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The effects of car traffic on breeding bird populations in woodland. I. Evidence of reduced habitat quality for willow warblers (*Phylloscopus trochilus*) breeding close to a highway

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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^{-1}) than in zones with a comparable habitat at a greater distance (3·3 ha^{-1}).
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 in the road zone 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).

Key-words: source–sink, habitat occupancy, return rate, breeding success, mating success, density.

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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. Räty 1979; van der Zande, ter Keurs & van der Weijden 1980; Reijnen, Thissen & Bekker 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, Krebs & Kacelnik 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 of reduced quality are delayed settlement of males (Sæther 1989; Brooke 1979; Järvi 1983; Jakobsson 1988) and an increased proportion of yearlings (Greenwood & Harvey 1982; Gezelius *et al.* 1984; Lanyon & Thomopson 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 focuses 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 50000 cars per day). It consisted of willow *Salix* sp. coppices (±150 ha) and poplar *Populus* sp. plantations (±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 three territories per year). Data were collected from 1988 to 1991.

Because of the regular cutting of the willow coppices (every 3 years), 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 homogeneous throughout the whole study area and a comparison

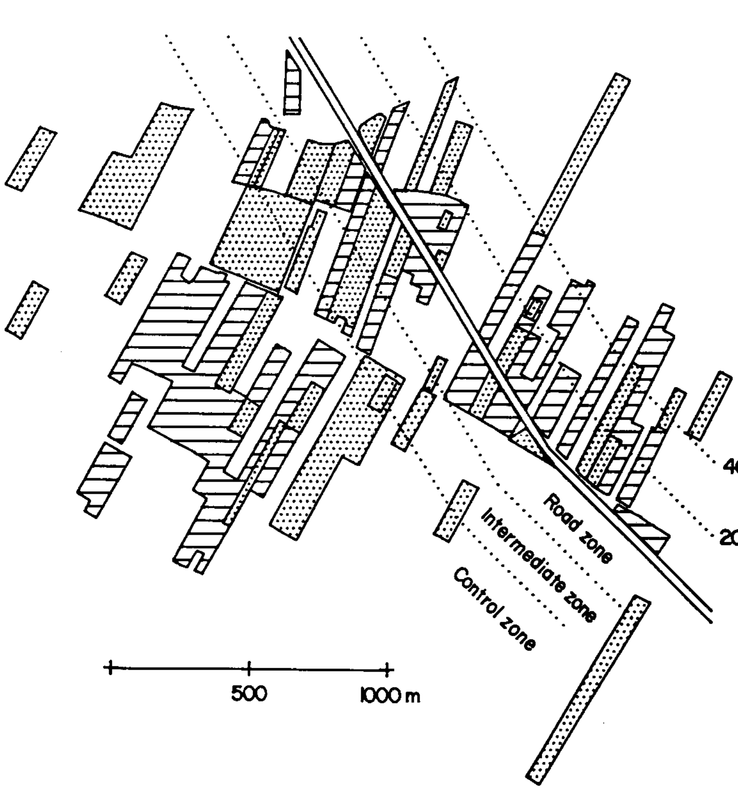

Fig. 1. The study area 'Bolgerijen-Autena' with the highway (double line). The hatched parts indicate the selected willow coppices, the dotted parts the other wooded vegetations (willow coppice and poplar wood). The remaining parts are meadows. The three zones are indicated by the dotted lines.

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 zone and 30% for the control zone).

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 a unique combination of coloured rings, so they could be distinguished individually. Females were not included in the ringing efforts because they were 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 & LaPointe 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 to 80%.

However, yearlings could be identified because they had a consistently different response to song-recordings 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 yearlings (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 until 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) recommended 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

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

	Road/intermediate zone ($n = 11$)		Control zone ($n = 11$)		
Estimate	Mean	SD	Mean	SD	Sign.
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^{-1})	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 estimate in the road/intermediate zone and the control zone.

NS, $P > 0{\cdot}10$.

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 22 March, when the first willow warbler arrived, until 16 April, the study area was visited frequently (nine times). These visits each took 2–3 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 easily, 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 to 1991 the total number of territories in the study area varied from 162 to 186 and most (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 & 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.

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

Table 2. Numbers (*N*) and densities (*D*) of willow warbler (territories ha^{-1}) 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

	Road		Intermediate		Control		
Year	*N*	*D*	*N*	*D*	*N*	*D*	Sign.
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 χ^2 tests comparing the numbers in the three zones and taking account of differences in area. Tests have 2 degrees of freedom.
NS, $P>0{\cdot}10$, ** $P<0{\cdot}01$.

Table 3. Numbers (*N*) and densities (*D*) of willow warbler (territories ha^{-1}) 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

	Road		Intermediate		Control		
Year	*N*	*D*	*N*	*D*	*N*	*D*	Sign.
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 χ^2 tests comparing the numbers in the three zones and taking account of differences in area. Tests have 2 degrees of freedom.
NS, $P>0{\cdot}10$, † $P<0{\cdot}10$, * $P<0{\cdot}05$, *** $P<0{\cdot}001$.

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

	Road			Intermediate			Control			
Year	Y	O	PY	Y	O	PY	Y	O	PY	Sign.
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 χ^2 tests comparing the numbers in the three zones and taking account of differences in area. Tests have 2 degrees of freedom.
NS, $P>0{\cdot}10$, † $P<0{\cdot}10$, ** $P<0{\cdot}01$, *** $P<0{\cdot}001$.

strongly influenced by the older males, because only these showed significant differences in the density between the three zones (Table 5).

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, $P>0{\cdot}10$). The yearlings, however, occupied their territories significantly later in the road zone (Mann-Whitney *U*-test, $P<0{\cdot}05$, Fig. 2).

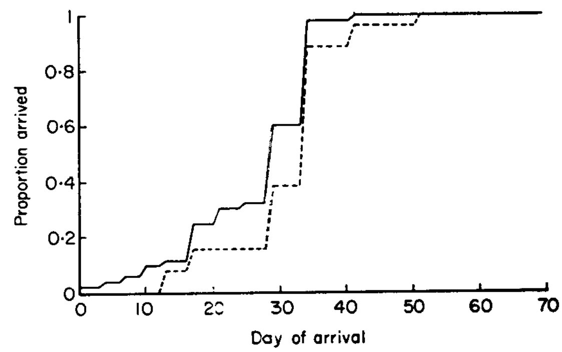

Fig. 2. Settlement pattern of yearling males in the road zone (dotted) and the control zone (solid).

BREEDING PERFORMANCE

Since willow warblers produce one brood per year (Schönfeld 1984) and in only a few cases (<2%) was bigamy 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 (χ^2 test, 1 df, $P<0{\cdot}05$).

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

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

	Yearlings				Older males			
Year	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 χ^2 tests comparing the numbers in the three zones and taking account of differences in area. Tests have 2 degrees of freedom.
NS, $P>0{\cdot}10$, * $P<0{\cdot}05$, ** $P<0{\cdot}01$, *** $P<0{\cdot}001$.

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 1990–91. The road zone (I) is 0–200 m, the intermediate zone (II) 200–400 m and the control zone (III) >400 m from the highway

	Mating success				Breeding success			
	Road	Intermediate	Control	Sign.	Road	Intermediate	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 χ^2 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, $P>0{\cdot}10$, * $P<0{\cdot}05$.

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, $F=0{\cdot}53$, $P=0{\cdot}76$)

	Road zone			Intermediate zone			Control zone		
	n	Mean	SD	*n*	Mean	SD	*n*	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

between the three zones, neither for yearling and older males, nor for both age groups combined (Table 8). There were also no significant differences between the two age groups (χ^2 tests, 2 df, $P>0{\cdot}10$). 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 (χ^2 test, 1 df, $P>0{\cdot}10$, Table 9), but the numbers are low and hardly allow statistical testing.

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

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

Table 8. Return rate (RR) of yearlings and older males during 1988–91 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, the intermediate zone 200–400 m and the control zone >400 m from the highway

	Road			Intermediate			Control			
	N	*R*	*RR*	*N*	*R*	*RR*	*N*	*R*	*RR*	Sign.
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 χ^2 tests comparing the return rate (*RR*) in the three zones. Tests have 2 degrees of freedom.
NS, $P>0{\cdot}10$.

Table 10. Estimates of male willow warbler annual productivity and recruitment in the study area (1989–91 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

	Road zone			Intermediate + control zone		
Estimates	O	Y	O+Y	O	Y	O+Y
Density of males (ha^{-1})	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^{-1})*	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^{-1})†	0·2	0·2	0·4	0·5	0·4	0·9
Total output of males (ha^{-1})	0·6	0·9	1·5	1·3	1·1	2·4

* (density) × (return rate).
† (recruitment per male) × (% successful males) × (density).

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 (red-winged 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 predation, such as the vegetation structure (Robertson 1972) or the amount of edge (Andrèn & 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 be considered unmated rather 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 number of nests (especially for age-groups separately), this assumption is not totally reliable.

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 no 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 effects 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 might be important.

An obvious explanation for noise having an important effect on numbers, 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, Davies & Mosca 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 does not seem very likely, since there were no important possible 'source' areas 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 under-estimation 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 (0·20–0·30), 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 & Fonstadt (1981).

The consequence for the whole willow warbler population may also be less important if the lower reproductive output in the road zone is (partly) due to accumulation of poorer yearling males. This implies that these males had a more equal distribution in the study area before the highway was built. However, the percentage of unmated males in our whole study area (on average at least 20% per year) was still much higher than that 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 has been negatively influenced by the presence of the highway. Because density in poor habitats 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 increased emigration of territorial males. The significance of this phenomenon is discussed elsewhere (Foppen & Reijnen 1994).

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