caused the lower density, is similar to results found for the whinchat *Saxicola rubetra* (Labhardt 1988). A lower proportion of successful males in poor habitats compared with good habitats, is also known for many species and usually is related to a decreased mating success (Kirtland's warbler *Dendroica kirtlandii*, Probst & Hayes 1987; whinchat *Saxicola rubetra*, Labhardt 1988) or an increased nest predation (redwinged blackbird *Agelaius phoeniceus*, Robertson 1972). Labhardt (1988) showed that the decreased breeding success for the whinchat also predominantly concerned the yearling males.

It is unlikely that increased nest predation caused the lower proportion of successful males in the road zone. Habitat features which can influence the predation level, such

as the vegetation structure (Robertson 1972) or the amount of edge (Andr  n & Angelstam 1988; Small & Hunter 1988), did not show significant differences between the zones. Although the mating success was lower in the road zone, it did not differ significantly from the mating success in the intermediate and control zones. However, there were indications that the mating success was still the crucial factor. Part of the observed 'nesting failures' could be due to 'divorces' before actual nest building, which means that the males involved should rather be considered unmated than mated. Anecdotal observations in the study area support this assumption and showed that yearling males especially in the road zone were involved (see also Labhardt 1988).

The reproductive success and survival rate of yearling and older males was not different between the zones. This indicates that the quality of males is not lower in the road zone. However, because the data on reproductive success of males were based on a low numbers of nests (especially for age-groups separately), this assumption is not totally reliable.

**Table 10.** Estimates of male willow warbler annual productivity and recruitment in the study area (1989-1991 average, Y = yearling, O = older than yearling). All demographic data were based on the observed values in the zones separately. Only for the return rate of nestlings the total value of the study area was taken, because the number of ringed birds in the road and intermediate zones was very low. The road zone is 0-200 m, the intermediate/control zone > 200 m from the highway.

Estimates	Road zone			Intermediate + control zone		
	O	Y	O+Y	O	Y	O+Y
Density of males(ha <sup>-1</sup> )	0.7	1.5	2.2	1.8	1.5	3.3
Return rate	0.60	0.45	0.50	0.42	0.49	0.45
Output of O-males(ha <sup>-1</sup> ) <sup>1</sup>	0.4	0.7	1.1	0.8	0.7	1.5
Number of male nestlings	2.8	2.8	2.8	2.9	2.8	2.9
Return rate	0.14	0.14	0.14	0.14	0.14	0.14
Recruitment per male	0.4	0.4	0.4	0.4	0.4	0.4
Proportion successful males	0.69	0.40	0.49	0.74	0.65	0.70
Output of Y-males(ha <sup>-1</sup> ) <sup>2</sup>	0.2	0.2	0.4	0.5	0.4	0.9
Total output of males(ha <sup>-1</sup> )	0.6	0.9	1.5	1.3	1.1	2.4

<sup>1</sup>(density) x (return rate)

<sup>2</sup>(recruitment per male) x (% successful males) x (density)

### Possible causes of reduced habitat quality

Little is known about how road traffic affects breeding-bird populations, but it is generally assumed that collisions, air pollution, visual stimuli and noise load should be relevant (e.g. van der Zande *et al.* 1980). Most of these causes, however, did not seem to affect the willow warbler population in our study area. An increased mortality due to collisions, which is the most clear cause-effect relationship, was unlikely because the return rate of the males in the road zone was not lower than in the other zones. Air pollution caused by road traffic can affect abundance and size of insects adjacent to roads (Przybylski 1979; Bolsinger & Flückinger 1989) and therefore might reduce the availability of insects as a food source for birds, but the range of the effect on insects is very small (up to 50 m from the road). Disturbance by visual stimuli could not have been important in the study area, because the sight of cars did not reach farther than 10–25 m from the road. Very little is known about noise as a possible causal factor, but relatively high levels occurred up to 500 m from the road (when using the method of Moerkerken & Middendorp 1981, the predicted mean value for 24 hours was about 50 dB(A) at a distance of 500 m). So, of the possible causes mentioned, the noise load might be important.

An obvious explanation of the noise load being an important cause of the effect, would be distortion of the song of the males in the road zone. The results indicate that males, especially yearlings, in the road zone experienced difficulties in attracting or keeping a female. The greater vulnerability of yearlings compared with older males can be explained by the fact that in the willow warbler older males usually have a more experienced song than young males, and females favour males with a more experienced song (Järvi 1983; Radesäter & Jakobsson 1989). Because car traffic noise can cause stress in birds (Helb & Hüppop 1991), an alternative or supplementary explanation could be that birds (females more than males) avoid the road zone.

### Evidence of sink effects near the highway

For a better understanding of the effect of car traffic in our study area, it is important to know whether the reproductive output in the road zone could have supported the observed densities or not. If not, the road zone should be considered as a 'sink'. In that case the persistence of a breeding population of the willow warbler in this zone would depend on immigration from more reproductive 'source' areas nearby, viz. the intermediate/control zone (Pulliam 1988; Howe *et al.* 1991).

However, the reproductive output in both the road zone and the intermediate/control zone was too low to compensate for the yearly losses due to mortality, which indicates that the whole area acted as a 'sink'. This seems not very likely, since important possible

'source' areas were not nearby (Foppen & Reijnen 1994) and the population had been quite stable for at least 4 years. Furthermore, the reproductive output of successful males appeared to be normal (see e.g. Schönfeld 1984) and the return rate of adults (used here as an indication for the survival rate) agrees with the highest values found in other studies (Lawn 1982; Tiainen 1983). On the other hand, the return rate of nestlings (used here as an indication of the survival rate of fledglings), even outside the road zone, was much lower (0.14) than normally is found for small passerine fledglings (0.20-0.30, see e.g. Bulmer & Perrins 1973; Schmidt & Hantge 1954; Von Haartman 1971; Probst & Hayes 1987).

Because an underestimation of the return rate of nestlings or fledglings can occur very easily (see e.g. Clobert & Lebreton 1991), it is possible that a (much) higher rate should be considered for the willow warbler in our study area. When we assume 'normal' values (between 0.20 and 0.30), then the road zone still remains a 'sink', but the intermediate/control zone can become a 'source'.

### Population consequences

The presence of a number of unsuccessful, respectively unmated males does not necessarily mean that the reproductive output of a population is decreased. The number of non-breeding females might be rare because of polygyny (see e.g. Arvidsson & Klaesson 1984) or a skewed sex ratio (more males than females). However, the percentage of bigamous males in our study area was low (<2% per year), which is in between values found in other studies, e.g. Tiainen (1983), 0.2%; Lawn (1982), 6.3%. Even if this is an underestimate, it is probably of no importance in compensating for the loss of reproduction due to the large amount of unmated/non-successful males in the road zone. In addition, a relatively large number of non-breeding females should have been present in our study area. In the chaffinch *Fringilla coelebs* evidence for females staying unmated, was shown by Sæther & Fonstad (1981).

The consequence for the whole willow warbler population might also be less important, if the lower reproductive output in the road zone is (partly) due to an accumulation of poorer yearling males. This implies, that these males had a more equal distribution in the study area before the highway was build. However, the percentage of unmated males in our whole study area (on average at least 20% per year) was still much higher than found in other studies, e.g. Lawn (1982), 12%; Tiainen (1983), 4%. Also, known differences in reproductive success between poor and good habitats for other species (Lundberg *et al.* 1981; Robertson 1972; Lemel 1989) between yearling and older males respectively (Sæther 1989) are very small.

So, there is much evidence that the lower density in the road zone means, that the population size of the whole study area was negatively influenced by the presence of the

highway. Because in poor habitats density can fluctuate more than in good habitats (e.g. Kluyver & Tinbergen 1953; Gezelius *et al.* 1984; O'Connor & Fuller 1985) the reduction of the population size probably also fluctuates. This means that habitats in the zone adjacent to and influenced by the highway will act as a buffer area for habitats further away. Although natal dispersal is a supposed mechanism in linking poor and good habitats (Pulliam 1988; Howe *et al.* 1991), the high proportion of yearlings in the road zone suggests an increased emigration of territorial males. The significance of this phenomenon is discussed elsewhere (Foppen & Reijnen 1994).

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### 3.3 BREEDING DISPERSAL OF MALE WILLOW WARBLERS (*PHYLLOSCOPUS TROCHILUS*) IN RELATION TO THE PROXIMITY OF A HIGHWAY

#### SUMMARY

1. In this study the dispersal activity of male willow warblers *Phylloscopus trochilus* breeding next to a highway carrying heavy traffic was investigated.
2. Breeding dispersal distances of yearling males along the road were larger than at further distances and were in the same order of magnitude as natal dispersal distances (medians being 303 and 515 m, respectively).
3. A simulation of dispersal directions, adjusted for actual landscape features, indicated that breeding dispersal was actively directed away from the road.
4. There appeared to be a relation between dispersal and breeding performance for yearling males, unsuccessful males moving more frequently and further (median 294 m) than successful males (median 120 m).
5. At the individual level the increased dispersal activity of yearlings close to the highway constitutes an 'escape' mechanism from low quality areas. At the population level it possibly stabilizes source populations. Dispersal characteristics should be incorporated into spatial population models.

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## INTRODUCTION

The proportion of yearling males in breeding bird populations is often higher in marginal habitats than in high quality habitats (e.g. Krebs 1971; Brooke 1979; Baeyens 1981; Ulfstrand *et al.* 1981; Gezelius *et al.* 1984; Labhardt 1988; Holmes & Sherry 1992). This larger proportion of yearlings might reflect an increased emigration of adult males. Alternatively it could be the result of an increased mortality rate in poor habitat. Movements from one territory to a better one, usually following an unsuccessful breeding season, have been reported in several studies (e.g. Brooke 1979; Greenwood & Harvey 1982; Weatherhead & Boak 1986; Gavin & Bollinger 1988). Since by definition breeding success is lower in marginal habitats, a larger proportion of the population in a given year is expected to disperse from such habitats. However, for many passerine birds it has been shown that breeding dispersal distances (distances between two succeeding breeding sites) usually are much shorter than natal dispersal distances (distance between site of birth and first site of breeding) (Villard 1991). So it is questionable whether breeding dispersal distances are large enough to allow redistribution over habitats. Evidence for movements from low to high quality habitats is rare (see e.g. Krebs 1971).

Habitats next to our study highway showed many characteristics of a low quality habitat. Breeding success was significantly lower close to the road than in areas further away. High proportions of yearling males were found and there was evidence that the high proportion of yearling males was not caused by an increased mortality (Reijnen & Foppen 1994).

This paper examines the extent and direction of breeding dispersal for a population of willow warblers (*Phylloscopus trochilus* L.) breeding next to a highway, and the relationship between dispersal and breeding success.

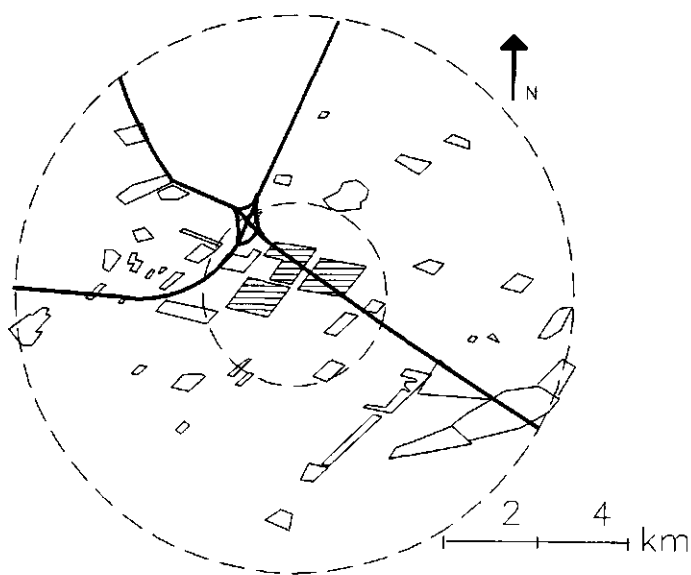
## STUDY AREA AND METHODS

The study area, total size about 165 ha, is located in the center of the Netherlands along a highway carrying heavy traffic. For a detailed description see Reijnen and Foppen (1994).

During the years 1988-91, territorial males were caught and given individual colour-ring combinations. Although ageing adult willow warblers based on plumage characteristics is almost impossible (Hogstad 1988), a yearling male group (against a group of older males) could be distinguished (Reijnen & Foppen 1994). All the observations of males were plotted on territory maps, and from this the center of the territory was determined graphically.

To analyse the data the area was divided into zones, starting from the road verge: a 'road' zone up to 200 m from the road; an intermediate zone from 200 to 400 m; and a control zone farther than 400 m. Data from corresponding zones on both sides of the road were combined since no influence of road side was to be expected.

To collect data on breeding dispersal, we looked for banded individuals in the study area, but also in all suitable habitat in the neighbourhood up to a distance of 1 kilometer from the boundary. The extent of the area surveyed was based on breeding dispersal data from the literature (Tiainen 1983; Lawn 1982). Breeding dispersal distance between subsequent years in the period 1989-91 was calculated as the difference between the centres of the breeding territories. In order to relate dispersal to breeding performance, data on breeding success published elsewhere were used (Reijnen & Foppen 1994). In 1990, 222 nestlings from 40 nests were colour-ringed. Since natal dispersal distances usually exceed breeding dispersal distances, a much larger area was surveyed in the spring of 1991. Suitable habitat in a 5-km circle around our main study area was checked for colour-ringed birds (Fig 1.).



**Figure 1.** Map of the study area and its surroundings. Hatched areas indicate the main study sites. Indicated are the two circles of 1 and 5 km radius where all available habitat patches (clear areas) were surveyed for colour-ringed individuals (for further information see text).

To test whether dispersing males moved randomly or actively avoided the areas next to the road, a Monte Carlo test (Manly 1990) was carried out. As a test statistic the mean displacement relative to the road was used, meaning the difference between the distance to the road in year  $x+1$  minus the distance to the road in year  $x$ . Simulations of the null model of random dispersal directions were conditional on the former territory centres. Thus, for each male, a circle was drawn based on the former territory centers with the dispersal distance as the radius. Those parts of the circle laying in non-habitat (meadows, clearings) were omitted. Next, random points on the remainder of the circle were chosen and distance to the road was measured. To derive a frequency distribution of mean displacements under the null model this procedure was carried out 200 times. The Monte Carlo significance level  $P$  is then the rank number for the observed test statistic divided by the number of simulations + 1 (Manly 1990).

## RESULTS

### Dispersal distance

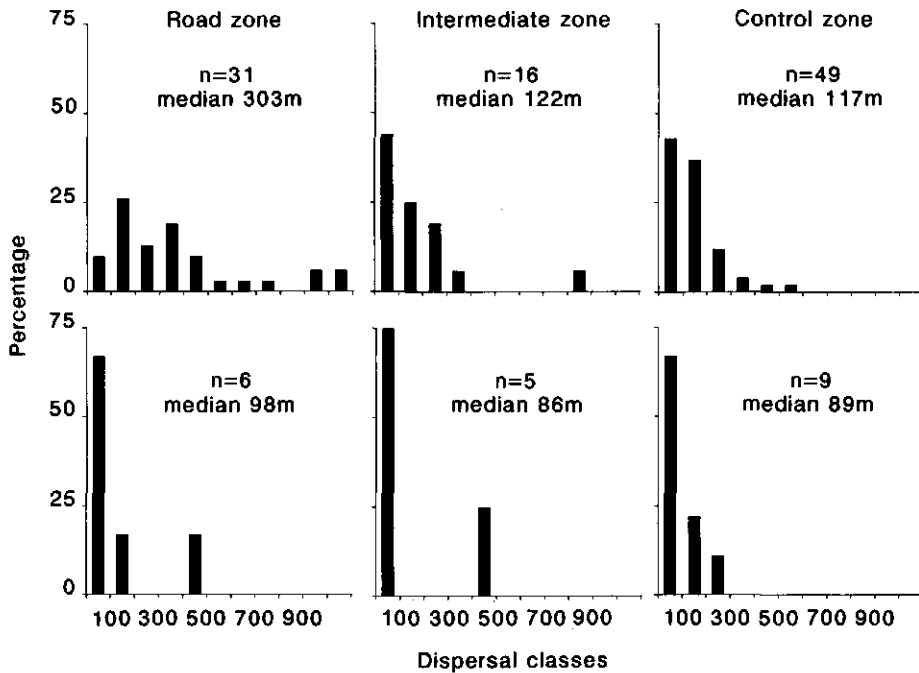
Because territory size covers about 0.2-0.3 ha (radius about 30 m) males that moved less than 50 m were considered site-tenacious. Although many males tended to be very site-tenacious, low site-faithfulness was observed for yearling males in the road zone (Table 1). In this zone the proportion of dispersing yearling males was significantly larger than for older males (chi-square test, 1 df,  $P < 0.01$ ). In the other zones older males tended to be also more site-tenacious than yearling males, but these differences were not significant, possibly due to small sample sizes.

**Table 1.** Percentage of site-tenacious males in the different zones for yearling and older males. The total number of males is shown in parentheses.

Zone	Total (%)	Yearling (%)	Old (%)
Road	18(45)	6(33)	50(12)
Intermediate	38(34)	36(25)	45(9)
Control	36(91)	35(75)	44(16)

The same picture arises from the analysis of dispersal distances. Usually, dispersing males stayed within 300 m of their former territory centre (Fig. 2), but yearling males in the road zone exhibited significantly longer dispersal distances. The median distance

moved was about 3-4 times as high as in other zones (see Fig. 2) and differed significantly from that in the other combinations of age and zone (Kruskal-Wallis test, 5 df,  $P < 0.005$ ). Again, the difference between yearlings and older males was significant only in the road zone (Mann Whitney  $U$ -test,  $P < 0.02$ ).



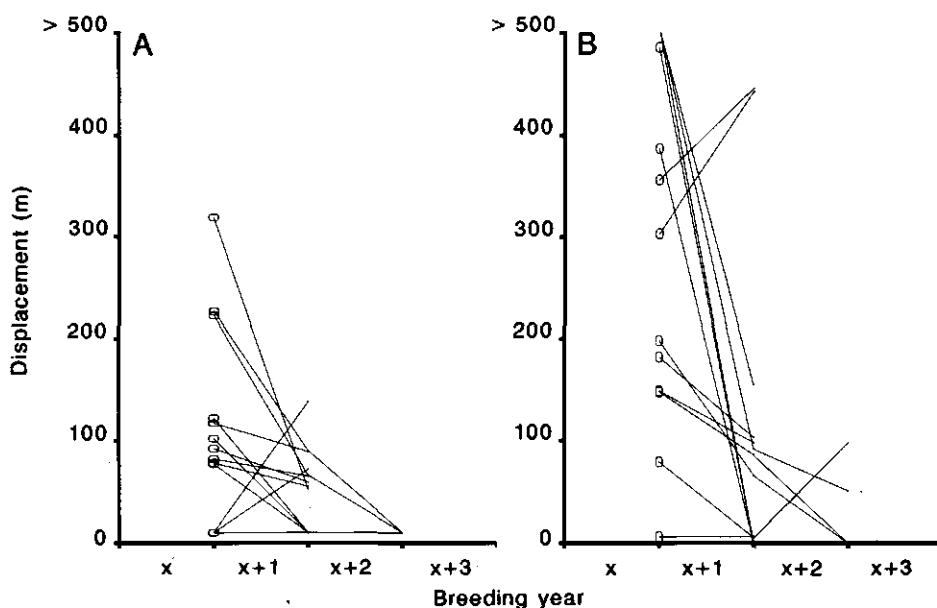
**Figure 2.** Frequency distributions of dispersal distances for yearling (above) and older males (below) in the three zones. Dispersal distances are shown in classes of 100 m; distances above 1000 m are combined.

When comparing successive breeding dispersal distances for a set of individuals the breeding dispersal distance for the first year was significantly longer than in subsequent years (Fig. 3). The difference was greatest for males in the road zone (mean difference 310 m, Wilcoxon matched-pairs test,  $P < 0.01$ ), but also applied to the other zones (pooled data: mean difference 40 m, Wilcoxon matched-pairs test,  $P < 0.05$ ).

In conclusion, yearling males close to the road almost all disperse, and they move much farther than older males or yearlings in other zones.

To judge the extent of these increased breeding dispersal distances, comparisons were

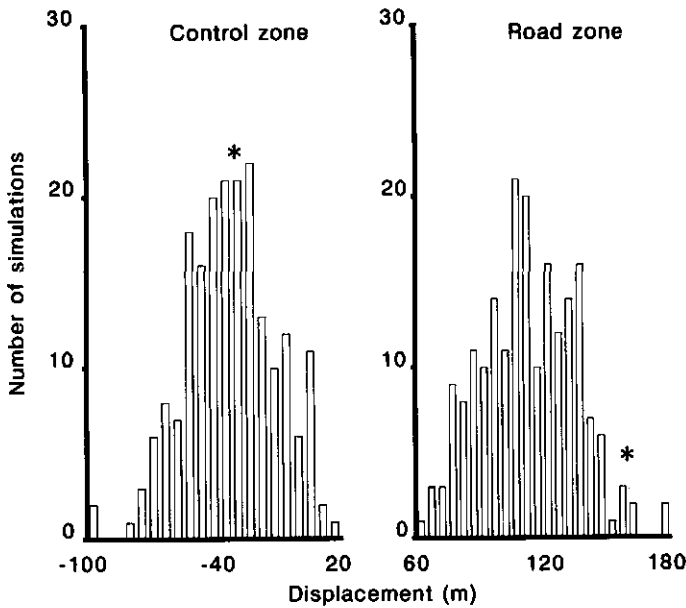
made with natal dispersal data for the same population. A total of 905 territorial males was checked for colour-rings in the 5-km circle. In total, 16 yearling males were found which were ringed as nestlings in our main study area the year before (7% return). Site-tenacious males included, median (515 m) and maximum (4125 m) natal dispersal distances are considerably longer than breeding dispersal distances of old males (median 55 m, maximum 446 m), but were not even twice as large as the breeding dispersal distances of yearlings in the road zone (median 282 m, range 3000 m). Direction of natal dispersal seemed random. Nestlings from zones close to the road ended up in the control zone and vice versa. The small sample size did not permit statistical analysis of this pattern.



**Figure 3.** Individual displacements of males which held territories in more than two years. Lines connect dispersal of individuals after first year of breeding ( $x$ ) and subsequent years ( $x+1$  or  $x+2$ ). In A individuals breeding for the first time in the intermediate and control zone, in B individuals breeding for the first time in the road zone.

### Direction of breeding dispersal

During the 1988-91 period, 40 between-year movements of males breeding in the road zone were recorded. More than half of these males (63%) moved out from this zone and occupied territories mostly in the intermediate (50%) but also in the control zone (13%). In interpreting these data, it should be noted that a withdrawal from the road zone is to be expected by random movement: when a male close to the road moves, the probability of moving even closer to the road is very small. Furthermore, the landscape structure surrounding the territory probably influences random dispersal. However, the observed distances to the road also appeared to be larger than expected on the basis of our generated random model (Fig. 4, 40 males, Monte Carlo test, one-tailed,  $P=0.03$ ). On the other hand, in the control zone, observed directions did not differ from a randomly generated pattern (Fig. 4, 38 males, Monte Carlo test one-tailed,  $P=0.51$ ).



**Figure 4.** Frequency distributions of simulated mean perpendicular displacements from the road for the group of males along the road and the group in the control zone (each 200 simulations). Asterisk (\*) indicates the actual recorded mean displacement to the road. A negative value means a displacement towards the road, a positive a displacement away from the road.

### Effect of former breeding performance on breeding dispersal

The relationship was examined between the dispersal data of individuals in 1991 and their breeding performance in 1990. For yearlings, dispersal probability was significantly correlated to their breeding performance in the previous year (Table 2). Among yearlings, successful males (having raised at least one young) dispersed less often than unsuccessful males. The breeding performance of old males did not correlate with their probability of dispersal (Table 2). Only for unsuccessful yearling males were there sufficient data to compare dispersal distances among the three zones. Distances moved in the road zone were clearly larger than in the other zones combined (median 294 and 120 m respectively, Mann-Whitney *U*-test,  $P < 0.05$ ).

**Table 2.** Relation between former breeding performance and amount of site tenacity of male willow warbler. The numbers of individuals are compared and tested by a chi-square test (1 df).

	Age			
	Yearling		Older	
	Moved	Not moved	Moved	Not moved
Successful	9	10	5	9
Unsuccessful	15	3	2	3
	$P < 0.05$		NS	

## DISCUSSION

### Breeding dispersal activity

The results support the idea that the high proportion of yearlings in the road zone is a consequence of a higher breeding dispersal from this zone than from those further from the road. Dispersal distances were quite large in the road zone and areas at a longer distance from the road were favoured. For most passerines, breeding dispersal distances reported do not exceed 2 or 3 times the territory size or 150 m (e.g. Darley *et al.* 1977; Harvey *et al.* 1979; Lanyon & Thompson 1986; Nyholm 1986; Drilling & Thompson 1988; Pärt & Gustafsson 1989; Winkel & Frantzen 1991). Short dispersal distances have also been reported in adult willow warblers (Lawn 1982; Tiainen 1983; Jakobsson 1988). Even in long-distance migrants, males are believed to disperse only short distances between years in order to occupy better quality territories in familiar areas around their own territory (Beletsky & Orians 1987). Indeed, it has been shown that males are able to increase their breeding success the year after dispersal (Baeyens 1981; Beletsky & Orians 1987; Pärt & Gustafsson 1989). In contrast, Lanyon and Thompson (1986)

consider territory improvement for painted buntings *Passerines ciris* to be hampered by strong site-tenacity.

Although yearling males of passerines have been reported to have an increased probability of dispersing (e.g. Rheinwald & Gutscher 1969; Greenwood & Harvey 1976; Mikkonen 1983; Labhardt 1988), only in a few cases breeding dispersal movements over long distances (several hundred metres or even a few kilometres) have been observed. Krebs (1971) observed young males of the great tit *Parus major* moving from hedgerows (marginal) to woodland (optimal) after removing territory holders in the latter habitat. However, these movements took place during the breeding season and the short replacement time indicated that the moving males also 'knew' their future territories. Few other studies have shown males switching from low quality areas to higher quality areas after their first breeding season. To our knowledge, in passerines this has been reported only in the whinchat (Labhardt 1988) and magpie (Baeyens 1981). In the nuthatch *Sitta europea* Matthysen (1990) also found changes to higher quality territories, however this concerned birds moving before their first breeding season.

The reason why long-distance breeding dispersal is very rarely observed might be due to the fact that in many studies the study areas are too small to allow detection of such long-distance dispersal. This might result in low return rates due to males settling far from their former breeding site. Indeed, lower return rates have been reported quite often for yearling males or for males in marginal habitats (Solonen 1979; Gauthreaux 1982; Nyholm & Myrberg 1983; Labhardt 1988; Holmes & Sherry 1992). The possibility that part of these low return rates is caused by an increased mortality rate must not be ruled out (Pärt & Gustafsson 1989), but this was certainly not the case in our study area (Reijnen & Foppen 1994).

#### **Effect of former breeding performance on breeding dispersal**

Breeding success seems to act as a proximate cue for dispersal. Yearling males that experience poor breeding success are more likely to move away from their previous territories. Probably males react according to their total former breeding experience rather than to their most recent breeding performance and this causes the observed differences in influence of former breeding success between yearling and older males (see also Beletsky & Orians 1987). There appears to be a trade-off between the risk of moving to a new area and the risk of another failure in the same area. Facing a poor breeding performance, old males, with a better knowledge of their present area, probably benefit most from staying, while yearling males benefit more from leaving. An identical relation between age, breeding experience and dispersal has been reported in the pied flycatcher *Ficedula hypoleuca* (Von Haartman 1949, Harvey *et al.* 1984), collared flycatcher *Ficedula albicollis* (Pärt & Gustafsson 1989), whinchat *Saxicola rubetra*



(Labhardt 1988), red-backed shrike *Lanius collurio* (Jakober & Stauber 1989) and magpie *Pica pica* (Baeyens 1981). The comparatively long dispersal distances shown by yearling males close to the road require another explanation in terms of decision-making. Probably males evaluate also the total quality of the breeding area by monitoring other males (Beletsky & Orians 1987). Based on both former breeding experience and the judgement on total quality of the area, they can make a decision about whether or not and how far to disperse. In the case of unsuccessful yearling males in low quality areas, this leads to long distance dispersal. In contrast, as expected, unsuccessful yearling males in the high quality areas did not disperse far away.

The proximate cause for the high numbers of yearling males starting to defend a territory in the road zone is yet unknown. Old males are dominant over yearlings (Jakobsson 1988) and we can confirm this by anecdotal observations. So probably a yearling male has only the option to fill vacant territories (about 50% of the total regarding the annual mortality). It is unknown whether yearling males immediately 'recognize' habitats further from the road as more suitable, whether individuals are forced out of these more preferred zones by other individuals, or whether the process follows a random distribution: filling open places in what appear to be suitable habitats in spite of the possible proximity of the road. Comparisons of clutch size and raised number of offspring do not support the idea that the potential of yearlings in the road zone is lower than in zones further from the road (Reijnen & Foppen 1994).

## Conclusions

At the individual level, dispersal constitutes a mechanism for yearling males to 'escape' from the highway-induced low quality habitat. Low reproductive success may occur in only one year. However, in small passerines most individuals will not survive until their second breeding season, so a large proportion of males in the road zone will never reproduce. For a short-lived species such as the willow warbler (mean life expectancy less than 2 years) this means that also the lifetime reproduction figure for those males will be much lower (Smith 1988).

Long-distance breeding dispersal of yearling passerine males in poor quality habitats seems to be a common phenomenon based on the high proportion of young males that disperse, and the return rates recorded for yearlings. It constitutes an effective mechanism to 'escape' from low-quality habitats and it optimizes habitat distribution without losing all advantages of being site-tenacious.

The willow warbler dispersal flow from areas next to the road to areas far from the road is quite large since not only are the distances large, the number of individuals involved is also quite considerable. In the opposite direction, there will be a net natal dispersal flow directed towards the road, since it was shown that offspring production

close to the road is much smaller than in control areas and probably also insufficient to compensate for yearly losses (Reijnen & Foppen 1994).

It has been suggested that low quality habitats are not only spill-overs for high quality habitats, but that they contribute to the stability of the latter populations and act as a buffer (Kluyver & Tinbergen 1953; Brown 1969; Bernstein *et al.* 1991). Howe *et al.* (1991), using simulation modelling, showed that the natal dispersal flow out of relatively large sink areas can stabilize a source population. The extra breeding dispersal flow towards 'source areas' also contributes to the stabilization of these populations and on the other hand it strengthens the 'sink' character of low quality habitats. Age-dependent dispersal characteristics therefore can not be neglected when modelling source-sink situations, though usually modelling is primarily based upon natal dispersal features (e.g. Pulliam *et al.* 1992).

Little is known about how dispersal is influenced by the configuration of the landscape. Field data are scarce and development of theoretical tools (e.g. modelling techniques) has only recently started (Johnson *et al.* 1992). Our data contribute to a better understanding of how animals respond to habitat patchiness and what kind of mechanisms are involved. However, at least for passerines, the conclusions probably only are applicable to situations where low and high quality areas are not greatly separated spatially (possibly not more than a few kilometres). A patchy environment probably alters the habitat selection and redistribution of birds over habitat (Verboom *et al.* 1991) and the challenge of clarifying this influence remains.

## ACKNOWLEDGEMENTS

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**DISTURBANCE BY CAR TRAFFIC IN THE  
NETHERLANDS: EVALUATION OF THE EFFECT**

## SUMMARY

In wildlife considerations in planning and managing road corridors few attention has been given to the effects of disturbance by car traffic on breeding bird populations. Recent studies, however, show evidence of strong reduced densities of many species of woodland and open habitat in broad zones adjacent to busy roads. The density reduction is related to a reduced habitat quality and car traffic noise is probably the most critical factor. Because density can underestimate the habitat quality, the effects on breeding populations are probably larger than established. In consequence, species that did not show an effect on the density, still might be affected by car traffic noise. Based on this recent knowledge methods are developed that can be used in spatial planning procedures related to main roads and in road management practice and some practical points are discussed. An example of application shows that the effects are probably very important in The Netherlands with a dense network of extremely crowded main roads. For 'meadow birds', which are of international importance, the loss of population in the west of The Netherlands may amount to 16%. Because breeding birds suffer from many other environmental influences, there is also a great risk of an important cumulation of effects.

*With Geesje Veenbaas and Ruud Foppen*

*Submitted to Biodiversity and Conservation*

*Original title: Disturbance by car traffic of breeding birds in The Netherlands: evaluation of the effect and considerations in planning and managing road corridors.*

## INTRODUCTION

Wildlife considerations in planning and managing road corridors point out that habitat loss is probably the most important factor that can reduce the population size of breeding birds. Although car traffic kills large numbers of birds annually, it is assumed that this will not likely cause a significant increase of the overall mortality of species (e.g. Ellenberg *et al.* 1981; Leedy & Adams 1982; Bernard *et al.* 1985; Bennett 1991). However, little attention has been given to the effect of disturbance by car traffic. A few earlier studies indicated that several species had depressed densities in habitats adjacent to main roads and highways (Clark & Karr 1979; R  ty 1979; Ferris 1979; Van der Zande *et al.* 1980; Adams & Geis 1981; Illner 1992a). Recently, evidence is shown that these effects can be very important (Reijnen *et al.* 1995, in press; Reijnen & Foppen in press). It was found that in open habitat as well as in woodland adjacent to busy roads, the majority of the species had lower densities in areas close to the road than in control areas further away. Moreover, in many species disturbance distances were very large and the reduction of the density over these distances very high.

The aim of this paper is to stress the importance of considering the 'disturbance' effect in planning and managing road corridors. We discuss the following points:

1. evidence illustrating the nature and extent of the disturbance effect in breeding birds;
2. methods to implement such knowledge in planning and managing road corridors;
3. how application works out in exploring the dimensions of the problem for The Netherlands with a dense network of extremely crowded motorways.

## BIRD POPULATION RESPONSE TO DISTURBANCE BY CAR TRAFFIC

### The effects on breeding density

In earlier studies depressed densities of breeding birds adjacent to roads were found in only a few species belonging to quite different taxonomic groups, such as warblers, waders and tetraonids (Clark & Karr 1979; R  ty 1979; Ferris 1979; Van der Zande *et al.* 1980; Adams & Geis 1981; Illner 1992a). Since the total number of investigated species in these studies was rather small, it is difficult to interpret whether the density-depressing effect of roads is a common phenomenon or not. However, from the results given in the recent papers of Reijnen *et al.* (1995, in press) and Reijnen & Foppen (in press) it can be concluded that the effect is widely spread in breeding birds. Along heavily travelled roads in The Netherlands 33 of the 45 investigated bird species in woodland showed an effect and 7 of the 12 investigated species in agricultural grassland. The affected species cover almost all taxonomic groups present in these data (Table 1).

**Table 1.** Number of affected species by car traffic in different taxonomic groups.

Taxonomic group <sup>1</sup>	Number of investigated species in woodland		Number of investigated species in agricultural grassland	
	Total	Affected	Total	Affected
<i>Anatidae</i>	1	0	4	1
<i>Accipitridae</i>	1	1	-	-
<i>Phasianidae</i>	1	1	-	-
<i>Rallidae</i>	- <sup>2</sup>	-	1	1
<i>Haematopodidae</i>	-	-	1	1
<i>Charadriidae</i>	-	-	1	1
<i>Scolopacidae</i>	1	1	2	1
<i>Columbidae</i>	3	2	-	-
<i>Cuculidae</i>	1	1	-	-
<i>Picidae</i>	3	2	-	-
<i>Alaudidae</i>	-	-	1	1
<i>Motacillidae</i>	1	1	2	1
<i>Troglodytidae</i>	1	1	-	-
<i>Prunellidae</i>	1	0	-	-
<i>Turdidae</i>	4	3	-	-
<i>Sylviidae</i>	8	8	-	-
<i>Muscicapidae</i>	2	1	-	-
<i>Aegithalidae</i>	1	0	-	-
<i>Paridae</i>	6	4	-	-
<i>Sittidae</i>	1	0	-	-
<i>Certhidae</i>	1	1	-	-
<i>Oriolidae</i>	1	1	-	-
<i>Corvidae</i>	3	2	-	-
<i>Sturnidae</i>	1	0	-	-
<i>Fringillidae</i>	2	2	-	-
<i>Emberizidae</i>	1	1	-	-
Total	45	33	12	7

<sup>1</sup>nomenclature follows Voous (1973, 1977)<sup>2</sup>no species presentSource: Reijnen *et al.* 1995, in press; Reijnen & Foppen in press

Rough estimations of disturbance distances and density reductions over these distances in some of the earlier studies indicate that the effect might also be important quantitatively. For two wader species in open field habitat, Van der Zande *et al.* (1980) estimated disturbance distances ranging from 625 m for a secondary road to 2000 m for a busy highway (Van der Zande *et al.* 1980). Tetraonid species in woodland were disturbed up to a distance of 500 m near relatively quiet highways (Räty 1979). In both studies the density reduction in the disturbed zone amounted to 50% or more.

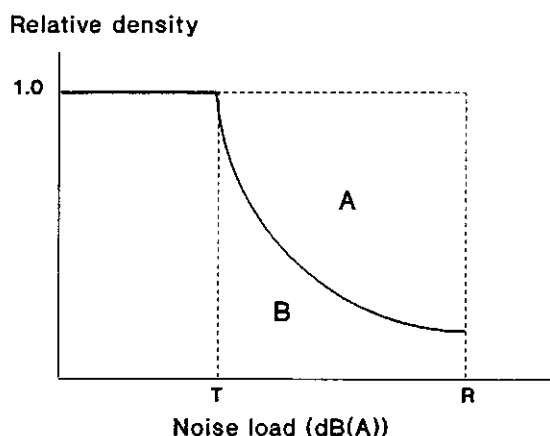
Accurate quantitative data of many species from the recent studies of Reijnen *et al.* (1995, in press) and Reijnen & Foppen (in press) show, that such large disturbance distances and high density reductions are not exceptional. They quantified the relationship between traffic load and density with regression by using a threshold model with car traffic noise (in dB(A)) as the explanatory variable (see for explanation Reijnen *et al.* 1995 and Fig. 1). Disturbance distances were derived from these equations by transforming the threshold value in dB(A) into distance from the road (m). To compare the results of these studies we converted values for 5000 cars a day to 10 000 cars a day (grassland) and values for 60 000 cars a day to 50 000 cars a day (woodland). Estimated disturbance distances of grassland breeding birds vary from 30 to 2180 m at 10 000 cars per day and from 75 to 3530 m at 50 000 cars per day. Woodland breeding birds have a similar range of disturbance distances, from 30 to 1500 m and from 60 to 2800 m, respectively. For the density of all species combined the estimated disturbance distance in open grassland is 190 m at 10 000 cars a day and 560 m at 50 000 cars a day, in woodland 50-1500 m and 100-2800 m respectively.

However, it was pointed out that the very large disturbance distances might be unrealistic because they are based on regressions in which a threshold is absent (lowest noise level was taken as the threshold). If we disregard these regressions, estimated disturbance distances remain very large but they do not exceed 1000 m anymore (Table 2). Also, the range of threshold values in dB(A) for species and for all species combined now becomes very similar in both habitat types (Table 3).

The reduction of the density over the disturbance distances varies greatly between species, but is never smaller than 30%. In both habitat types, several species even show a density reduction of almost 100%. This means that dense car traffic, in particular, can cause an important loss of population of species. Because many species are affected, there is also an significant reduction of the total density, in open agricultural grassland 39% and in woodland 35%.

In some previous studies also higher densities of breeding birds close to roads were found (Clark & Karr 1979; Ferris 1979; Adams & Geis 1981). However, this can be explained by habitat conditions being much more favourable close to roads than farther away and therefore should not be interpreted as a positive effect of car traffic (see

Reijnen *et al.* 1995). There are no indications that species might be favoured because of competition (increase of density if there is an effect on related species) or better feeding conditions due to the presence of road victims (Reijnen *et al.* 1995). This is in accordance with the fact that total bird density is also reduced.



**Figure 1.** Estimation of the relationship between traffic noise and breeding density of birds. T = threshold value, R = noise load in the verge of the road. The decrease factor of the density = area of A / (area of A+B).

Source: Reijnen *et al.* 1995

**Table 2.** Maximum size of the disturbed zone adjacent to main roads (in m) that has a reduced density of breeding birds, when probable unrealistic values are not considered.

Habitat	Species		All species combined	
	10 000 cars per day	50 000 cars per day	10 000 cars per day	50 000 cars per day
Open grassland	365	930	190	560
Woodland	305	810	125	365

Based on Reijnen *et al.* (1995, in press) and Reijnen & Foppen (in press).

### Possible causes and mechanisms

Reijnen *et al.* (1995) found almost no effects on species along roads when the noise load due to car traffic was relatively low. This indicates that the presence of a road *per se* is



not very important in affecting densities of breeding birds. Also, it is not probable that mortality due to collisions is an important causal factor. Although the numbers of road victims can be rather large (e.g. Adams & Geis 1981; Hodson & Snow 1965, Füllhaas *et al.* 1989; Van den Tempel 1993), it was assumed that they are in general not sufficient to cause a significant increase of the total mortality of species (Leedy & Adams 1982; Ellenberg *et al.* 1981; Reijnen *et al.* 1995). Support for this assumption is given by Reijnen & Foppen (1994), who observed equal survival rates of male willow warblers *Phylloscopus trochilus* close to a busy highway and in areas at a distance of several hundred meters. Only for owls, in particular barn owl *Tyto alba*, road mortality might influence population size significantly (Joveniaux 1985; Illner 1992b; Van den Tempel 1993).

**Table 3.** Threshold values for traffic noise (dB(A)) of breeding birds; probable unrealistic values are shown in parentheses. Below the threshold the density is not affected.

Habitat	Species	All species combined
Woodland	(23)36-58	(23)42-52
Open grassland	(27)43-60	47

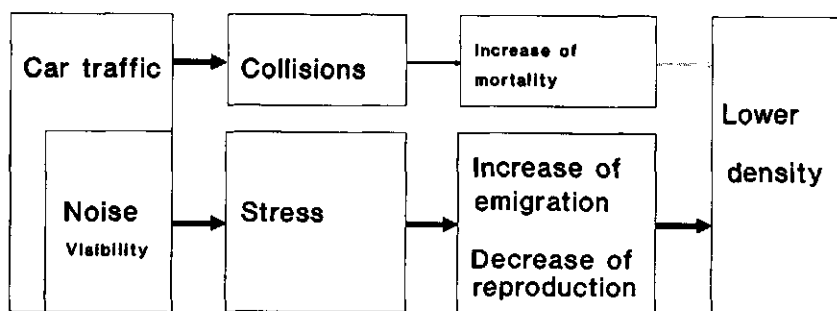
Source: Reijnen *et al.* (1995, in press) and Reijnen & Foppen (in press)

This implies that possible causes will rather be related to emission of matter and energy by road traffic, such as pollution, visual stimuli and noise (Van der Zande *et al.* 1980; Leedy & Adams 1982; Ellenberg *et al.* 1981). Reijnen *et al.* (1995) show evidence that in woodland noise is probably the most critical factor in causing reduced densities close to roads. In regression analysis using noise and visibility of cars as response variables, noise appeared to be the best and in many species also the only predictor of observed depressed densities close to the road. A reduction of the total density could only be explained by noise. Furthermore, they made it plausible that other possible causal factors, such as pollution and visual stimuli, are not very important, because they operate at a very short distance from the road and have in all probability a limited effect. With respect to visual stimuli this might not hold true in open landscape. Here, visual stimuli reach much farther than in wooded areas and breeding birds might respond differently (Reijnen *et al.* in press). On the other hand, a study of Illner (1992a) showed that by absence of visual stimuli (road bordered by hedge rows) grey partridge *Perdix perdix* densities in open arable farmland were still heavily depressed up to several hundred meters from busy highways. Also, breeding birds of open grassland and woodland respond very similarly to disturbance by car traffic (Table 3). This indicates

that noise is also the most critical factor in open landscape.

Very little is known about how noise could cause reduced densities of breeding birds. For the willow warbler it has been shown that close to a highway many males experience difficulties in attracting or keeping a female and because of the lack of reproductive success move out of the road zone in the following year (Reijnen & Foppen 1994; Foppen & Reijnen 1994). This could point to distortion of the song of males as a possible mechanism (cf. Reijnen & Foppen 1994). However, there is some evidence that disturbance of the vocal communication between birds is probably not a general mechanism in causing reduced densities (Reijnen *et al.* 1995). An alternative, or more likely a supplementary explanation is that birds avoid areas close to roads because of stress (Reijnen *et al.* 1995; Illner 1992a).

Fig. 2 summarizes the probable relationships between car traffic and density of breeding birds.

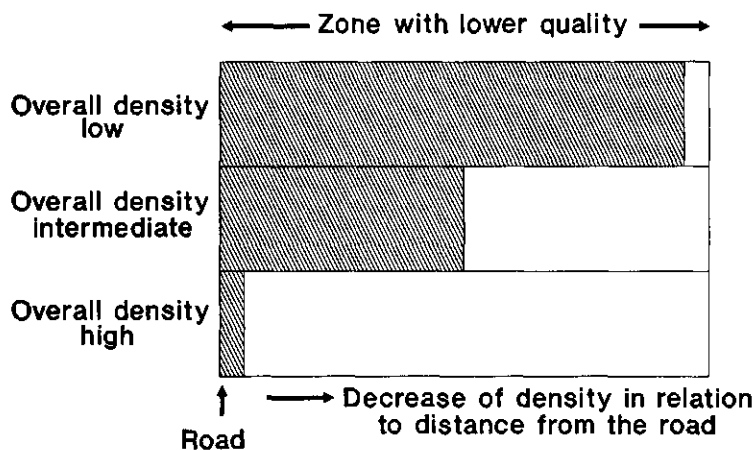


**Figure 2.** Probable relationships between car traffic and density of breeding birds.

### **Effects on habitat quality in relation to density**

There is much evidence that the reduction of the density is related to a reduction of the habitat quality (Reijnen & Foppen 1994; Reijnen & Foppen in press). On the other hand it is known that density is not always a good indicator of habitat quality and might be even misleading (Fretwell 1972; Van Horne 1983). In several territorial bird species it has been shown that, when overall density is high, less-preferred habitat is more strongly occupied than when overall density is low (Kluyver & Tinbergen 1953; Glas 1962; O'Connor & Fuller 1985). Similar relationships were found between habitats close to roads and habitats further away (Reijnen & Foppen in press). This means that the size

of zones adjacent to roads, that have a lower quality due to disturbance by car traffic, can easily be underestimated when it is based on density data (Fig. 3). The study of Reijnen & Foppen (in press) indicates that in woodland birds such underestimation can be substantial, since many species only had a depressed density in years with a relatively low overall density. By consequence, species that did not show an effect on the density, still might be affected by car traffic.



**Figure 3.** Schematic representation of the effect of disturbance by car traffic on habitat quality (hatched + open) and density (hatched) of breeding birds in relation to overall population size.

### Consequences for breeding populations

To understand the consequences of the effect of disturbance by car traffic on breeding bird populations the reduction of the habitat quality is probably the most important. There are many indications that the size and persistence of breeding populations mainly depend on areas with a high quality (Wiens & Rotenberry 1981; Bernstein *et al.* 1991). In consequence, the largest effects on the overall population size can be expected when disturbance causes a major loss of high-quality areas. Also a further degradation of habitats with a low quality can have some effect, because they may contribute significantly to the overall population size (Howe *et al.* 1991). This is supported by a study of Foppen & Reijnen (1994), who found that there is a quantitatively important breeding dispersal flow of male willow warblers from highway-induced low-quality habitat to high-quality habitat nearby.

Finally, one should also consider possible risks of cumulation of effects.

## APPLICATION

### General considerations

In applying the recent knowledge on the relationship between car traffic and breeding bird populations in spatial planning procedures we distinguish between (1) assessment of the size of the problem and (2) selection of effective measurements that reduce the effects.

The use of noise to quantify the traffic load has the advantage of describing the relationship between car traffic and density in a rather universal way. Noise takes into account many characteristics of car traffic that might be important in affecting breeding birds (such as number of cars, type of cars, speed) and, as mentioned before, probably also is the most critical factor. Furthermore, there are appropriate mathematical models to calculate the noise load along roads (Moerkerken & Middendorp 1981; Huisman 1990; see also Reijnen *et al.* 1995) and basic data are readily available or can be easily measured.

The available data give adequate information to establish effects of car traffic on main roads in woodland (deciduous and coniferous) and open agricultural grassland. Sampling plots were distributed all over The Netherlands and the range of traffic densities involved was rather large (3000-75 000 cars per day). Furthermore, application of the results in other habitat types seems allowable. The species studied are representative for the whole group of breeding bird species in The Netherlands and many of them can also be found breeding outside woodland and open agricultural grassland. It is likely that the results are also applicable in areas outside The Netherlands that have a similar bird fauna. However, in hilly areas the established relationships between noise and density might not be valid. In that case and in all other very different situations additional investigations are needed.

Effect curves in which a threshold was absent resulted in very large and probable unrealistic disturbance distances and it is better not using them. On the other hand, evidence was shown that the available data can underestimate the size of the disturbed zone considerably. To reduce this risk, for the remaining effect curves one can concentrate on the largest effect found for the total density and the effect for the most sensitive species. These effect curves also have relatively narrow confidence limits. A side-advantage of this approach is that it makes extrapolation to other habitat types more easy.

Because noise is probably the most critical factor, one can expect that a reduction of the noise load will reduce the effects on the density. Although further experimental evidence is needed, there are probably no important restrictions to apply this knowledge. Measurements that reduce the noise load, such as the construction of walls of earth or

concrete materials, will also reduce or eliminate the other traffic related factors.

A reduced density adjacent to roads can also be compensated for by developing new favourable habitats outside the disturbed zone. Improvement of the habitat quality within this zone, in general, will have a limited effect, since the observed density reductions were very large. However, since the reduction of the density decreases with increasing distance from the road, it might have some effect in the part of the disturbed zone far from the road.

To favour the application of the present knowledge on the effects of car traffic on breeding bird populations in spatial planning procedures related to main roads, such as EIA and in road management practice, we compiled a manual that makes application easier (Reijnen *et al.* 1992). Partly based on this manual we now discuss some practical points.

### **Reducing effects along existing roads**

A sufficient reduction of the noise load along roads in order to reduce the effects of car traffic on breeding bird populations can only be achieved by constructing noise muffling devices. However, to obtain a substantial reduction, the length of these devices should be very large and their height rather high. Moreover, in open areas, such devices may also act as a source of disturbance themselves, because many birds of open grassland avoid the vicinity of hedgerows, wooded banks and dikes up to several hundred meters (e.g. Klomp 1954; Van der Zande *et al.* 1980; Altenburg & Wymenga 1991). So, application seems only appropriate for major problems (large disturbance distances in important areas for breeding birds). Finally, in constructing noise muffling devices, one should take into account that they might act as a further barrier for other animal species. If under- or overpasses for wildlife are constructed to reduce the barrier effect of the road itself, this might give less problems. Openings in muffling devices at the ground level are probably not very effective, since, in particular, for small animals, the barrier effect of the road itself is probably much more important (e.g. Oxley 1974; Mader 1984; Mader *et al.* 1990). However, they might be useful for animals to escape from the road area.

Compensation for loss of population along roads by creating new habitats outside the disturbed zone, has the disadvantage that in general it will take many years before the habitat is fully developed. Moreover, in The Netherlands with a dense human population, application is probably limited. At present, reallocation plans afford the best opportunity, in particular with respect to birds of agricultural grasslands. Extensification of agricultural management in areas outside the disturbed zone (which improves the habitat quality), can be compensated for by intensifying the agricultural management close to roads (cf. Reijnen *et al.* in press). One should take care that such measurements do not

cause loss of other natural values in the disturbed zone, such as interesting plant communities.

As discussed before, improvement of habitat quality of disturbed areas near the road will not be of great value since the reduction of the density of many species is very strong. Moreover, it can increase the number of road kills (Van den Tempel 1993). In view of this, one should also have low expectations of positive effects of roadside management for breeding birds in general. This does not mean that roadside management to maintain or improve natural qualities, is not effective from a conservation point of view. In particular, when roadside habitat comprises remnants of natural vegetations, it can be valuable for many plant species and animals, such as small mammals, butterflies, carabids and other invertebrates (e.g. Bennett 1991; Sykora *et al.* 1993; Hochstenbach 1993). If road sides connect other habitat patches, they also can function as a corridor, which might have positive effects on the size and persistence of the overall population (see e.g. studies on carabids, Vermeulen 1993, 1994). In large agricultural areas, the occurrence of many species, including birds, may depend on roadside habitat (see e.g. Bennett 1991).

Although it is now rather well established that the development of new natural areas for breeding birds should not be taken place close to main roads, still in The Netherlands this sometimes happens. Recently, in the reallocation plan for the 'Eempolders', a nature reserve for meadow birds was situated adjacent to a highway. This resulted in discussions how to reduce the effects of disturbance!

### **Minimizing effects in planning roads**

The best way to minimize the effects of new roads is to avoid disturbance of important areas for breeding birds. This can be achieved by using knowledge on disturbance distances in the first phase of the EIA-procedure, to which all plans for main roads are subjected. In exploring possible solutions for transportation routes, one should take into account a sufficient distance from these areas, based on expected traffic densities. In general, 1000 m to both sides of the road seems an adequate distance.

When effects are inevitable, one should consider measurements to compensate for or to reduce effects. As discussed before, development of natural areas in or adjacent to roadsides are in general not a useful strategy with respect to breeding birds.

## **EXAMPLE OF APPLICATION: EXPLORING THE DIMENSIONS OF THE PROBLEM IN THE NETHERLANDS**

### **Estimation of the total disturbed area**

The Netherlands has a dense network of main roads (ca. 0,3 km per 100 ha, total ca. 3000 km)(Anonymous 1993a) with high traffic densities varying from 10 000 to more than 140 000 cars per day (Anonymous 1988, 1993b)(Fig. 4). This network of main roads adsorbs the majority of the traffic volume on all paved roads outside the urbanized areas (Anonymous 1992), and therefore it accounts for most of the effects of car traffic on breeding bird populations.

To obtain a rough indication of the consequences for breeding bird populations we made an estimation of the total disturbed area along the network of main roads. This was carried out for the present situation (1986) and for a scenario in 2010 (Anonymous 1988), which is mainly based on an ongoing increase of the traffic density. Two estimates were made, one for all species combined and one for the most sensitive species (as recommended before). This was done for birds of woodland and open agricultural grassland separately, because they have somewhat different disturbance distances. The actual disturbed area will be in between these two values. Calculations were carried out by using the computerprogram SILENCE (Anonymous 1988).

In 1986 the estimated size of the disturbed zone for all species combined covered more than 8% of the land area of The Netherlands and for the most sensitive species more than 15% (Table 4). In 2010 these values could be 30-40% higher (Table 4). Although it was not possible to show which part of actual habitats is affected, it is very likely that such a large disturbed area should have important consequences for breeding bird populations of many species, in particular the more sensitive ones.

### **Exploration of consequences for meadow bird populations**

To support the assumption that disturbance by car traffic has important consequences for breeding populations of species, we made a rough analysis for birds of moist and wet grasslands. Many of these grasslands, in particular in the north and west of The Netherlands, are well known for their rich communities of so-called 'meadow birds', which are of international importance (Beintema 1986). The most typical species is the black-tailed godwit *Limosa limosa*, of which 80-90% of the European population nests in these grasslands (Van Dijk *et al.* 1989).



**Figure 4.** Pattern of main roads in The Netherlands in 1986. The traffic density varies from 10 000 to > 100 000 cars per day. The thickness of the lines reflects the area that has a noise load of > 50 dB(A). Source: Anonymous 1991.

For practical reasons the survey was restricted to the west of The Netherlands, which has the highest density of main roads (Fig. 5). Data on the distribution of moist and wet grasslands were taken from Bakker *et al.* (1989), which reflect the pattern of 1986. Because detailed data on the distribution of 'meadow birds' were not readily available, we made only two categories to indicate differences in habitat quality: 'important' (many



species and high densities, based on Bakker *et al.* 1989) and 'less important' (on average few species and low densities, see e.g. Vogelwerkgroep Avifauna West-Nederland 1981). For the black-tailed godwit, the most abundant species, the number of breeding pairs between 1979-1987 in this region was on average 20 000 (Van Dijk *et al.* 1989).

**Table 4.** Estimated size of disturbed area by car traffic along main roads in The Netherlands in 1986 and for a scenario in 2010, which is based on an ongoing increase of the traffic density.

Estimate	Disturbed area			
	Size x 100 ha <sup>1</sup>		% of total land area in The Netherlands <sup>2</sup>	
	1986	2010	1986	2010
All species combined <sup>3</sup>	2786-3901	3965-5377	8.2-11.5	11.7-15.9
Most sensitive species <sup>3</sup>	5324-5872	7114-7776	15.8-17.4	21.1-23.0

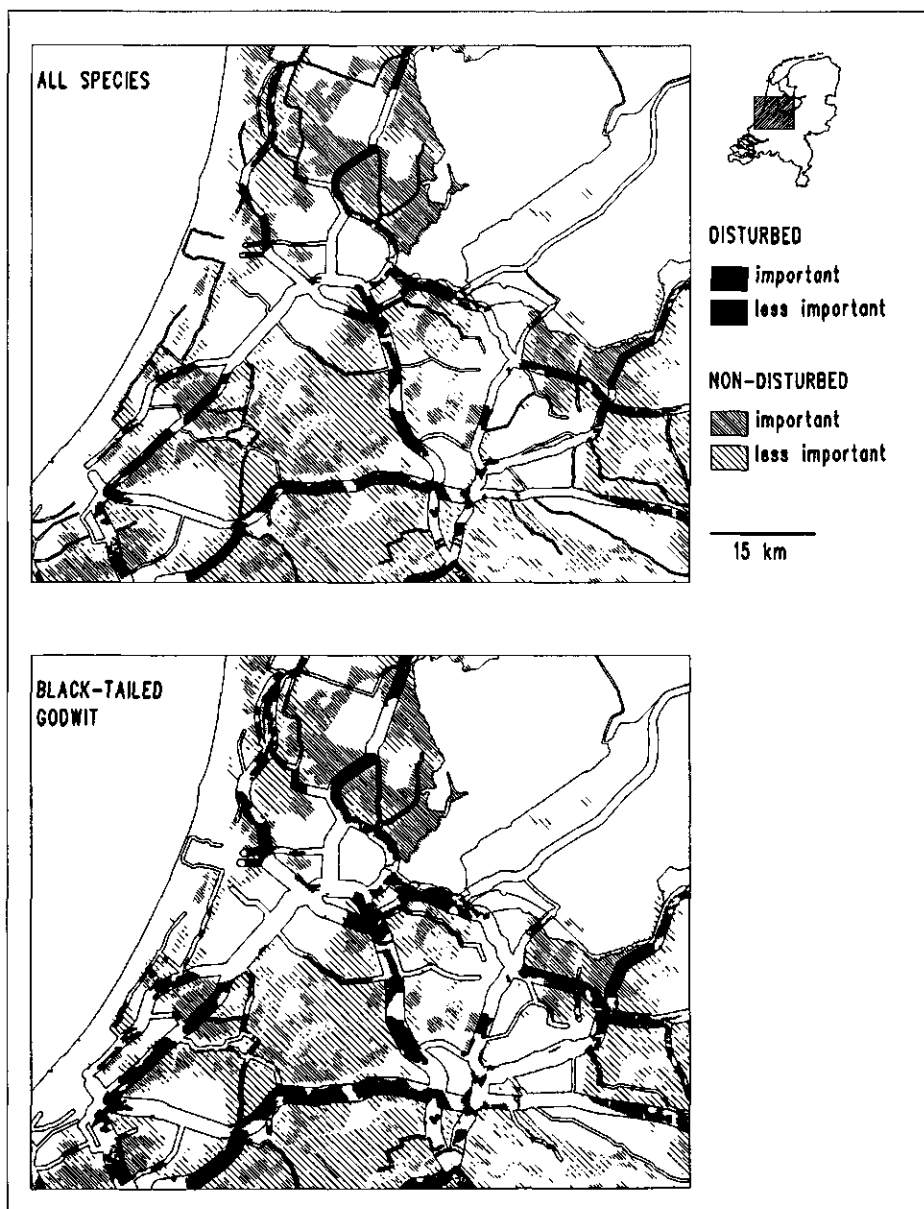
<sup>1</sup>area of pavement and verges excluded.

<sup>2</sup>total land area is ca. 33 800 km<sup>2</sup>

<sup>3</sup>lowest value is based on woodland birds, highest value on grassland birds.

All roads that had traffic densities of more than 10 000 cars per day were considered. Traffic data of 1986 were available in reports of the national and provincial authorities. Calculation of disturbance distances was carried out according to Reijnen *et al.* (in press) and the size of the disturbed area was estimated by using overlay-techniques in a GIS system (ARC/INFO). This was done for all species combined and for the black-tailed godwit and for the two habitat categories separately.

It appeared that in 1986 a substantial proportion of both 'important' and 'less important' areas for meadow birds was disturbed by car traffic (Table 5 and Fig. 5). If we take into account observed reductions of the density in the disturbed zone (39% for all species combined and 47% for black-tailed godwit; Reijnen *et al.* in press) and assume that densities in the 'important' habitat were five times higher than in the 'less important' habitat (based on Vogelwerkgroep Avifauna West-Nederland 1981), this points to a loss of population that amounts to 12 % for all species combined and to 16% for the black-tailed godwit (approximately 3200 breeding pairs). Because of the ongoing strong increase of traffic densities (Anonymous 1990), the effects only will become more important. Based on a scenario for 2010 (see Anonymous 1988), this could lead to an expected population loss of approximately 30%. So, in meadow birds, there is strong evidence that disturbance by car traffic has a significant impact on the size of breeding populations in the west of The Netherlands.



**Figure 5.** Disturbed area for grassland breeding birds by car traffic on roads with > 10 000 cars a day in the west of The Netherlands in 1986 (see also Table 5).

**Table 5.** Estimated size of disturbed area by car traffic on roads with >10 000 cars a day for grassland breeding birds in the west of The Netherlands in 1986 (see also Fig. 5).

Estimate	Disturbance of important area		Disturbance of less important area	
	Size in ha	% of total <sup>1</sup>	Size in ha	% of total <sup>2</sup>
All species combined	6800	11	30 200	21
Black-tailed godwit	12 000	19	44 700	32

<sup>1</sup>total size 140 700 ha, area of pavement and verges excluded

<sup>2</sup>total size 62 000 ha, area of pavement and verges excluded

### Implications for nature conservation

To understand the consequences of the effects of disturbance by car traffic for breeding bird populations, one should also consider other threats. Breeding birds in The Netherlands suffer from many other environmental influences, of which eutrophication of ground water and surface water, ammonium deposition from agricultural emissions, lowering of the water table, and habitat fragmentation are considered of greatest importance (e.g. Canters & De Snoo 1993; Bink *et al.* 1994; Vos & Zonneveld 1993) and this increases the risk of an important cumulation of effects. The first three factors cause a decline of the habitat quality (or even a loss of habitat), which may affect the size of local populations. If the population size becomes very small there will be an increased risk of extinction due to demographic chance processes (Goodman 1987; Shaffer 1987). Habitat fragmentation can reinforce this process. It increases the risk of extinction due to demographic chance processes and it may reduce the chance that dispersers rescue small local populations from extinction; eventually, this will affect whole network populations (e.g. Opdam *et al.* 1993; Verboom *et al.* 1993). Evidence for these effects have been shown in several studies (see Opdam 1991; Opdam *et al.* 1993; Opdam *et al.* in press). For meadow birds such cumulative effects might be important. They are heavily suffering from agricultural activities (Beintema 1991) and the distribution pattern in the east of The Netherlands becomes more and more fragmented.

A further exploration of which breeding bird species or groups of species are most threatened by car traffic and indications for an important cumulation of effects, therefore, should get much attention in nature conservation strategies.

## **ACKNOWLEDGEMENTS**

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## SUMMARY

This study investigates the poorly understood but potentially important effect of disturbance by car traffic on the density of breeding birds. It shows that adjacent to busy roads in The Netherlands 33 of the 45 investigated species in woodland and 7 of the 12 investigated species in agricultural grassland have depressed densities. This indicates that the effect is a common phenomenon in breeding birds. The size of the disturbed zone increases strongly with growing traffic densities. For a busy highway (50 000 cars per day) the disturbance distances vary from 75 to 930 m in open agricultural grassland and from 60 to 810 m in woodland, depending on bird species. If the summed density of all species is considered, the disturbed zone is larger in agricultural grassland than in woodland, 560 and 365 m respectively.

The reduction of the density over the disturbance distance varies greatly between species, but is never smaller than 30%. In both habitat types, several species even show a reduction of almost 100%. This means that the loss of population of species can become a very significant phenomenon. Because many species are affected, there is also an important reduction of the total density in the disturbed zone, in open agricultural grassland 39% and in woodland 35%.

Car traffic noise is probably the most critical factor in causing density reductions adjacent to roads. In woodland, the relationship between disturbance by car traffic and the reduction of density of breeding birds is much better explained by noise than by visual stimuli. This is related to the fact that in woodland visual stimuli in general only operate at a very short distance from the road. In open meadow landscape, however, visual stimuli reach much farther and might be more important than in woodland. Available studies do not point to significant effects of pollution at the population level of species. Possible mechanisms of the disturbance effects are interference with the vocal communication between birds (noise) and stress (noise and visual stimuli).

There is much evidence that the reduction of the density is related to a reduction of the habitat quality. However, density is not always a good indicator of habitat quality. This means that the size of zones adjacent to roads which have a lower quality due to car traffic, can easily be underestimated. For woodland birds it was shown that such underestimation can be substantial, since many species only had a depressed density in years with a relatively low overall density. By consequence, species that did not show an effect on the density, still might be affected by car traffic.

To understand the consequences of the effect of disturbance by car traffic on breeding bird populations the reduction of the habitat quality is probably the most important. It is generally assumed that the size and persistence of breeding populations

mainly depend on areas with a high quality. As a result, the largest effects can be expected when disturbance causes a major loss of such areas. Also a further degradation of habitats with a low quality can have some effect, because they may contribute significantly to the overall population size. The fact that there is a quantitatively important breeding dispersal flow of male willow warblers from highway-induced low-quality habitat to high-quality habitat nearby supports this assumption.

To favour the application of the results, methods are developed that can be used in spatial planning procedures related to main roads and in road management practice. Some practical points are discussed. An example on application shows that the effects are probably very important in The Netherlands, a country with a dense network of extremely crowded main roads. For 'meadow birds', which are of international importance, the population loss in the west of The Netherlands may amount to 16%. Because breeding birds suffer from many other environmental influences, cumulation of effects might be very important. This should get much more attention in nature conservation strategies.

# **SAMENVATTING**

## **WEGEN EN VERKEER ALS PROBLEEM VOOR BROEDVOGELS**

De opkomst van gemotoriseerde voertuigen heeft het transport over de weg ingrijpend veranderd. Het vervoer van goederen en personen nam een enorme vlucht, waardoor uitgebreide netwerken van zeer drukke verkeerswegen zijn ontstaan. In Nederland ontwikkelde het autosnelwegennet zich van 87 km in 1938 tot 2600 km in 1991. De verkeersintensiteit op deze wegen varieert momenteel van 10.000 tot meer dan 100.000 auto's per dag.

Deze ontwikkelingen hebben tot grote problemen voor het milieu en de natuur geleid. De aanleg van wegen vernietigt biotopen en leidt tot een toename van de versnippering van het landschap. Het intensieve gebruik door autoverkeer beïnvloedt de omgeving door verontreiniging en geluidsoverlast en maakt talloze slachtoffers onder de fauna.

Bij de gevolgen voor broedvogels hebben biotoopvernietiging en verkeersslachtoffers tot nu toe veel aandacht gekregen. Biotoopverlies is een belangrijk effect, omdat hierdoor het aantal broedparen afneemt. In een versnipperd landschap (als gevolg van wegaanleg, landbouwontwikkelingen e.d.) kan dit effect bovendien worden versterkt. Recent onderzoek laat zien dat de overlevingskans van kleine populaties afneemt naarmate de afstand tot andere populaties groter wordt. Sterfte door verkeer is een opvallend effect en daardoor uitgebreid onderzocht. Ondanks de grote aantallen slachtoffers zijn er echter geen duidelijke aanwijzingen dat hierdoor de omvang van broedvogelpopulaties wordt beïnvloed. Alleen voor een enkele soort, zoals de kerkuil, is er mogelijk een probleem.

Aan de andere kant laat onderzoek aan enkele vogelsoorten zien zijn dat de dichtheid tot op grote afstand van vooral drukke wegen aanzienlijk is verlaagd. Dit wijst erop dat een andere factor, namelijk verstoring door verkeer wel eens erg belangrijk zou kunnen zijn. Er is echter nog geen duidelijk beeld in hoeverre dit effect algemeen voorkomt bij broedvogels.

## **ONDERZOEKVRAGEN EN ALGEMENE OPZET**

Dit onderzoek richt zich op het nog weinig onderzochte effect van verstoring door verkeer op de dichtheid van broedvogels langs wegen. Inzicht in de betekenis en omvang van dit effect is van groot belang bij het maken van wegenplannen en het beheer en de inrichting van wegen en wegbermen. Belangrijke vragen hierbij zijn:

1. Bij hoeveel soorten komt het effect voor en hoe groot is de verstoringafstand en de afname van de dichtheid over deze afstand?
2. Welke factoren veroorzaken de verstoring?
3. In hoeverre is dichtheid een goed indicator om de afname van de kwaliteit van broedgebieden vast te stellen?

De ideale opzet voor het vaststellen van de effecten is metingen te verrichten in gebieden voor en na de aanleg van een weg en deze te vergelijken met metingen in gebieden waar geen veranderingen hebben plaats gevonden (controle). Een dergelijke longitudinale opzet is echter vanwege praktische redenen moeilijk uitvoerbaar. Daarom is het effect onderzocht door van broedvogelsoorten de dichtheid in gebieden met een verschillende mate van verstoring door verkeer met elkaar te vergelijken (transversale opzet). Andere factoren die de dichtheid kunnen beïnvloeden, zoals verschillen in de vegetatiestructuur, zijn daarbij constant gehouden. Het onderzoek is gericht op vogels van bossen en open weidegebied. Deze landschapstypen worden in Nederland het meest doorsneden door drukke wegen.

Zoals hiervoor al aangegeven, is gekozen voor een transversale correlatieve aanpak. Alle verkeersfactoren die verstoring tot gevolg kunnen hebben (geluid, visuele prikkels, luchtverontreiniging), nemen in intensiteit af met een toenemende afstand tot de weg. Nader inzicht in het belang van afzonderlijke factoren is derhalve alleen te verkrijgen door de invloed ervan te scheiden. Dit is op twee manieren gedaan: (1) door het selecteren van proefgebieden die verschillen in waarde voor één factor maar niet voor de andere(n) en (2) door na te gaan of er binnen de verstoringafstand verschillen zijn in reikwijdte van de invloed van factoren.

Een afname van de dichtheid van broedvogels langs wegen duidt op verslechterde leefomstandigheden. Dit is belangrijk, omdat de kwaliteit van broedgebieden in belangrijke mate de omvang en duurzaamheid van vogelpopulaties bepaalt. Aan de andere kant is bekend dat dichtheid niet altijd een goede maat is om verschillen in kwaliteit van broedgebieden weer te geven. Dit houdt verband met de voorkeur van vogels om zich te vestigen in goede gebieden. Als de populatieomvang van een soort klein is (bijvoorbeeld van de winterkoning na een strenge winter), blijven er weinig vogels over voor gebieden die minder geschikt zijn en zal de dichtheid hier relatief laag zijn. Naarmate de populatieomvang echter toeneemt zal een groter aantal vogels zich ook in minder geschikte gebieden vestigen. Het gevolg hiervan is dat het verschil in dichtheid tussen goede en minder goede gebieden kleiner wordt en eventueel zelfs kan verdwijnen. Dit betekent dat bij het gebruik van dichtheid als maat om de effecten van verstoring te meten, de afname van de geschiktheid van gebieden kan worden onderschat of zelfs niet wordt waargenomen. Het belang hiervan is onderzocht door de effecten op de dichtheid



in een aantal gebieden gedurende meer dan één jaar te meten. Er is nagegaan of verschillen in effect tussen jaren ook daadwerkelijk samenhangen met veranderingen in de populatiegrootte. Voor een nadere bewijisvoering, is van een soort, de fitis, de populatie in een gebied bij een drukke snelweg gedurende een aantal jaren nauwkeurig bestudeerd. Hiermee is vast te stellen of de geschiktheid dichtbij de weg inderdaad geringer is en welke mechanismen daarbij een rol spelen.

## EFFECT OP DICHTHEID

Het onderzoek is uitgevoerd langs auto(snel)wegen met een verkeersintensiteit variërend van ca. 5000 tot 60.000 motorvoertuigen per dag. Langs deze wegen blijkt een verlaagde dichtheid van broedvogels een algemeen verschijnsel te zijn. Bij 33 van de 45 onderzochte soorten in bos en bij 7 van de 12 onderzochte soorten in open weidegebied is een effect vastgesteld. Vrijwel alle soortgroepen zijn hierbij vertegenwoordigd. In bos o.a. roofvogels, duiven, spechten, lijsters, mezen, zangers en kraaiachtigen en in open weidegebied eenden, steltlopers en zangvogels. Daarnaast is er ook een effect op de totale dichtheid (van alle soorten).

Om de verstoring te meten is de geluidsbelasting door verkeer als maat genomen. Het voordeel hiervan is, dat met allerlei kenmerken van weg, verkeer en omgeving die de intensiteit van verstoring kunnen bepalen, wordt rekening gehouden. De meest belangrijke zijn aantal voertuigen, snelheid, type voertuigen, type wegdek, afstand tot de weg en opgaande begroeiing langs de weg. Voor het verkrijgen van verstoringafstanden, worden grenswaarden voor het geluidsniveau (waarden waaronder geen effect op de dichtheid meer is vast te stellen) omgerekend in afstand tot de weg. Vastgestelde grenswaarden voor de geluidsbelasting verschillen sterk tussen soorten, ook wanneer rekening wordt gehouden met de betrouwbaarheidsintervallen. Hiervan afgeleide verstoringafstanden worden vooral bepaald door de verkeersintensiteit (aantal motorvoertuigen per dag) en de verkeerssnelheid en in bosgebied ook door de hoeveelheid bos langs de weg. Bij een aantal mtv van 10.000 per dag en een snelheid van 120 km per uur heeft al ruim 40% van de soorten in zowel open weidegebied als boslandschap (aandeel bos 75%) een verstoringafstand groter dan 100 m en bij 50.000 mtv per dag 70%. De hoogste waarden in bos zijn 305 m respectievelijk 810 m (koekoek) en in open weidegebied 365 m respectievelijk 930 m (grutto). Voor alle soorten gezamenlijk is de verstoringafstand bij 10.000 mtv per dag 120 m (bos) en 190 m (open weidegebied) en bij 50.000 mtv per dag 365 m (bos) en 560 m (open weidegebied).

De verlaging van de dichtheid in de verstoorde zone is voor de gevoelige soorten

altijd meer dan 30% en zelfs waarden van bijna 100% komen regelmatig voor. Voor de totale dichtheid van alle soorten gezamenlijk is de verlaging in de verstoringzone in open weidegebied 39% en in bos 35%. Dit betekent dat vooral bij grote verstoringafstanden het verlies aan broedterritoria zeer aanzienlijk wordt.

## MOGELIJKE OORZAKELIJKE FACTOREN

Er zijn duidelijke aanwijzingen dat het effect op de dichtheid vooral wordt veroorzaakt door verstoring. Het detailonderzoek aan de fitis ondersteunt de veronderstelling dat verkeerssterfte geen invloed heeft op de dichtheid van broedvogels langs wegen. Bij een verkeersintensiteit van 50.000 mvt per dag is de sterfte in gebieden vlakbij de weg niet groter dan in gebieden verder van de weg vandaan. Verder is het ook niet aannemelijk dat de aanwezigheid van de weg zelf de dichtheid kan verlagen. Voor proeflocaties met een geringe verstoring door verkeer (geluidsbelasting) is een effect op de dichtheid niet meer aantoonbaar.

In bos is de geluidsbelasting waarschijnlijk de belangrijkste versturende factor. Een eerste aanwijzing hiervoor is dat op grotere afstand van de weg alleen van geluid nog een meetbare invloed is vast te stellen. Dit wordt ondersteund door het gegeven dat het verband tussen verstoring en dichtheid beter kan worden verklaard door geluid dan door visuele prikkels, een factor die alleen op korte afstand van de weg opereert. Bovendien zijn er aanwijzingen dat visuele prikkels ook op korte afstand van de weg maar een beperkt effect hebben. Wanneer er geen verschillen zijn in geluidsbelasting, neemt het effect niet toe bij een groter wordende visuele belasting. Andersom is er wel een toename van het effect als de visuele belasting gelijk blijft en de geluidsbelasting groter wordt. Een beperkt effect van verontreiniging door verkeer op vogels blijkt uit resultaten van door anderen verricht onderzoek. Een verhoging van de sterfte of een verlaging van de reproductie kon niet worden aangetoond.

In open weidegebieden is het moeilijker oorzakelijke factoren te analyseren. Met name geluid en visuele prikkels zijn hier beide tot op grote afstand van de weg waar te nemen. Bovendien zijn vogels van open gebieden mogelijk gevoeliger voor visuele prikkels dan vogels van bossen. Uit ander onderzoek blijkt echter dat bij afwezigheid van visuele prikkels (lage heg langs de weg), patrijzen toch sterk verlaagde dichtheden vertoonden tot op grote afstand van de weg. Dit wijst erop dat in open gebieden geluid in elk geval geluid een belangrijke factor is.

Er is weinig bekend over hoe geluid vogels kan beïnvloeden. Verstoring van de vocale communicatie tussen individuen zou een rol kunnen spelen. Het detailonderzoek aan de fitis laat zien dat veel mannetjes aan de weg ongepaard blijven. Dit is mogelijk

te verklaren doordat ze minder aantrekkelijk zijn voor vrouwtjes omdat de zang wordt verstoord. Daarnaast geeft onderzoek van anderen een aanwijzing dat stress door geluid een rol kan spelen.

## **EFFECT OP DE KWALITEIT VAN BROEDGEBIEDEN IN RELATIE TOT DE DICHTHEID**

Meerjarig onderzoek naar het effect op de dichtheid in een aantal proefgebieden in bossen toont aan dat de effecten op de dichtheid sterk kunnen variëren. In 1988 was het aantal soorten met een lagere dichtheid langs de weg veel geringer (4) dan in 1984 en 1986 (10 respectievelijk 14). Een overeenkomstig patroon is aanwezig voor de effectgrootte (verstoringsafstand x dichtheidsafname) van afzonderlijke soorten en voor alle soorten gezamenlijk. De verschillen blijken negatief gecorreleerd met de algehele populatieomvang van de soorten: in 1984 en 1986 was deze voor de meeste soorten veel lager dan in 1988.

Deze resultaten zijn in overeenstemming met de hypothese dat gebieden vlak langs de weg een verlaagde kwaliteit hebben. Als het totale aantal vogels groter wordt neemt het aantal vestigingen in deze gebieden sterker toe dan in niet verstoorde gebieden. Het gevolg hiervan is wel dat het effect op de kwaliteit van broedgebieden in veel gevallen zal zijn onderschat.

Het detailonderzoek aan de fitis ondersteunt de hiervoor gegeven interpretatie. Dit is uitgevoerd in een ongeveer 160 ha groot griendencolplex langs de A2 bij Vianen. Gedurende vier jaar zijn hier van 160-180 gekleurde mannetjes gegevens verzameld over leeftijdsopbouw, paar- en broedsucces en verplaatsingen tussen jaren. Het blijkt dat mannetjes in de eerste 200-300 m vanaf de weg (wegzone) ruim 30% minder jongen produceren dan mannetjes in gebieden verder van de weg vandaan (controle). Dit wijst duidelijk op een verlaagde kwaliteit. Bovendien is de lage reproductie in de wegzone onvoldoende om de waargenomen dichtheid in stand te houden. Er is dus extra aanvoer van elders (uit betere gebieden) nodig.

Voor het verschil in reproductief succes tussen weg- en controlegebied zijn vooral de eerstejaars mannetjes verantwoordelijk. Hun broedprestatie in het weggebied is veel lager dan in het controlegebied doordat een groot deel ongepaard blijft. Bovendien is het aandeel eerstejaars vogels in het weggebied veel groter dan in het controlegebied. Dit wordt veroorzaakt doordat de mannetjes die ongepaard zijn gebleven het volgende jaar verhuizen naar ongestoorde gebieden verder van de weg vandaan. Nieuwe éénjarige mannetjes waarvan een deel is geboren in naburige goede gebieden nemen hun plaats dan weer in. Tussen de eerstejaars mannetjes in het controlegebied en de ouderejaars

mannetjes in zowel het controle- als het weggebied bestaan geen verschillen in reproductief succes.

Tijdens de onderzoeksperiode bleef de totale fitispopulatie in het onderzoekgebied vrij constant. De waargenomen processen maken het echter zeer aannemelijk dat het aantal mannetjes in het weggebied veel meer worden beïnvloed door algehele populatieschommelingen dan het aantal mannetjes in het aanliggende controlegebied. Het feit dat het wegtrekken van eerstejaars mannetjes uit het weggebied daarbij een belangrijke rol speelt is een nieuw gezichtspunt.

## **GEVOLGEN VOOR BROEDVOGELPOPULATIES**

Het is te verwachten dat een verlaging van de kwaliteit van broedgebieden langs de weg een negatief effect zal hebben op de omvang en duurzaamheid van populaties. Wanneer een lokale populatie geheel binnen de verstoorde zone terecht komt, is de kans groot dat deze zal verdwijnen. Bij een gedeeltelijke verstoring zal het effect over het algemeen groter zijn naarmate de kwaliteit van het verstoorde deel hoger was. Als gebieden met een hoge kwaliteit worden verstoord kunnen ze niet meer functioneren als een bron van waaruit gebieden met een lagere kwaliteit worden bevolkt. De aantallen in de gebieden met een lage kwaliteit zullen hierdoor sterk afnemen. Waarschijnlijk heeft dit ook een negatief effect op de aantallen in de gebieden met een hoge kwaliteit zelf.

## **TOEPASSING**

Dit onderzoek laat zien dat het belangrijk is om aandacht te besteden aan de effecten van verstoring door verkeer op broedvogels. De verkregen kennis is hiervoor goed bruikbaar. Hoewel deze alleen betrekking heeft op vogels van bossen en open weidegebieden, lijkt toepassing in andere biotopen mogelijk. De onderzochte soorten zijn representatief voor de hele groep van Nederlandse broedvogels en een relatief groot aantal komt ook in andere biotopen voor.

Voor het vaststellen van de grootte van het effect kan men in het algemeen het beste uitgaan van de relatie tussen geluid en de dichtheid van alle soorten gezamenlijk. Niet voor alle soorten die een effect vertonen is een dergelijk verband beschikbaar en bovendien kan van soorten die geen effect vertonen het leefgebied wel zijn verstoord. Bovendien maakt deze benadering het mogelijk om de resultaten ook in andere landschapstypen toe te passen. Om een indruk te krijgen van de maximale breedte van de verstoorde zone kan het verband tussen geluid en dichtheid voor de meest gevoelige

soort worden gebruikt.

Een vermindering van het effect is op verschillende manieren te bereiken. Wanneer de geluidsbelasting kan worden verlaagd, is het verwachten dat ook het effect zal afnemen. Een andere mogelijkheid is de verlaagde dichtheid langs de weg te compenseren door nieuwe biotopen te ontwikkelen of, indien mogelijk, van bestaande biotopen de kwaliteit te verbeteren. Dit zal het meeste resultaat opleveren indien dit geheel of grotendeels buiten de verstoorde zone plaats vindt.

Bij nieuw te plannen wegen is het vermijden van effecten de beste strategie. In het algemeen zal voor drukke wegen een afstand van 1000 m tussen de weg en broedgebieden van vogels toereikend zijn. Maatregelen om de effecten te verminderen moeten alleen worden overwogen als een verstoring niet is te vermijden. Voor het oplossen van problemen bij bestaande wegen is men hier echter op aangewezen. Een substantiële verlaging van de geluidsbelasting is te bereiken met geluidsbeperkende voorzieningen. Dit geeft echter wel een aantal praktische problemen. Voor een efficiënte werking moeten deze voorzieningen vrij hoog zijn en over een grote lengte worden aangebracht. Met name in open gebieden kan dit vanwege landschappelijke overwegingen ongewenst zijn. Bovendien vermijden vogels van open gebied opgaande elementen in het landschap tot op een afstand van vaak honderden meters. Een ander nadeel is dat het aanbrengen van geluidswerende voorzieningen de barrièrewerking van wegen voor andere organismen zal vergroten. Compensatie, door het ontwikkelen van nieuwe vergelijkbare biotopen op grotere afstand tot de weg, is daarom in veel gevallen waarschijnlijk een betere strategie. In een druk bevolkt land als Nederland zal realisering hiervan echter niet altijd eenvoudig zijn. Daarom moet ook worden nagegaan in welke mate een verbetering van de kwaliteit van biotopen een bijdrage kan leveren. Meer aandacht voor natuurwaarden bij het beheer van wegbermen heeft naar verwachting een gering positief effect voor broedvogels. Hiervoor is de verstoring door verkeer vlakbij de weg te groot. Bovendien zijn er aanwijzingen dat dit leidt tot een toename van het aantal verkeersslachtoffers.

Om de toepassing van de resultaten te bevorderen is een handleiding voor praktisch gebruik samengesteld, die elders is gepubliceerd (Reijnen, Veenbaas & Foppen 1992). In diverse diverse milieueffectrapportages voor nieuw aan te leggen wegen is hier al ervaring mee opgedaan. Aandacht voor vermindering van de bestaande effecten is echter ook zeer belangrijk. Een eerste verkenning laat zien dat het hoofdwegenet in Nederland momenteel 8-15% van de landoppervlakte minder geschikt maakt voor broedvogels. Uitgaande van een verkeersscenario voor het jaar 2010 kan dit toenemen tot 16-23%. Wat dit betekent voor weidevogels is uitgewerkt voor het westelijk deel van Nederland. Verstoring door wegen veroorzaakt hier een verlaging van de gezamenlijke dichtheid van 12% en voor de grutto van 16%. Voor de grutto houdt dit een verlies in van ongeveer 3200 broedparen.

Bij de beoordeling van de effecten is het van belang ook andere bedreigingen dan verstoring door verkeer in beschouwing te nemen. Door cumulatie van effecten kunnen de gevolgen voor broedvogelpopulaties belangrijk toenemen. Hieraan moet in het verdere onderzoek nadere aandacht besteed worden.

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### **On referring to parts of this thesis**

Most parts of this thesis are accepted by or published in scientific journals. It is kindly requested to refer to the papers in these journals, rather than to parts of this thesis when possible.

## NAWOORD

De eerste jaren van dit onderzoek heb ik uitgevoerd op de afdeling Adviezen en Algemeen Onderzoek van het toenmalige Rijksinstituut voor Natuurbeheer (RIN). Daan Kruizinga ben ik erkentelijk voor de ruimte die ik daarbij heb gekregen. Het onderzoek is daarna voortgezet op de afdeling Landschapsecologie (RIN en IBN-DLO), waarbij ik de werksfeer als bijzonder stimulerend heb ervaren.

Aan het onderzoek hebben vele personen een wezenlijke bijdrage geleverd. Johan Thissen heeft mij geholpen bij de opzet van het onderzoek. Henk Meeuwsen, Dick Jonkers, Jaap Mekel, Carl Derks, Ton Eggenhuizen, Fetze Andringa, Max Klasberg en Frieda van Noordwijk namen een groot deel van het veldwerk voor hun rekening en voerden de eerste bewerking van de gegevens uit. Dick Bekker en Bart Veenstra droegen waardevolle ideeën aan in het kader van hun afstudeeronderwerp in de biologiestudie. Bouke den Ouden en Henk Meeuwsen ben ik erkentelijk voor het schrijven van gebruikersvriendelijke computerprogramma's, waarmee de grote hoeveelheden data efficiënt konden worden verwerkt. Zonder Willibrord Huisman had ik nooit de geluidsbelasting door verkeer in bosgebieden kunnen bepalen. Samen met René Beekwilder paste hij de bestaande rekenmethode voor het bepalen van de geluidsbelasting voor dit doel aan. Daarnaast wist hij op mijn vragen over de voortplanting van geluid altijd een praktisch toepasbaar antwoord te geven. Cajo ter Braak en Johan Thissen hebben veel tijd gestoken in het ontwikkelen en programmeren van de regressiemethode voor de kwantitatieve analyse van de gegevens. Vanuit hun positie als opdrachtgever hebben Geesje Veenbaas en Theo Goeman het onderzoek begeleid en ik ben hun erkentelijk voor het feit dat ze steeds oog hadden voor de complexiteit van dit soort effectenonderzoek.

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De uitvoering van het onderzoek is ook mede mogelijk gemaakt door de toestemming van vele natuurbeherende instanties, boscigenaren en boeren om hun terreinen te mogen betreden. In het bijzonder wil ik noemen Piet en Ina Bogerd die vele jaren gastvrijheid verleenden in het studiegebied in de polder Bolgerijen-Autena van het Zuidhollands Landschap. Voor de hulp bij het vervaardigen van een aantal figuren ben ik Henk Meeuwsen en Ruut Wegman erkentelijk.

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## CURRICULUM VITAE

Rien Reijnen werd geboren op 2 januari 1946 te Nijmegen. In 1962 slaagde hij voor het MULO diploma en werkte daarna tot 1968 als analist aan de Katholieke Universiteit van Nijmegen. Tijdens deze periode volgde hij de opleiding voor chemisch analist 1e deel. Na het behalen van het staatsexamen 'artikel 3' in 1968, studeerde hij biologie aan de KU te Nijmegen. Het MO en aansluitend kandidaatsexamen werd afgelegd in 1972. Het doctoraal werd behaald in 1974 met geobotanie als hoofdvak (prof. dr. V. Westhoff en dr. E. van der Maarel) en dierecologie (dr. H. Oomen) en genetica (dr. H. Kroon) als bijvakken. Voor het hoofdvak en het bijvak Dierecologie voerde hij met zes medestudenten een ecologische kartering uit van de groene ruimte tussen Arnhem en Nijmegen en werd een rapport geschreven over de effecten van een geplande waalbochtverlegging op de natuurwaarden in de Ooypolder bij Nijmegen. Tevens werd met twee andere studenten een vegetatiekartering uitgevoerd van de Oude Rijnstrangen bij Zevenaar. Voor het bijvak Dierecologie en in dienstverband van de Provincie Gelderland werkte hij ook mee aan een ecologische inventarisatie en evaluatie van het streekplan Midden-Gelderland. Na afloop van de studie werd dit werk gedurende anderhalf jaar voortgezet voor andere streekplannen. In 1977 trad hij in dienst van het Rijksinstituut voor Natuurbeheer (RIN) te Leersum. Aanvankelijk was hij betrokken bij een groot aantal kortlopende projecten verspreid over geheel Nederland, die waren gericht op het karteren en evalueren van natuurwaarden ten behoeve van ruimtelijke planning en natuurbeheer. Een kartering en evaluatie van de gevolgen van grondwaterwinning voor de vegetatie in het gebied ten zuiden van Breda, vormde de aanzet tot een nadere studie samen met anderen met als resultaat een voorspellingsmodel voor de effecten van grondwaterwinning op de vegetatie. Hij werkte tevens mee aan het vervaardigen van een boek over Vogelinventarisatie. De betrokkenheid bij een aantal onderzoeken naar de invloed van verstoring op vogels door militaire oefeningen, recreatie en verkeer, kreeg een vervolg in een uitgebreide studie naar de effecten van verstoring door verkeer op broedvogelpopulaties in opdracht van de Dienst Weg- en Waterbouwkunde van Rijkswaterstaat. Dit proefschrift is daaruit voortgekomen. Momenteel is hij werkzaam op de afdeling Landschapsecologie van het DLO-Instituut voor Bos en Natuuronderzoek te Wageningen (IBN-DLO, ontstaan door een fusie van RIN en 'De Dorschkamp') en verricht en begeleidt onderzoek naar de effecten van versnippering op vogels en planten.

**Stellingen behorende bij het proefschrift 'Disturbance by car traffic as a threat to breeding birds in The Netherlands' door Rien Reijnen.**

1. In studies naar het effect van versturende invloeden van de mens op broedvogels waarbij de dichtheid van territoria als maatstaf wordt genomen, is de kans groot dat de effecten aanzienlijk worden onderschat.

*(dit proefschrift)*

2. Biotopen langs drukke wegen fungeren voor de fitis en waarschijnlijk voor veel andere vogelsoorten als een 'ecologische val'.

*(dit proefschrift)*

3. Ecologisch bermbeheer en natuurontwikkeling in de directe nabijheid van snelwegen moeten worden beschouwd als maatregelen die verloren gegane natuurwaarden slechts gedeeltelijk kunnen vervangen.

*(dit proefschrift)*

4. Omdat bij de verstoring van broedvogelpopulaties langs wegen de geluidsbelasting een belangrijke rol speelt *(dit proefschrift)*, is langs vooral drukke spoorwegen ook een effect te verwachten.

5. Door vogelbeschermingsinstanties wordt naar verhouding te veel aandacht besteed aan het leed van aangereden vogels in plaats van aan de op populatieniveau veel belangrijker effecten van verstoring door verkeer.

*(Van den Tempel, R. 1992. Vogelslachtoffers in het wegverkeer. Vogelbescherming Nederland, Zeist)*

6. De geringe kennis van het effect van verstoring door recreatie op de fauna en de beperkte middelen voor verder onderzoek staan niet in verhouding tot de huidige maatschappelijke drang om bos- en natuurgebieden geheel open te stellen voor recreatief medegebruik.

7. Het is te verwachten dat we in de toekomst zullen moeten leren leven met veel geringere aantallen van een aantal in Afrika overwinterende broedvogelsoorten.

*(Beintema, A.J. & Diemont, W.H. 1994. Wetlands and migratory waterbirds in West Africa. IBN Research Report 94/5, IBN-DLO, Wageningen)*

8. Het ontwikkelen van praktisch toepasbare (ruimtelijke) dynamische populatiemodellen is van groot belang om aan het begrip duurzame natuur meer inhoud te kunnen geven.

9. Een te grote marktgerichtheid van onderzoeksinstellingen en universiteiten kan de omvang van het fundamenteel ecologisch onderzoek in Nederland op een onaanvaardbaar laag niveau brengen.

10. Bij het toepassen van onderzoeksresultaten ten behoeve van beleid en beheer ontkomt een onderzoeker er niet aan om regelmatig 'spitsroeden te moeten lopen'.

11. Monitoring van flora en fauna door vrijwilligers is onmisbaar voor een verantwoord natuurbeleid en de coordinatie hiervan dient derhalve structureel te worden ondersteund door rijks- en provinciale overheden.

12. Bij het opnemen van vluchtelingen in de westerse landen moeten de problemen van de vluchtelingen zelf de meeste aandacht krijgen.