Predicting the effects of motorway traffic on breeding bird populations

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The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to the proximity of main roads

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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 analysed 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 per day to 70–2800 m for a road with 60 000 cars per day (120 km h^{-1} 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.

Key-words: noise load, visibility of cars, pollution, road mortality, road planning and management.

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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; Räty 1979; Ferris 1979; van der Zande, ter Keurs & van der Weijden 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)

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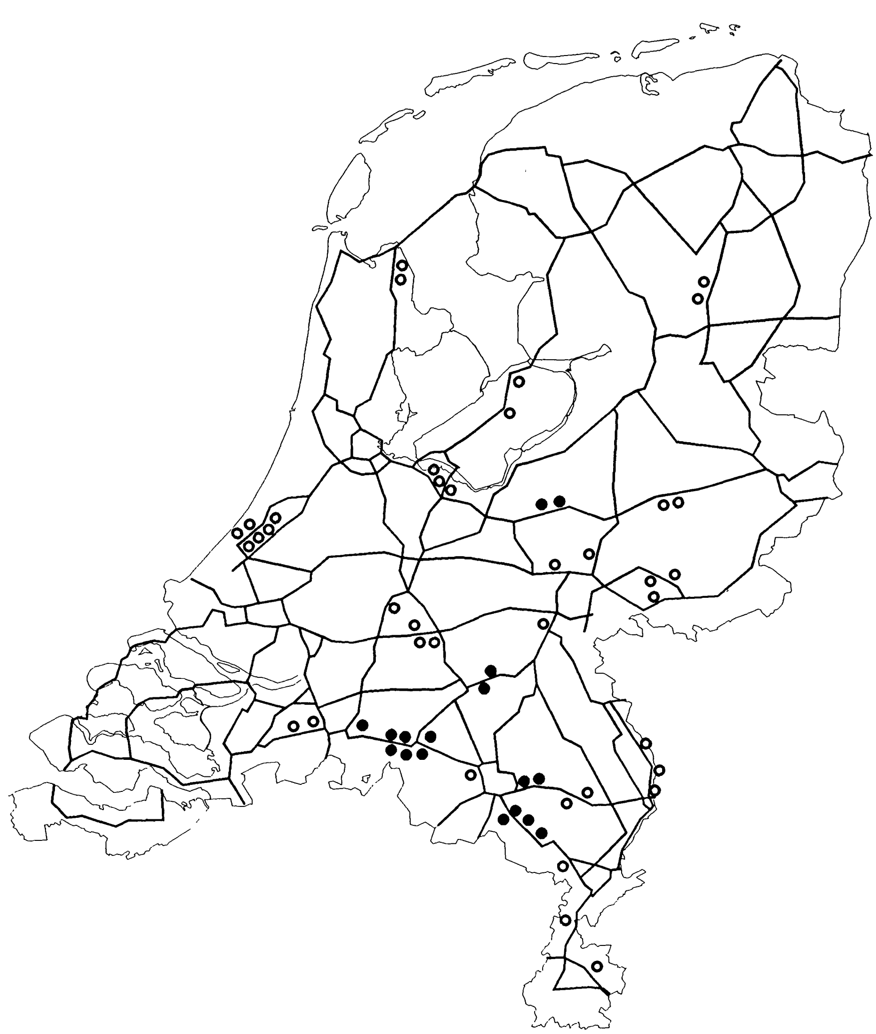

Fig. 1. Main roads in The Netherlands (bold lines) and location of paired plots in deciduous woodland (black dots) and coniferous woodland (open dots).

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

How car traffic causes densities to be reduced is 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's size (e.g. van der Zande *et al.* 1980; Leedy & Adams 1982; Ellenberg, Müller & Stottele 1981). This implies that possible causes are probably 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 was to determine which woodland species showed 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 per day and in areas with coniferous woodland 29 000–69 000 (mean 45 319) cars per 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

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 ($n = 38$)			Coniferous woodland ($n = 17$)		
	Road	Control	Sign.	Road	Control	Sign.
Cover of vegetation layers (%)						
<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	**			
Tree characteristics						
Circumference (cm)	87	86	NS	63	63	NS
Distance between (m)	3·1	2·8	NS	18·8	20·4	NS
Height (m)	16·4	17·0	NS	12·5	12·6	NS
Size and edge						
Size (ha)	4·04	4·24	NS	7·20	8·20	NS
Borderline with open area (%)	53	53	NS	55	46	NS

NS = $P > 0·10$; ** $P < 0·01$.

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* sp.) 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 (mostly *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 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 the percentage of registrations) was included in the calculation of density.

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

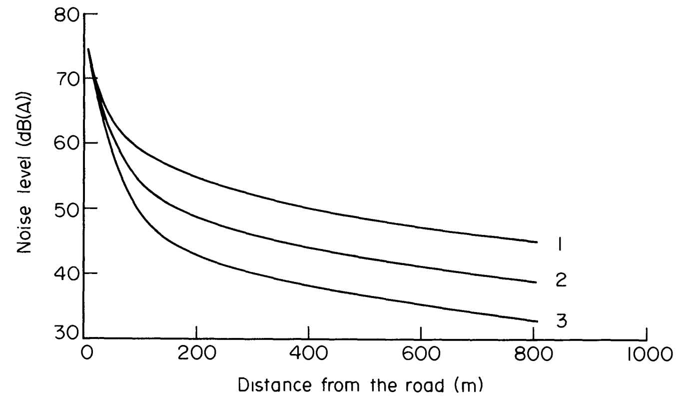

Fig. 2. Estimation of the noise load of car traffic along a highway with 50 000 cars per day and a speed of cars of 120 km h^{-1} based on Moerkerken & Middendorp (1981) and Huisman (1990) (see Methods for further explanation). 1 = open field; 2 = proportion of woodland along the road 0·5; 3 = proportion of woodland along the road 1·0.

were investigated, but the calculated values were all strongly correlated with the 1 m data, $r = >0{\cdot}90$).

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 multiplicated 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 per day), the visual experience of traffic remains constant.

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 5 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.

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

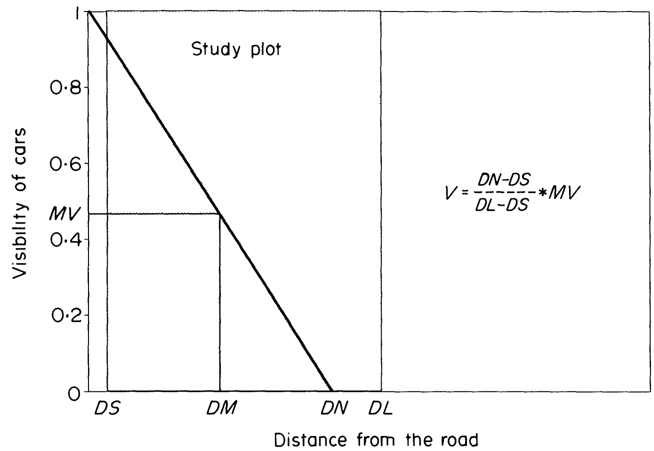

Fig. 3. Estimation of a relative value for the visibility of cars (V) in woodland (see also methods). DS = mean smallest distance of plot to the road; DN = mean largest distance of plot to the road; DL = mean distance from the road where traffic cannot be seen any more; DM = mean distance from the road 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.

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.

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.

ANALYSIS

In accordance with the study design (paired plots), the data were analysed 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 ($r = 0{\cdot}95$), 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 high ($r = 0{\cdot}63$), 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, ter Braak & van Tongeren 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 relationship 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 log linear Poisson regression with

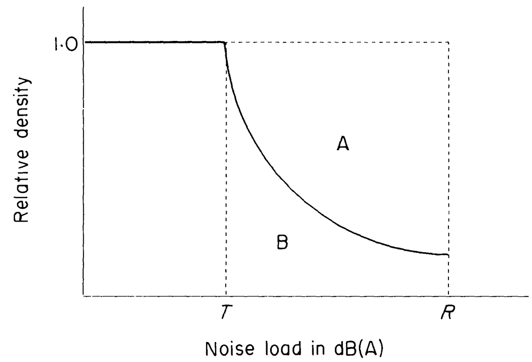

Fig. 4. Estimation of the decrease factor of the density based on loglinear Poisson regression using a threshold model (see methods). T = threshold value in dB (A), R = noise load in dB (A) in the verge of the road. The decrease factor = area of A/(area of A + B).

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 by product 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 independence 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.

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 $P < 0{\cdot}05$, a significance level of $P < 0{\cdot}10$ was 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.

Results

DENSITY IN DECIDUOUS WOODLAND

Of the 50 species present in the 38 paired plots, 41 (see Table 3) were sufficiently numerous for analysis. By using the Wilcoxon signed-ranks test, the density of 12 of the 41 species was reduced close to the road (at $P < 0{\cdot}10$, six species at $P < 0{\cdot}05$, 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 $P < 0{\cdot}10$, one species at $p < 0{\cdot}05$, Table 3). Despite the negative effect on several species, the density of all species combined was not significantly reduced close to the road (Table 3).

With regression the model with only noise load resulted in a significant reduction of the density for seven of the 12 species (at $P < 0{\cdot}10$, five species at $P < 0{\cdot}05$, Table 4) which showed an effect with the paired test and also for four additional species (at

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	n	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 = $P > 0{\cdot}10$; *** $P < 0{\cdot}001$.

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[1]

Species	NP	NT	R	C	Sign.
Anas platyrhynchos	10	16	0·10	0·05	NS
Buteo buteo ()	18	64	0·16	0·21	NS
Phasanius colchicus	13	60	0·13	0·22	*
Cuculus canorus	13	35	0·04	0·16	*
Scolopax rusticola	11	42	0·11	0·09	NS
Columba oenas ()	14	37	0·08	0·12	NS
Columba palumbus ()	30	186	0·59	0·54	NS
Picus viridus	7	27	0·05	0·12	NS
Dendrocopus minor	10	11	0·02	0·05	*
Dendrocopus major ()	28	85	0·25	0·25	NS[1]
Anthus trivialis	8	33	0·09	0·08	NS
Troglodytus troglodytus ()	34	289	0·91	0·96	NS
Prunella modularis ()	16	41	0·16	0·14	NS
Erithacus rubecula ()	34	357	1·09	1·00	NS
Phoenicurus phoenicurus	10	17	0·05	0·06	NS
Turdus merula ()	38	350	1·15	1·04	NS
Turdus philomelos ()	24	112	0·29	0·32	NS
Acrocephalus palustris	5	11	0·04	0·15	†
Hippolais icterina	7	16	0·11	0·15	*
Sylvia borin ()	28	175	0·70	0·82	NS
Sylvia atricapilla ()	35	172	0·56	0·62	NS
Phylloscopus sibilatrix	10	22	0·04	0·10	NS
Phylloscopus collybita ()	35	222	0·87	0·90	NS
Phylloscopus trochilus ()	26	264	0·70	0·98	**
Regulus regulus	7	23	0·05	0·07	†
Muscicapa striata ()	26	85	0·27	0·24	NS
Ficedula hypoleuca ()	13	27	0·09	0·06	NS
Aegithalos caudata ()	25	39	0·17	0·13	NS
Parus montanus	18	31	0·09	0·19	NS
Parus palustris ()	23	65	0·17	0·20	NS
Parus caeruleus ()	33	252	0·79	0·75	NS
Parus major ()	37	504	1·63	1·45	NS
Sitta europaea ()	18	65	0·22	0·17	NS
Certhia brachydactyla ()	30	142	0·44	0·44	NS[1]
Oriolus oriolus	10	33	0·04	0·20	†
Garrulus glandarius ()	29	146	0·50	0·40	NS
Pica pica ()	17	66	0·20	0·23	NS[1]
Corvus corone ()	29	185	0·83	0·71	NS
Sturnus vulgaris ()	20	121	0·41	0·45	NS
Coccothraustes coccothraustes	10	18	0·03	0·06	†
Fringilla coelebs ()	32	238	0·72	0·85	NS
All species combined ()	38	4493	14·76	15·53	NS

[1] Significantly 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* $P < 0{\cdot}01$ ($N = 0{\cdot}21$, $F = 0{\cdot}41$), *Certhia brachydactyla* $P < 0{\cdot}10$ ($N = 0{\cdot}50$, $F = 0{\cdot}66$), *Pica pica* $P < 0{\cdot}10$ ($N = 0{\cdot}33$, $F = 0{\cdot}56$).

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 = $P > 0{\cdot}10$; † $P < 0{\cdot}10$; * $P < 0{\cdot}05$; ** $P < 0{\cdot}01$.

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.
Buteo buteo	N	1/45	2·88	≤23 (?−50)	−0·050	*
Phasanius colchicus	N	2/28	5·15	53 (45−58)	−0·253	*
	V	1/29	2·92	0 (?−7)	−0·009	*
Scolopax rusticola	N	2/28	2·53	56 (53−62)	−2·191	†
Cuculus canorus	N	2/31	8·28	49 (40−52)	−1·143	**
	V	1/32	18·60	0 (?−24)	−0·064	***
Dendrocopus minor	N	2/23	2·84	50 (43−56)	−3·207	†
	V	2/23	3·81	46 (33−59)	−1·191	*
Phylloscopus sibilatrix	N	1/24	5·41	≤26 (?−62)	−0·052	*
Phylloscopus trochilus	N	2/61	4·30	39 (?−60)	−0·034	*
	V	2/61	4·30	62 (44−81)	−0·077	*
Oriolus oriolus	N	1/27	14·0	≤23 (?−39)	−0·121	***
	V	1/27	13·0	0 (?−57)	−0·038	***
Pica pica	N	2/43	2·95	46 (40−56)	−0·086	†
Coccothraustes coccothraustes	N	1/30	3·30	≤26 (?−56)	−0·067	*
Fringilla coelebs	N	1/66	2·51	≤23 (?−60)	−0·013	†
All species combined	N	1/81	1·98	≤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 = $P > 0{\cdot}10$, † $P < 0{\cdot}10$, * $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$.

$P < 0{\cdot}10$, two species at $P < 0{\cdot}05$, Table 4). Moreover, there was an effect on the density of all species combined (at $P < 0{\cdot}10$, 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 $P < 0{\cdot}05$, 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.

Effect distances (threshold value in m) were

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

		Decrease factor up to 250 m	
Species	Decrease factor up to threshold	10 000 cars per day	60 000 cars per day
Buteo buteo	0·62	0·76	0·81
Phasanius colchicus	0·77	0·14	0·28
Scolopax rusticola	0·97	0·14	0·27
Cuculus canorus	0·96	0·25	0·52
Dendrocopus minor	0·98	0·24	0·43
Phylloscopus sibilatrix	0·61	0·73	0·79
Phylloscopus trochilus	0·38	0·28	0·45
Oriolus oriolus	0·82	0·95	0·98
Pica pica	0·58	0·20	0·49
Coccothraustes coccothraustes	0·68	0·81	0·86
Fringilla coelebs	0·25	0·32	0·36
All species combined	0·09	0·11	0·13

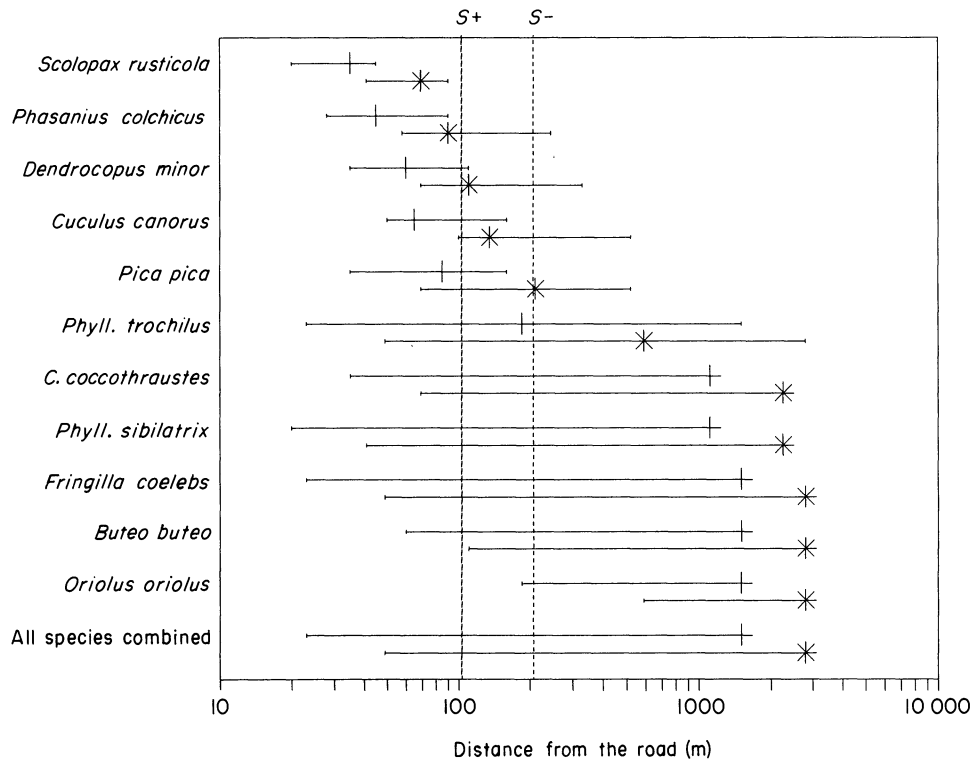

Fig. 5. Effect distances (m) with confidence limits in deciduous woodland for 10 000 cars per day (---ı---) and 60 000 cars per day (---*---). The car speed was fixed at 120 km h^{-1} and the amount of woodland along the road at 70%. Effect distances were derived from the regression with noise load as 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 (−).

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 per day. Other variables which influenced the effect distance were kept constant, such as speed of cars (120 km h^{-1}) and amount of woodland along the road (70% = mean value for the plots). For 10 000 cars per day the effect distances of species varied from about 40 to 1500 m, and for 60 000 cars per day from 70 to 2800 m (Fig. 5). However, the confidence limits were very large, especially for the large effect distances. The decrease factor of the density 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 per day, median 0·33; 60 000 cars per day, median 0·49) (Table 5).

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 $P < 0{\cdot}10$, 3 species at $P < 0{\cdot}05$, Table 6), but there was a clear effect on the density of all species combined (at $P < 0{\cdot}05$, Table 6).

Because there was a strong correlation between noise load and visibility of cars ($r = > 0{\cdot}90$), the regression was carried out with noise load only. Of the five species which showed an effect (at $P < 0{\cdot}10$, two species at $P < 0{\cdot}05$, 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 $P < 0{\cdot}05$, 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 per day and from 100 to 1750 m for 60 000 cars per day (Fig. 6). The decrease factor of the density in the zone between the road and the threshold 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^{-1}: median 0·23; 60 000 cars day^{-1}: median 0·60) (Table 8).

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 $P < 0{\cdot}10$, four at $P < 0{\cdot}05$, Table 9) and only two in the subset with a low noise load (at $P < 0{\cdot}05$, Table 9). Moreover, in the subset with a low noise load all

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[1]

Species	NP	NT	R	C	Sign.
Columba palumbus ()	11	48	0·32	0·63	*
Anthus trivialis ()	10	30	0·13	0·23	NS
Troglodytus troglodytus ()	14	37	0·16	0·22	NS
Erithacus rubecula ()	16	55	0·32	0·26	NS
Turdus merula	13	25	0·09	0·15	NS
Sylvia atricapilla	5	11	0·04	0·05	NS
Phylloscopus collybita ()	8	23	0·10	0·11	NS
Phylloscopus trochilus	8	24	0·11	0·25	*
Regulus regulus ()	14	41	0·22	0·36	*[1]
Parus montanus	12	19	0·06	0·11	NS
Parus cristatus ()	16	48	0·29	0·33	NS
Parus ater ()	15	29	0·17	0·29	†
Parus caeruleus	8	12	0·05	0·09	NS
Parus major ()	17	49	0·26	0·27	NS
Garrulus glandarius	13	39	0·12	0·32	NS
Pica pica ()	10	59	0·31	0·26	NS
Corvus corone ()	11	108	0·42	0·38	NS
Fringilla coelebs ()	13	77	0·45	0·52	NS
All species combined ()	17	256	2·35	3·39	*

[1] 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* $P<0{\cdot}01$ (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 = $P>0{\cdot}10$; † $P<0{\cdot}10$; * $P<0{\cdot}05$, ** $P<0{\cdot}01$.

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 (seven species at $P<0{\cdot}05$, 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 $P<0{\cdot}05$, 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 $P<0{\cdot}10$, one species at $P<0{\cdot}05$, Table 11) and three with a low visibility of cars (at $P<0{\cdot}10$, two at $P<0{\cdot}05$, 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 $P<0{\cdot}10$, one species at $P<0{\cdot}05$, Table 12) and one in low visibility plots (at $P<0{\cdot}10$, Table 12). In none of these cases was an effect on the density of all species combined found.

Discussion

REDUCTION OF DENSITIES

Of the 43 species that could be analysed 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 $P<0{\cdot}10$), there still remain 18 species with a significant effect at $P<0{\cdot}05$ (= 42%). This is considerably more than the few available studies indicate (Ferris 1979; Adams & Geis 1981; Reijnen & Thissen 1987). 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 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 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 relatively small numbers of observations at a greater distance from the road.

POSSIBLE CAUSES OF REDUCED DENSITIES

The fact that significant relationships were found between traffic related factors and breeding density

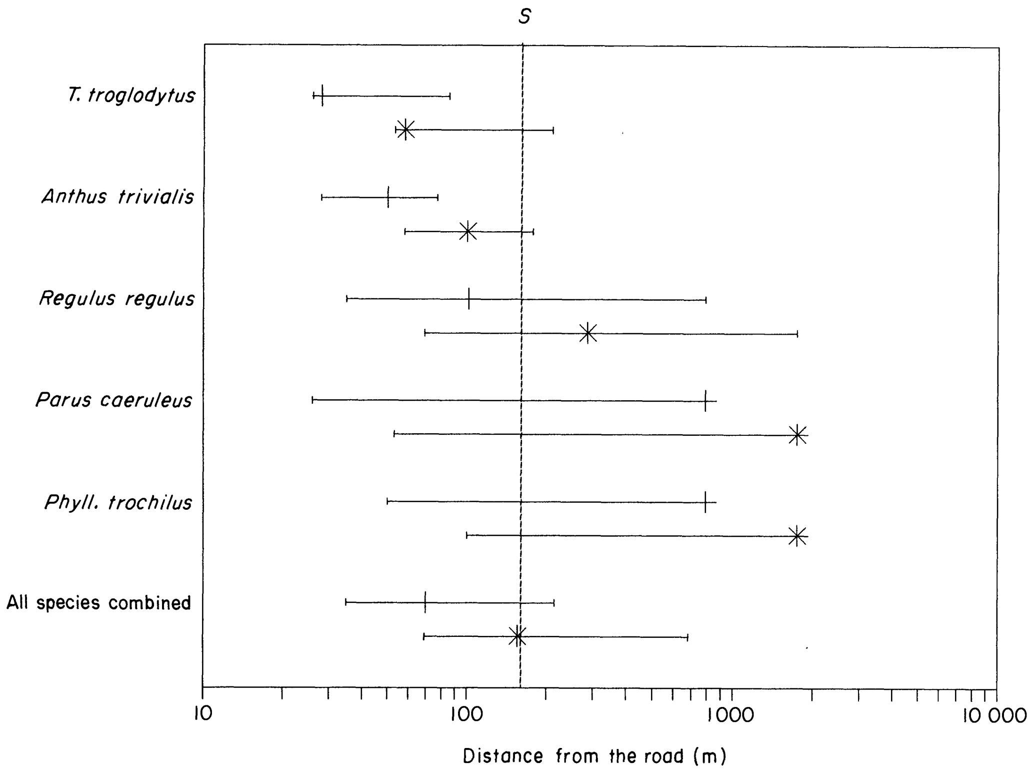

Fig. 6. Effect distances (m) with confidence limits in coniferous woodland for 10 000 cars per day (---ı---) and 60 000 cars per day (---*---). The car speed was fixed at 120 km h^{-1} and the amount of woodland along the road at 70%. Effect distances were derived from the regression with noise load as explanatory variable and a conversion of noise load to distance in m (see Methods). S = mean range of visibility of cars.

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.

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.
Anthus trivialis	2/23	4·12	52 (47–58)	−2·618	*
Troglodytes troglodytus	2/25	2·72	58 (46–59)	−6·846	†
Phylloscopus trochilus	1/17	3·00	≤29 (?–52)	−0·043	*
Regulus regulus	2/28	3·54	44 (?–56)	−0·080	†
Parus caeruleus	1/19	2·46	≤29 (?–59)	−0·057	†
All species combined	2/30	5·84	48 (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. † $P<0{\cdot}10$; * $P<0{\cdot}05$; ** $P<0{\cdot}01$.

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 per day	Decrease factor up to 250 m: 60 000 cars per day
Anthus trivialis	0·98	0·20	0·39
Troglodytus troglodytus	0·99	0·11	0·23
Phylloscopus trochilus	0·53	0·62	0·69
Regulus regulus	0·58		0·60
Parus caeruleus	0·61	0·23	0·78
All species combined	0·35	0·10	0·22

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 (±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 metres. 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 a 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 (Lowell, Best & Prather 1977; Grue *et al.* 1986), 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. L.P. Kuggeleijn (personal communication) estimated that in woodland concentrations of exhaust gases and other pollutants reach background levels within 50 m from a highway with dense traffic (40–50 000 cars per day). The majority of the species in this study (75%), however, showed maximum effect distances between 100 and 1500 m (see Figs 5 & 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, Foppen & Huisman 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 to 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

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 (see footnote). 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

	Noise load high				Noise load low			
Species	NP	R	C	Sign.	NP	R	C	Sign.
Phasanius colchicus	9	0·07	0·28	**	5	0·19	0·17	NS
Buteo buteo	9	0·15	0·12	NS	8	0·17	0·29	NS
Scolopax rusticola	6	0·12	0·07	NS	5	0·11	0·11	NS
Colomba oenas	8	0·09	0·08	NS	6	0·06	0·15	NS
Columba palumbus ()	14	0·53	0·49	NS	16	0·62	0·55	NS
Dendrocopus major ()	11	0·22	0·25	NS[1]	17	0·28	0·25	NS[1]
Troglodytus troglodytus ()	17	0·70	0·78	NS	17	1·11	1·14	NS
Prunella modularis	9	0·19	0·18	NS	7	0·12	0·10	NS
Erithacus rubecula ()	16	1·15	1·11	NS	18	1·00	0·90	NS
Turdus merula ()	19	1·07	0·99	NS	19	1·24	1·10	NS
Turdus philomelos ()	13	0·40	0·41	NS[1]	10	0·20	0·25	NS
Sylvia borin ()	14	0·62	1·13	*	14	0·78	0·51	NS
Sylvia atricapilla ()	17	0·48	0·72	†	17	0·65	0·57	NS
Phylloscopus collybita ()	18	0·78	0·94	†	17	0·96	0·86	NS
Phylloscopus trochilus ()	13	0·69	1·12	**	13	0·72	0·83	NS
Muscicapa striata ()	13	0·26	0·24	NS	13	0·28	0·25	NS
Aegithalos caudata	12	0·14	0·16	NS	13	0·19	0·10	NS
Parus montanus	8	0·10	0·14	NS	10	0·08	0·23	NS
Parus palustris	11	0·20	0·25	†	12	0·14	0·15	NS
Parus caeruleus ()	17	0·78	0·74	NS	16	0·79	0·75	NS
Parus major ()	19	1·58	1·54	NS	18	1·67	1·36	NS
Sitta europaea	9	0·21	0·18	NS	9	0·23	0·16	NS
Certhia brachydactyla ()	15	0·42	0·44	NS[1]	15	0·46	0·44	NS[1]
Garrulus glandarius ()	15	0·53	0·42	NS	14	0·47	0·38	NS
Pica pica ()	8	0·15	0·16	NS	9	0·24	0·30	NS
Corvus corone ()	14	0·82	0·46	NS	15	0·84	0·97	NS
Sturnus vulgaris	10	0·45	0·59	NS	10	0·36	0·31	NS
Fringilla coelebs ()	16	0·61	0·87	NS	16	0·82	0·83	NS
All species combined ()	19	13·3	15·8		19	14·1	13·3	NS

[1] 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 = $P > 0·10$; † $P < 0·10$; * $P < 0·05$; ** $P < 0·01$.

between 100–200 Hz and 0·5–4 kHz (Huisman & Attenborough 1991). So, if disturbance of communication is an important mechanism, those species producing songs 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 no clear pattern (chi-squared test, 2df, $P > 0·10$, 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 probably, a supplementary explanation could be that birds avoid road habitats because of this aspect (cf. Reijnen & Foppen 1994).

Table 10. Significant regression 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.
Phasanius colchicus	2/15	5·28	40 (?–58)	−0·099	*
Scolopax rusticola	2/11	3·99	56 (55–61)	−2·515	*
Sylvia borin	1/27	3·24	≤23 (?–54)	−0·024	*
Sylvia atricapilla	1/37	4·20	≤23 (?–48)	−0·036	*
Phylloscopus trochilus	2/29	5·73	38 (?–50)	−0·046	**
Pica pica	2/22	3·45	46 (33–56)	−0·092	*
Fringilla coelebs	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. * $P<0{\cdot}05$; ** $P<0{\cdot}01$.

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 [1]

	Visibility of cars high				Visibility of cars low			
Species	NP	R	C	Sign.	NP	R	C	Sign.
Phasanius colchicus	5	0·21	0·24	NS	8	0·05	0·20	**
Buteo buteo	9	0·18	0·25	NS	8	0·13	0·16	NS
Columba palumbus ()	15	0·55	0·59	NS	15	0·63	0·49	NS
Dendrocopus major ()	16	0·32	0·28	NS	12	0·17	0·21	NS[1]
Troglodytus troglodytus ()	17	0·92	0·96	NS	17	0·89	0·90	NS
Prunella modularis	8	0·16	0·13	NS	8	0·15	0·16	NS
Erithacus rubecula ()	20	1·21	1·26	NS	15	0·76	0·81	NS
Turdus merula ()	19	1·36	1·10	NS	19	0·94	0·98	NS
Turdus philomelos ()	15	0·26	0·33	NS	9	0·33	0·32	NS
Sylvia borin ()	13	0·54	0·48	NS	15	0·86	1·16	NS
Sylvia atricapilla ()	18	0·50	0·61	†[1]	16	0·63	0·67	NS
Phylloscopus collybita ()	17	0·74	0·85	NS	18	1·00	0·96	NS
Phylloscopus trochilus ()	12	0·26	0·66	**[1]	14	1·14	1·40	†
Muscicapa striata ()	14	0·35	0·28	NS	13	0·41	0·41	NS
Aegithalos caudata	13	0·18	0·14	NS	12	0·15	0·12	NS
Parus palustris	15	0·25	0·32	NS	8	0·10	0·08	NS
Parus montanus	7	0·08	0·13	NS	11	0·10	0·25	NS
Parus caeruleus ()	18	0·94	0·86	NS	15	0·63	0·64	NS
Parus major ()	19	1·83	1·58	NS	19	1·28	1·28	NS
Sitta europaea	11	0·35	0·22	NS	7	0·09	0·12	NS
Certhia brachydactyla ()	18	0·53	0·62	NS[1]	12	0·35	0·26	NS
Garrulus glandarius ()	15	0·51	0·42	NS	14	0·50	0·38	NS
Pica pica ()	7	0·16	0·15	NS	10	0·23	0·31	NS
Corvus corone ()	14	0·54	0·59	NS	15	1·07	0·83	NS
Sturnus vulgaris	14	0·68	0·67	NS	6	0·14	0·22	NS
Fringilla coelebs ()	17	0·82	0·97	NS	15	0·61	0·73	NS
All species combined ()	15	13·0	13·7	NS	16	11·7	12·5	NS

[1] 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* $P<0{\cdot}01$ (N = 0·18, F = 0·45), *Sylvia atricapilla* $P<0{\cdot}10$ (N = 0·45, F = 0·63), *Phylloscopus trochilus* $P<0{\cdot}05$ (N = 0·17, F = 0·84), *Certhia brachydactyla* $P<0{\cdot}10$ (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 = $P>0{\cdot}10$; † $P<0{\cdot}10$; * $P<0{\cdot}05$; ** $P<0{\cdot}01$.

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.
Phasanius colchicus	H	2/7	3·38	50 (11−71)	−0·058	†
Phylloscopus trochilus	H	1/27	12·16	0 (?−41)	−0·017	**
Fringilla coelebs	L	1/33	2·74	0 (?−57)	−0·01	†

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. † $P<0{\cdot}10$; ** $P<0{\cdot}01$.

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 relationships 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 lowered 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 & 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 lowered 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 in 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, Krebs & Kacelnik 1991), the reduction of 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 the 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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