ELSEVIER

Landscape and Urban Planning 841 (2001) 1–13

LANDSCAPE AND URBAN PLANNING

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Reduced bird occurrence in pine forest fragments associated with road proximity in a Mediterranean agricultural area

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Received 15 November 2000; received in revised form 18 June 2001; accepted 28 August 2001

Abstract

This study investigated the effect of road and highway proximity on the occurrence of bird species in isolated secondary pine forest fragments in an agricultural matrix. We assessed the effects of road proximity separately for three different groups of bird species in order to detect ecological responses related to species biology. Bird occurrence was mainly related to fragment size but also to vegetation structure and fragment connectivity. When corrected for patch characteristics, we found that fragments up to 2 km away from a main highway contained less forest species, both generalists and specialists than fragments more distantly located. This pattern was independent of the side of the highway analysed. Considering each bird species separately, we found consistent lower occurrence probabilities near the highway in 50% of forest species. This difference was not found for ubiquitous species that were to some extent positively influenced by proximity of other major roads. Our results suggest that highway proximity, but not that of other major roads, decrease occupancy probability of forest birds in isolated forest fragments, thus reducing probability of metapopulation persistence. Although low habitat quality as a result of noise disturbance is likely to account for some of the results, the long distance effect detected strongly suggests that other factors rather than direct traffic disturbance alone are involved in lower bird occurrences near the highway. Decreased connectivity among forest fragments associated to avoidance of areas near the highway is an alternative explanation to the results obtained. We suggest that these findings should be included in strategic environmental impact assessment studies conducted to determine the ecological impact of large transport infrastructures across highly fragmented landscapes.

Keywords: Fragmentation; Metapopulation; Highways; Roads; Forest birds

1. Introduction

In fragmented forest habitats, bird populations are often organised in metapopulations in which habitat quality and connectivity determine the occurrence of a given species in the remaining patches of suitable habitat (Verboom et al., 1991; Opdam, 1991; Wiens, 1994). The distance between these habitat patches and to possible source areas as well as their size and quality are decisive factors determining species presence in forest fragments (Hanski, 1998). Habitat barriers between habitat patches will further affect connectivity, and interfere species mobility and dispersal (Forman, 1995; Verhulst et al., 1997; Desrochers et al., 1999; Bélisle et al., 2001). In such cases, metapopulation dynamics will be affected and specific risk of local extinction will increase accordingly (Saunders et al., 1991; Hanski, 1998).

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0169-2046/01/$20.00 © 2001 Published by Elsevier Science B.V.
PII: S0169-2046(01)00191-8

Roads are important features of humanised landscapes that function as barriers for the movements and the dispersal of many species (Forman and Alexander, 1998). Furthermore, traffic load on transport infrastructure such as roads and highways often reduce the quality of habitat for vertebrates such as forest or grassland birds, through noise production or visual disturbance (see review in Forman and Alexander, 1998). A number of studies have assessed the effects of road proximity on bird abundance in continuous forest habitats (Räty, 1979; Reijnen and Foppen, 1994; Reijnen et al., 1995; Reijnen et al., 1996; Kuitunen et al., 1998; Meunier et al., 1999). However, no studies have been conducted so far on the effects of linear infrastructures on already isolated forest bird populations, which is a very common pattern in humanised landscapes. In this study, we investigated the effect of road and highway proximity on bird occurrence in secondary pine forest fragments in an agricultural matrix. We studied the effects of road proximity separately for three different groups of bird species in order to detect ecological related responses according to species biology. We predict that independently of size, isolation and vegetation features, fragments near roads will support a reduced number of species that those located further away, and such avoidance should be stronger in the case of heavily used highways.

2. Methods

2.1. Study area

Fieldwork was carried out in the Penedès area in the northeast of the Iberian peninsula (Fig. 1, 45°80′N, 3°90′W, 100 m a.s.l.). This zone is heavily cultivated, with vineyards dominating areas where the Holm oak (*Quercus ilex*) forest has been almost completely eliminated. Secondary forest fragments of varying size dominated by Aleppo pine (*Pinus halepensis*) can now be found among vineyards in patches not appropriate for farmland. Larger extensions of Aleppo pine forests affected to a variable extent by forest fires and exploitation are also found in the mountain ranges surrounding the Penedès plain. Transport infrastructures such as roads and a major highway (A2, Barcelona–Zaragoza) cross the area, thus allowing the study of their effects on animal distribution.

We sampled 40 forest fragments with sizes ranging from 0.1 to 38.4 ha ($X = 4.64$ ha Fig. 1). We included all the large forest fragments within the Penedès plain and a representative sample of those of smaller size throughout the plain. The size of each fragment and its distance to the nearest continuous forest (which could stand as 'sources' of dispersing individuals) were measured on aerial photographs. These distances were measured as linear distances between the edge of each forest fragment to the nearest edge of a large continuous Aleppo pine forests (>100 ha). Forested narrow stripes along small rivers are common in the area and they are likely to be used as potential dispersing corridors by birds. Therefore, we also measured the linear distance of each forest fragment to the nearest riparian habitat corridor.

The A2 highway is the main transport infrastructure of the area with the heaviest traffic load (mean of 47,000 vehicles per day, Direcció General de Carreteres, 1999, personal communication). Thus, given its strategic location dividing the Penedès plain in two parts, we specifically measured the minimum linear distance of each forest fragment to it. We did not expect to find linear responses of bird occurrence to distance from roads, rather negative effects are expected to occur within the first 1000 m (Forman and Alexander, 1998). Therefore, we decided to categorise distance variables according to our expectations of finding stronger effects near roads. We categorised forest fragments in four groups of increasing distance to the highway: A (0–500 m); B (0.5–1 km); C (1–2 km); D (>2 km). More fine grained categorisations became impossible due to the lower number of forest fragments very close to the highway.

We also wanted to determine the effect of road magnitude on species presence in forest fragments. Therefore, we also measured the minimum fragment distance to other roads, which were classified as main roads (5,000–20,000 vehicles per day) and roads of the local network (500–2,000 vehicles per day). This covered most of the main roads in the plain other than the highway. We categorised the fragments into two groups according to their minimum distance to other roads: A (0–200 m); B (200–500 m); C (0.5–1 km) and D (>1 km). In the case of local network roads, the last category D, (>1,000 m) was pooled with category C (500–1,000 m) because very few fragments were located far enough from a local road.

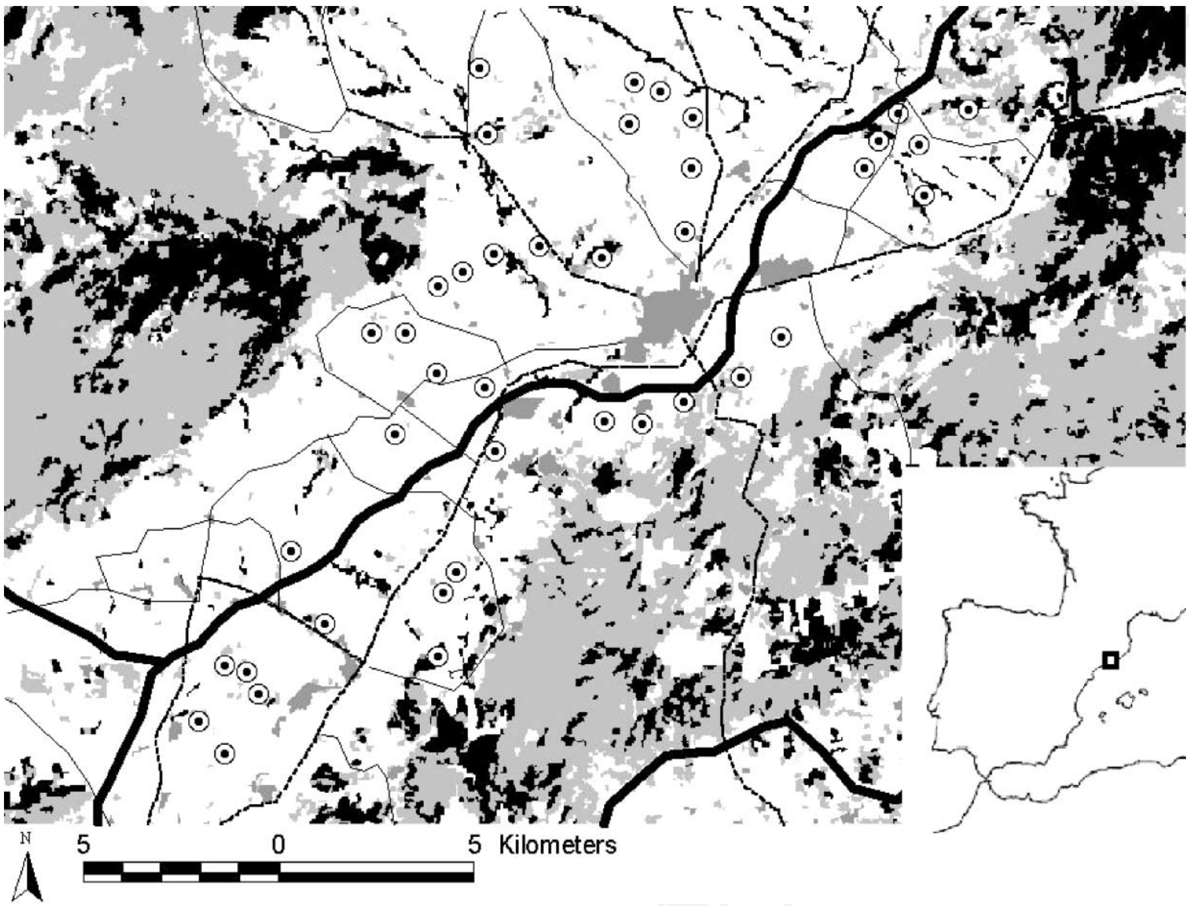

Fig. 1. Land-use map of the study area in 1997 containing the Penedès plain (in the centre) and surrounding, less humanised areas. Black areas represent forests, gray areas, shrubby vegetation or urban areas in the plain. White areas represent agriculture and other open areas. The small circles show the locations of the forest fragments. A2 highway can be located in the centre of the Penedès plain crossing the area in a south-west north-east direction. Other paved roads (main roads, thick broken lines, and local network, thin lines) are also shown.

2.2. Bird censuses

We conducted bird censuses in each fragment during the 1999-breeding season (April–July). We recorded the presence/absence of each bird species in two to four visits to each fragment, evenly distributed through the period studied (Hinsley et al., 1995; Díaz et al., 1998 for similar procedure). We did not attempt to measure the abundance of breeding birds since comparisons of abundance estimates between habitat patches of highly different sizes are misleading (reviewed by Haila et al., 1993; Opdam, 1991). Furthermore, in highly fragmented habitat, such as our forest patches, occurrence is a reliable measure of species distribution in the landscape and it has been widely used in metapopulation studies (Opdam, 1991; Hanski, 1998).

Censuses were made early in the morning and late in the afternoon in order to avoid central hours of the day, when bird activity is at its minimum. Small to medium size forest fragments (0.1–30 ha) were searched by walking a route established to get within 100 m of every point in the forest fragment in each visit (Sutherland, 1996). Along the routes, we noted all the birds seen or heard and the results from all the visits were pooled together. Raptors, owls and nightjars were not reliably detected with our census technique and so were excluded from the list of breeding species. The length of routes was established according to the size of the forest fragment and ranged from 30 min to 2 h in the larger fragments. We assumed a probability detection of 1 when the number of species did not increase after further visits. Since, the first visit to each fragment accounted for 95% of the total species recorded, we were quite confident that the list of species listed for each fragment was complete and no missing species were left out. The largest fragments (>30 ha) were also censused by means of repeated point counts distributed across the whole area of study. Both routes and point counts were established to sample the edges and the interior of each forest fragment.

Some of the species detected did not breed at all in the fragments studied, either because they nested in open areas and visited forests only occasionally (Bee-eater, *Merops apiaster*; aerial feeders such as swallows, swifts), or because they were late-season migrants that did not breed in the area studied (Pied flycatcher *Ficedula hypoleuca*). Also, some species records from the smallest fragments (<1 ha) could be attributable transient individuals breeding in some other forested areas nearby. To avoid this potential bias, such records were considered only when we obtained direct evidence for breeding in the fragment (e.g. nest construction or provisioning behaviour) or when we detected the species in at least two visits.

We classified the species found into three groups according to their dependency on forest habitats during breeding following Díaz et al., 1998 (Table 1). (i) Ubiquitous species, such as pigeons, sparrows and some finches, are able to nest and feed in other habitat types other than the forest (e.g. isolated shrubs, field margins or even croplands). (ii) Forest generalists, such as thrushes, some corvids and most finches, breed in forest but can also exploit the agricultural matrix surrounding them. Most forest generalist species are tree- or shrub-nesters and ground feeders. (iii) Forest specialists, such as most warblers and pariforms (tits and allies), are restricted to forest habitats for nestling and feeding. They place nests on trees and shrubs, and forage in tree and shrub canopies as well as on tree trunks and branches.

2.3. Vegetation composition and structure

The vegetation composition and structure of fragments were measured at the centre of each forest fragment immediately after bird censuses were completed. The vegetation structure at each forest fragment was measured within a 25 m radius around the centre of the forest fragment. In larger fragments, where birds were censused by means of point counts, vegetation structure was measured at each bird count station and a mean for the fragment was calculated. We estimated the cover of several vegetation layers (0–0.25, 0.25–0.5, 0.50–1, 1–2, 2–4, 4–8, 8–16 m), the relative cover of dominant tree and shrub species, and rock layer as habitat variables. The cover value was defined as the projection of the foliage volume of the layer (or rock layer) in a horizontal plane. We estimated this projection by comparison with the reference chart following the procedure by Prodon and Lebreton (1981). According to this method, the observer can reach a reliability of ±10%. The final number of shrubs and tree cover variables was selected after considering only species covering at least 10% of the surface in at least 10% of the study sites.

The original number of vegetation variables (Table 2) was summarised into a few independent factors by means of principal component analysis (PCA) carried out on the average values of each variable for each forest fragment. This procedure was established to reduce multicolonearity in the multivariate analysis of bird responses to forest traits (Hinsley et al., 1995; Díaz et al., 1998).

2.4. Data analyses

In order to control the effects of landscape and vegetation effects on bird occurrence on forest fragments, we performed a backward step-wise multiple regression (Crawley, 1993) using the following explanatory variables: size of the fragment, distance to the corridor, distance to nearest continuous forests and vegetation structure (as estimated from the three first factors obtained from the PCA analysis). The analyses were performed separately for the three different ecological groups, that is, for ubiquitous, forest generalists and forest specialist species (see Díaz et al., 1998). The size of the fragment and its distance to the nearest corridor and to the tract of continuous forest were previously normalised using logarithmic transformations.

We calculated the residuals from the best regression model selected for each group of birds to control for the effects of landscape and vegetation structure on

Table 1
The bird species found breeding in Aleppo pine fragments in the Penedès area[a]

Bird species	Group	No. of fragments occupied	Smallest fragment
Sylvia melanocephala (Syme) sardinian warbler	G	36	0.1
Carduelis chloris (Cach) greenfinch	G	26	0.1
Luscinia megarhynchos (Lume) nightingale	G	24	0.1
Turdus merula (Tume) blackbird	G	15	0.1
Eritacus rubecula (Erru) robin	G	10	1.1
Garrulus glandarius (Gagl) jay	G	6	1.2
Streptotelia turtur (Sttu) turtle dove	G	6	0.4
Picus viridis (Pivi) green woodpecker	G	3	1.2
Hyppolais polyglotta (Hypo) melodious warbler	G	1	5.9
Oriolus oriolus (Oror) golden oriole	G	1	1.8
T. viscivorus (Tuvi) mistle thrush	G	1	0.6
P. major (Pama) great tit	S	28	0.1
Certhia brachydactlyla (Cebr) short-toed treecreeper	S	18	0.6
P. cristatus (Pacr) crested tit	S	14	0.5
Troglodytes troglodytes (Trtr) wren	S	10	1.1
Aegithalos caudatus (Aeca) long-tailed tit	S	8	2.8
Regulus ignicapillus (Reig) firecrest	S	8	2.7
Phylloscopus bonelli (Phbo) Bonelli's warbler	S	6	1.6
S. atricapilla (Syat) blackcap	S	4	0.4
P. caeruleus (Paca) blue tit	S	3	1.2
Muscicapa striata (Must) spotted flycatcher	S	1	1.6
Serinus serinus (Sese) serin	U	39	0.1
C. carduelis (Caca) goldfinch	U	36	0.1
Pica pica (Pipi) magpie	U	36	0.1
Passer domesticus (Pado) house sparrow	U	32	0.1
Columba palumbus (Copa) wood pigeon	U	29	0.1
E. cirlus (Emci) Cirl bunting	U	13	0.1
Upupa epops (Upep) Hoopoe	U	12	0.5
Cettia cetti (Cece) Cetti's warbler	U	2	11.1
Alectoris rufa (Alru) red-legged partridge	U	1	3.3
S. decaoto (Stde) mourning dove	U	1	0.5
Sturnus vulgaris (Stvu) common starling	U	1	2.7

[a] Species were classified as ubiquitous (U), forest generalist (G) and forest specialists (S) according to their dependence on forest habitats during breeding. The number of fragments where each species was found (from a total of 40 fragments) and the size of the smallest forest fragment (ha) where the species was found are also shown.

species occurrence (Buckland and Elston, 1993). Then, using such residuals in a multiway factorial ANOVA, we first assessed separately the effects of road and highway proximity on bird's occurrence. We used distance from the nearest main road (four levels), distance to nearest local network road (three levels) and distance to the highway (four levels) as explanatory factors. To check for the consistency in the pattern observed in relation to highway distance, we included in a second analyses the side of the fragment as its location right or left from the highway. Given the similar exposure of the forest fragments across de Penedès plain to wind (Forman and Alexander, 1998), we expect no differences to be found between the patterns in the two sides of the highway.

We also analysed relationships between species presence and road proximity by means of logistic regression where only significant explanatory variables (landscape and vegetation), as judged by changes in deviance between different models, were included in the final model after a backward procedure (Crawley, 1993). Here, we use a similar approach to multiple regression models. First, we searched for the best model including landscape and vegetation fac-

Table 2
Variables describing the structure of the vegetation in the plantations studied, and factor loadings of each individual variable in the three first factors obtained in the principal component analysis of the vegetation structure of forest fragments[a]

Variable	Description	PC1	PC2	PC3
COVER25	Cover of herbaceous plants less than 25 cm tall (%)	−0.35*	0.14	0.16
COVER50	Cover of shrubs from 25 to 50 cm tall (%)	0.03	0.00	−0.85*
COVER1	Cover of shrubs from 50 cm to 1 m tall (%)	0.50*	0.06	−0.78*
COVER2	Cover of shrubs and small trees less than 2 m tall (%)	0.79*	0.04	−0.47*
COVER4	Cover of shrubs and trees less than 4 m tall (%)	0.62*	−0.39	−0.12
COVER8	Cover of trees less than 8 m tall (%)	0.02	−0.73*	0.22
COVER16	Cover of trees less than 16 m tall (%)	−0.05	0.84*	0.09
COVER+	Cover of trees more than 16 m tall (%)	0.42*	0.28	0.11
PINUS	Cover of Aleppo Pine *Pinus halepensis* (%)	−0.50*	−0.40*	0.14
QILEX	Cover of Holm oak *Quercus ilex* (%)	0.79*	0.25	−0.15
QCOCCIFERA	Cover of Kermes oak *Quercus coccifera* (%)	−0.19	−0.30	−0.54*
QCERRIOIDES	Cover of Spanish oak *Quercus cerrioides* (%)	0.73*	0.00	0.06
PISTACIA	Cover of Lentisk *Pistacia lentiscus* (%)	0.00	−0.13	0.45*
ROSMARINUS	Cover of Rosemay *Rosmarinus officinalis* (%)	−0.26	−0.43*	−0.10
OLEA	Cover of Olive trees *Olea europaea* (%)	−0.02	0.34	0.08
RUBUS	Cover of Blackberry *Rubus olmifolius* (%)	0.73*	0.30	0.07
HEDERA	Cover of Ivy *Hedera helix* (%)	0.63*	−0.14	0.16
	Eigenvalue	3.93	2.17	2.13
	Variance (%)	24.60	13.62	13.33

[a] PC1 was interpreted as an index of subarboreal original vegetation mainly associated with the presence of the Holm oak. Negative PC2 values in this factor were associated with dense medium-height pine forests with Mediterranean dry vegetation such as the rosemary (*Rosmarinus officinalis*). PC3 separated shrubby rich forests from those with less vegetation at lower layers.
* $P < 0.05$.

tors, and second, we studied whether road and highway distance added explanatory power to the basic models. Specific models were only calculated for species present in at least three of the fragments studied. In specific models, the effect of the distance to main roads and the highway was tested using two categories per variable in order to obtain an unambiguous comparison of close versus distant fragments. In case of finding clear patterns in the associations between species richness and distance to roads we used maximum affection distance as a criteria to separate close and distant fragments. If no clear pattern arose, we used a conservative criteria and used 500 m distance to separate distant and close fragments in species specific models. Deviations from random expectations in overall tendencies to occur more often near highways were studied using Sign-tests.

3. Results

The total number of species detected in the 40 fragments studied was 32 (mean = 10.77 species per fragment, range 4–20, Table 1). Vegetation composition and structure, mainly the presence of a developed shrubby layer associated with the Holm oak, considerably affected the number of both types of forest species present in fragments (Table 3).

Nevertheless, forest species presence was mainly associated with landscape characteristics such as fragment size (Table 3). Forest specialists were more likely to appear in fragments located near riparian corridors (Table 3). Only one landscape variable, fragment size, and one vegetation structure variable affected significantly the occurrence of ubiquitous species on forest fragments (Table 3). Best model for this group of birds explained much less variation in the data than that for forest species. Vegetation factors were not significantly correlated or very slightly associated with the spatial factors included (Table 4). Furthermore, none of the vegetation or landscape variables was significantly associated with distance to main roads or to the highway (Table 4). Therefore, interrelations between the factors studied were low enough to assume they did not affect the relative weight of each type of

Table 3
Multiple regression models for the concordance between the richness of breeding bird species and forest fragment features; size, distance to corridors, distance to nearest continuous forest and structures of vegetation ($n = 40$ forest fragments)[a]

Independent variable	Coefficient	S.E.	Variance (%)	*P*
Forest generalists				
Constant	1.96	0.26		<0.001
Fragment size	1.37	0.11	70.05	<0.001
PC1	0.75	0.19	7.38	<0.001
PC2	0.38	0.19	1.96	<0.05
			79.90	<0.001
Forest specialists				
Constant	2.27	0.55		
Fragment size	0.97	0.13	65.32	<0.001
Distance to corridors	−0.24	0.10	7.80	<0.01
PC1	0.33	0.19	1.35	<0.1
PC2	0.55	0.18	4.50	<0.01
			80.02	<0.001
Ubiquitous species				
Constant	3.53	0.26		
Fragment size	0.33	0.17	11.41	<0.05
PC3	−0.30	0.16	5.50	<0.1
			16.91	<0.05

[a] Results are given for ubiquitous and forest species (both generalists and specialists taken separately).

factors in explaining species occurrences in forest fragments.

After controlling for landscape and vegetation effects, fragments at different distances from main paved roads, either main ones or from the local network, did not differ in the number of species present for any of the ecological groups analysed (Table 5, Fig. 2). In contrast, significant associations were discovered between highway proximity and residual bird richness in fragments. ANOVA models of the residual number of species, for both forest generalists and specialists, explained significant amounts of variance ranging 35–40%. Fragments located up to 2 km from the highway had a lower residual number of forest species, both forest generalists and specialists, than fragments located further away (Fig. 2). Therefore,

Table 4
Correlation matrix of spatial and vegetation factors included in the study[a]

	Distance to local network road	Distance to main road	Distance to highway	CONTINUOUS	CORRIDOR	SIZE	PC1	PC2	PC3
Distance to local network road	1.00	0.27	0.07	0.20	0.08	−0.23	−0.14	0.13	−0.11
Distance to main road		1.00	0.25	−0.19	−0.14	−0.18	−0.05	−0.03	0.16
Distance to highway			1.00	0.05	−0.25	0.21	0.12	0.05	−0.07
CONTINUOUS				1.00	0.30	−0.07	0.35	0.22	0.07
CORRIDOR					1.00	−0.28	−0.12	−0.02	0.14
SIZE						1.00	0.04	−0.25	−0.11
PC1							1	0.00	0.00
PC2								1	0.00
PC3									1

[a] Correlation coefficients are Pearson coefficients. Distance to the highway (m); distance to the nearest main road (m); distance to nearest road of the local network (m); SIZE, fragment size (ha); CORRIDOR, the distance to the nearest corridor (m); CONTINUOUS, the distance to the nearest tract of continuous forest >500 ha (m), and the three multivariate gradients of vegetation structure (PC1, PC2 and PC3).

Table 5
ANOVA models for the residual species number in fragments ($n = 40$ forest fragments) according to distance to the highway (four categories) and proximity to other paved roads, main roads (four categories), local network (three categories)[a]

Factor considered	d.f.	*F*	*P*	Variance explained (%)
Ubiquitous				
Distance to main road	2.31	0.71	N.S.	
Distance to road local network	3.31	0.93	N.S.	
Distance to highway	3.31	0.29	N.S.	
R^2				13
Forest generalists				
Distance to main road	2.31	1.65	N.S.	
Distance to road local network	3.31	1.25	N.S.	
Distance to highway	3.31	3.83	<0.05	
R^2				40
Forest specialists				
Distance to main road	2.31	0.08	N.S.	
Distance to road local network	3.31	0.08	N.S.	
Distance to highway	3.31	3.54	<0.05	
R^2				35

[a] Results are given for ubiquitous and forest species (both generalists and specialists taken separately).

independently of vegetation and landscape factors, fragments located further than 2 km from the highway contained on average 1–2 species more than fragments near it (Fig. 2). The pattern observed was the same independently of the side of the highway studied (Table 6), suggesting a strong consistency in the measured effect. The model for ubiquitous species remained non-significant (Table 6), suggesting that this group of birds is not or slightly affected by highway proximity.

Species specific models showed that none of the ubiquitous species studied was significantly affected

Table 6
ANOVA models for the residual species number present in fragments ($n = 40$ forest fragments) according to distance to the highway (four categories) and side of the highway (two categories)[a]

Factor considered	d.f.	*F*	*P*	Variance explained (%)
Ubiquitous				
Side	1.32	0.40	N.S.	
Distance to highway	3.32	0.41	N.S.	
Interaction	3.32	0.63	N.S.	
R^2				10
Forest generalists				
Side	1.32	1.39	N.S.	
Distance to highway	3.32	3.75	<0.05	
Interaction	3.32	2.51	N.S.	
R^2				45
Forest specialists				
Side	1.32	0.33	N.S.	
Distance to highway	3.32	4.47	<0.01	
Interaction	3.32	1.31	N.S.	
R^2				33

[a] Results are given for ubiquitous and forest species (both generalists and specialists taken separately).

by highway proximity (Table 7). Furthermore, the overall tendencies in the occurrence probability of this group (whether significant or not) did not differ from the expected random distribution (four species showed a tendency to appear less near the highway, three to appear more often, Sign-test, $Z = 0.00$, N.S.). However, 50% (four out of eight) of forest generalists and 50% of forest specialists (four out of eight) were significantly less likely to appear in fragments near the highway than in those further away after including other landscape and vegetation factors in the models (Table 7). In this case, the overall tendencies in the occurrence probability of species, including also non-significant tendencies, differed from an expected random distribution (Sign-test, $Z = 2.474$, $P < 0.05$). All forest species (eight forest generalists and eight forest specialists, Table 7) were more likely to be present in fragments further than 2 km from the highway.

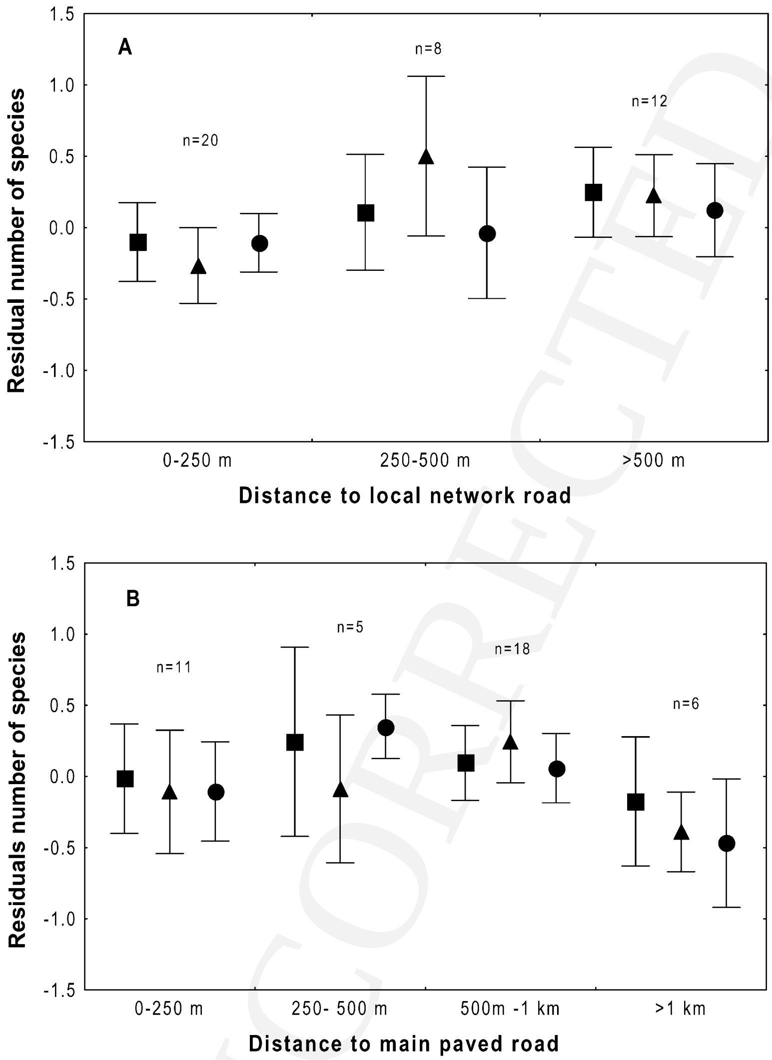

Fig. 2. Residual number of species, after vegetation and landscape variables have been accounted for, present in forest fragments at different distances from local network paved roads (A), main paved roads other than A2 highway (B) and A2 highway (C). The results are given for three different ecological groups of species: (●) ubiquitous species; (■) forest specialists species; (▲) forest generalist species. The number of fragments included in the analyses is included above the bars for each category.

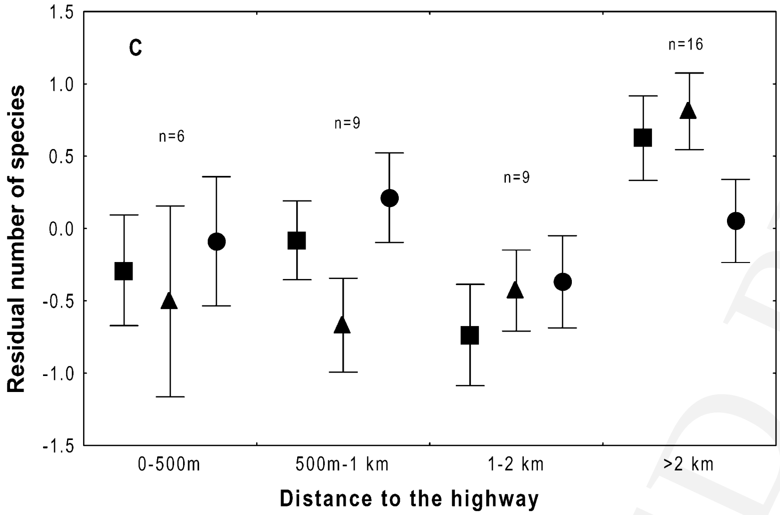

Fig. 2. (*Continued*).

4. Discussion

We showed that highway proximity diminishes probability of forest species occurrence in isolated forest fragments. We have shown that independently of factors related to habitat quality such as vegetation structure (see also López and Moro, 1997; Díaz et al., 1998), patch size and corridor connectivity (see also Opdam et al., 1985; Díaz et al., 1998), fragments near the highway contained a smaller number of forest species than those located further away. Compared with the effect induced by highway presence, the negative effects of other main roads for forest species was much lower and remained under detected, suggesting that effects on species occurrence in fragmented areas are dependent on the traffic load, size and location of the infrastructure (Forman and Alexander, 1998). However, some species such as the long-tailed tit or the wood pigeon did have lower occurrence probabilities near local network roads. On the other hand, proximity of main roads other than the highway had a positive effect on some ubiquitous species, such as the magpie or the house sparrow. Human activities are often concentrated along such main roads but not necessarily along highways, which are usually designed for long distance transport. Therefore, the presence of some ubiquitous species in forest fragments, often associated with human activities, may be indirectly favoured by road proximity.

Other studies have found negative effects of busy roads extending up to 1,000 m to the sides of the infrastructure (Van der Zande et al., 1980; Reijnen et al., 1995, 1996; Forman and Alexander, 1998). Roads with high traffic intensity have been identified as a major negative impact on habitat quality for several of forest bird species (Forman and Alexander, 1998). Direct visual disturbance or increased pollution near roads may affect habitat quality for forest bird species (Forman and Alexander, 1998). Also, noise load appears to have a major impact on forest bird populations since even small levels of noise affect bird song performance (Reijnen and Foppen, 1994; Reijnen et al., 1995, 1996). However, our study differs from previous ones in the larger extent in which we detected the negative effects of a busy highway. In our study, forest species occurrence seemed diminished in fragments located as far a 2 km from the highway. Different reasons may be behind this larger distance effect.

Noise effects expand further in open habitats (Reijnen et al., 1996). Therefore, its consequences on bird habitat quality may increase in agricultural areas in which small forest patches are embedded. Given that forests only occupy around 5% of the Penedès plain, the long-range effect of noise in open areas could partially explain why forest fragments located at relatively long distances form the highway contained less species. Further experimental studies should

Table 7
Step-wise logistic regression models for the probability of occupancy of forest fragments by each bird species as a function of the distance to the highway (DHIGHWAY, two levels, up to 2 km and further away), distance to other main roads (DMROAD, two levels, up to 500 m and further away), distance to other paved roads from the local network (DLROAD, two levels up to 500 m and further away), size of the fragment (SIZE (ha), log-transformed), the distance to the nearest corridor (CORRIDOR (m), log-transformed), the distance to the nearest tract of continuous forest (>100 ha, CONTINUOUS (m), log-transformed) and the three multivariate gradients of vegetation structure (PC1, PC2 and PC3)[a]

Bird species (species occurrence and highway proximity)	Variables included in the logistic regression model ($P < 0.05$)	Overall model classification (%)	χ^2	P
Copa (−)	CORRIDOR, PC3, CONTINUOUS, DLROAD−	66.20	14.23	<0.01
Sttu (−)	SIZE, PC1, PC2, DHIGHWAY−	100	33.20	<0.001
Upep (+)	SIZE, PC1, PC3	81.30	17.26	<0.0001
Pivi[*] (−)				
Tume (−)	CORRIDOR, SIZE, DHIGHWAY−	75.50	20.71	<0.0001
Trtr (−)	SIZE, PC1	88.30	30.84	<0.0001
Erru (−)	CORRIDOR, SIZE, PC1	100	44.90	<0.0001
Lume (−)	CONTINUOUS, SIZE, PC1, PC2, DHIGHWAY−	89.60	35.90	<0.0001
Syme (−)	PC3	63.56	8.90	<0.01
Syat (−)	CONTINUOUS, PC1, PC2, DHIGHWAY−	100	26.01	<0.001
Phbo (−)	SIZE, DHIGHWAY−	65.10	10.41	<0.001
Reig (−)	CORRIDOR, SIZE, PC1	100	41.36	<0.0001
Aeca (−)	SIZE, PC1, DLROAD−	100	36.43	<0.0001
Paca (−)	PC2	50.50	3.650	<0.05
Pacr (−)	CORRIDOR, SIZE, DHIGHWAY−	76.50	16.04	<0.001
Pama (−)	SIZA, PC2, DHIGHWAY−	83.90	23.90	<0.0001
Cebr (−)	SIZE, PC2	87.50	31.40	<0.0001
Pipi (+)	PC3, DMROAD+	74	14.08	<0.01
Gagl (−)	CORRIDOR, CONTINUOUS, SIZE, PC1	100	32.74	<0.0001
Pado (+)	SIZE, PC3, DMROAD+	66	9.41	<0.05
Sese[*] (−)				
Cach (−)	SIZE, PC3, DHIGHWAY−	72	15.17	<0.001
Caca (−)	PC1	58.92	6.80	<0.01
Emci (−)	DLROAD+	67.61	5.05	<0.05

[a] The percentage of fragments correctly classified as occupied [P (occupancy) >0.5] or unoccupied [P (occupancy) <0.5], as well as the significance level for the whole model, are also shown. Lower occurrences associated with highway proximity are designated with (−). See Table 1 for species abbreviations.

[*] No model containing any of the independent variables included was significant.

assess the exact role that noise may exert in avian communities inhabiting fragmented forests.

In agricultural landscapes, such as the one under study, forest patches are isolated to different degrees by a non-forest matrix, which makes interpatch movement difficult for forest birds (Bélisle et al., 2001). Some forest species are very reluctant to cross even small habitat gaps or open areas and often prefer to take longer paths through forested habitat (Desrochers et al., 1999). Indeed, we found that presence of forest specialists (but no that of generalists) was positively influenced by the proximity of riparian vegetation strips, possibly acting as dispersing corridors and suggesting a certain aversion of forest birds to use open areas for dispersal (Brotons and Herrando, 2001). Linear barriers such as heavily used roads may further decrease connectivity of remnant forest patches. In spite of their flying ability, some forest birds show a major resistance to busy road crossing (Forman and Alexander, 1998; Bélisle, personal communication). This may decrease dispersal movements at variable distances from the infrastructure and therefore, and diminish the arrival of new individuals to isolated forest patches near it. The role of busy roads as a factor decreasing landscape connectivity and therefore, diminishing probability of species presence in forest fragments seems supported by the long distance effect found in our study, on the limit of that attributable to other factors such as noise disturbance. Road magnitude and location may account for the lack of distance effect detected in other main roads compared to the highway. However, observational and experimental approaches are needed to study specific tendencies to cross roads of different widths and traffic loads, and to study hypothetical specific avoidance patterns during dispersal. Furthermore, birds which decide to cross a highway are more likely to be killed by the cars (Forman and Alexander, 1998) thus, diminishing individual dispersal abilities and further decreasing recolonisation probabilities of forest fragments near dangerous roads.

Our results have important implications in the conservation of fragmented populations affected by transport infrastructures. In fragmented agricultural landscapes under heavy human pressure, the size and quality of forest patches tend to decrease and landscape resistance tends to increase (Hinsley et al., 1995; Díaz et al., 1998). From a metapopulation perspective, roads, specially highways, seem an important factor behind this increase in landscape resistance. These transport infrastructures may shift balance between the rates of extinction and recolonisation to a point where, on average, a smaller number of patches is occupied (Opdam, 1991). First, proximity of high-density traffic roads may decrease the productivity of large and high quality forest fragments (i.e. source areas for forest species, Reijnen et al., 1996) thus, reducing individual flow towards other forest patches available (Días, 1996). Second, high-density traffic roads may also decrease habitat quality and immigration probability into isolated patches, which will be then more prone to species extinction. As the proportion of empty patches increases, the survival probability of the species in the landscape, as measured by metapopulation dynamics, will decrease (Hanski, 1998). Therefore, harmful effects of road proximity on forest bird metapopulations may be magnified in isolated forests, in which their long-term viability may become increasingly difficult.

In the Mediterranean agricultural areas, forest fragments are often important refuges for forest species that would be otherwise missing from local species pool (Tellería, 1992, Tellería and Santos, 1994). Special attention should, therefore, be taken when building linear infrastructures such as highways in the proximity of forest isolates, and specific actions should be carried out on already constructed highways to alleviate the negative effects of car circulation and infrastructure location on breeding avifauna (Reijnen et al., 1995).

Acknowledgements

Jacint Nadal, Carme Rosell and three anonymous referees commented previous drafts of the manuscript. This study is included in the research carried out by the Grup de Recerca de Qualitat 1198 of the University of Barcelona and received financial support from the CAICYT (PB-96-0224), the Museu de Gavà and the Generalitat de Catalunya (''Ajut ACOM''). Sergi Herrando received financial support from the Comissionat per a Universitats i Recerca de la Generalitat de Catalunya. Lluís Brotons was granted by ''Fundación Ramón Areces'' during the elaboration of the manuscript.

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