

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

Threshold distances to nearby cities and roads influence the bird community of a mosaic landscape

D. Palomino^{a,*}, L.M. Carrascal^b

^aUnit of Bird Study and Monitoring, Spanish Society of Ornithology (SEO/BirdLife), C/Melquiades Bencinto 34, 28053 Madrid, Spain

^bDepartment of Biodiversity and Evolutionary Biology, National Museum of Natural History (CSIC), C/José Gutiérrez Abascal 2, 28006 Madrid, Spain

ARTICLE INFO

Article history:

Received 22 January 2007

Received in revised form

23 July 2007

Accepted 26 July 2007

Available online 14 September 2007

Keywords:

Abundance

Birds

Environmental impact

Road network

Species richness

Urban ecology

ABSTRACT

Urban developments and road networks extend their impacts on the surrounding habitats along a variable distance, affecting birds living in natural environments. This study identifies the threshold distances upon which several cities and roads, located across a large mosaic landscape of ca. 300 km² in central Spain, alter the abundance patterns of the native avifauna. Total species richness, total bird abundance, and abundance of different guilds of birds which are potentially sensitive to human disturbances were modelled by means of tree regression analyzes. Nearby cities do not affect the total bird species richness in natural habitats of the study region. Total bird abundance increases near urban areas, mainly through its positive influence on urban-exploiter species. The effect of roads is negative and highly generalized, although threshold distances to roads vary among different groups of species. The bird communities of deciduous woodlands (ash groves, oak patches and poplars) show higher resilience to deleterious influences from nearby cities and roads. It would be desirable not to build new scattered urban developments within the remnant natural areas of this heavily fragmented region, because their existence and connection to the nearby cities by new roads would add 'invisible' negative effects on the native bird fauna (e.g. on some threatened species from open habitats), considering the buffer distances determining most significant impacts (400 m for urban areas, and 300 m for roads).

© 2007 Elsevier Ltd. All rights reserved.

1. Introduction

Because transport networks increase parallel to urbanization, roads and urban developments are usually treated like surrogate components in environmental assessments of anthropic disturbance (e.g. Bolger et al., 1997; Hennings and Edge, 2003; Fraterrigo and Wiens, 2005). However, the effects on ecosystems of impacts from urban or road origins may be very different (e.g. Sauvajot et al., 1998; Gutzwiller and Barrow, 2003; Zeng et al., 2005), and they may require different management to minimize deleterious impacts. With regard to the avifauna, urban developments stress the biotic homoge-

nization of the community (e.g. Beissinger and Osborne, 1982; Blair, 1996; Marzluff, 2001; Crooks et al., 2004; Clergeau et al., 2006; McKinney, 2006; Palomino and Carrascal, 2006), and act as sink-habitats for some populations (e.g. Vierling, 2000; Solonen, 2001; see a review on urban effects on the avifauna in Chace and Walsh (2006)). Moreover, roads also have several negative impacts on avian communities (Bennett, 1991; Forman and Alexander, 1998; Spellerberg, 1998), such as high mortality rates from car collisions in some populations (e.g. Mumme et al., 2000), the alteration of the distribution patterns of breeding birds due to the constant noise from cars (e.g. Reijnen et al., 1995; Kuitunen et al., 1998; Peris and

* Corresponding author. Tel.: +34 4340910.

E-mail address: dpalomino@seo.org (D. Palomino).

0006-3207/\$ - see front matter © 2007 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2007.07.029

Pescador, 2004), and the barrier-effects preventing the normal movements of birds (e.g. Bélisle and St.Clair, 2001).

The impact of each road/city may extend to surrounding habitats tens or thousands of meters, depending either on the type of disturbed habitat or the specific characteristics of the road/city (e.g. Forman et al., 2002; Reijnen et al., 1996). The effective buffer distance will also vary among organisms with different ecological characteristics and tolerance to disturbances (e.g. Findlay and Houlahan, 1997; Sauvajot et al., 1998). Therefore, a suitable management of city/road impacts requires study cases: (1) separating the distance effects from urban developments and roads; (2) covering a spatial extent large enough for allowing regional generalizations; and (3) considering a diverse array of organisms differing in their degree of sensitivity to anthropic impacts.

The northwestern part of Madrid province (central Spain) suffers from an intense urban pressure due to the housing demand of weekend residences, mostly by people living in the nearby large metropolitan area of Madrid city (approx. 3.5 million people, 40 km away). Urban sprawl and road development are currently primary features of the ecosystems of this region of ca. 300 km². However, the precise effects of this process on the regional conservation concerns is poorly known, especially considering the ongoing project of a large natural reserve in this area, where a more stringent control of negative effects from nearby roads/cities must be addressed (Ramp et al., 2006). This study identifies the threshold distances upon which several cities and roads alter the abundance and species richness patterns of the native avifauna,

comparing different groups of birds which are potentially sensitive to human disturbances.

2. Materials and methods

2.1. Study area and bird censuses

The study region is located in the southern slopes of the Guadarrama Range, of cold mediterranean–continental climate, with mean temperature and rainfalls during springtime of 14.5 °C and 130 mm, respectively. This area is a mosaic landscape of interspersed patches of forest of various seral stages, diverse shrubland types, and pastures, among 12 cities (Guadarrama, Los Molinos, Cercedilla, Alpedrete, Collado Mediano, Navacerrada, Becerril, Mataelpino, El Boalo, Moralarzal, Cerceda, and Manzanares) and several small developments, connected to each other by a dense road network (Fig. 1). These cities have a relatively homogeneous size (mostly 1–4 km² and 1,600–11,600 inhabitants in 2006), comprising several urban typologies such as densely built-up commercial cores, four- to seven-storey block buildings, small terraced-houses, and well-gardened detached houses (for more details see Palomino and Carrascal, 2006). The road network consists of narrow two-lane roads, 7–10 m wide, with a moderate traffic volume averaging 300 vehicles/h (obtained from direct field measurements during sampling days).

Bird censuses were assessed during May and early June (breeding season for all species) of four consecutive years

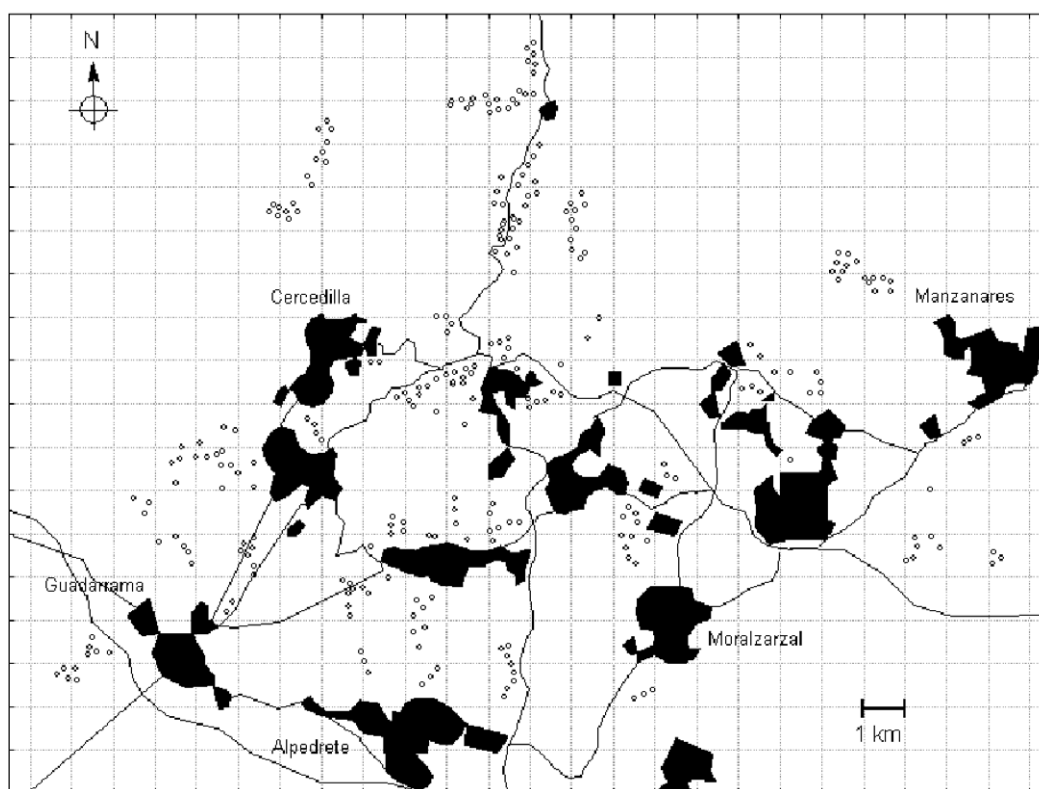


Fig. 1 – Study area, showing the urban developments (black patches, with the name of some cities), the road network (lines) and the 276 sampling plots performed (dots).

(2001–2004), by means of single-visit point-counts, 20 min long each, recording all birds heard or seen within 50 m radius. Overflying birds were not considered. A total number of different 276 census plots were obtained in the four years (every plot was censused during only one year to maximize a wide regional coverage). The censuses were carried out by the same person (DP) on windless and rainless weekdays, between sunrise and 1100 h GMT in the morning, or between 1800 h GMT and sunset in the evening. Data of early morning and late afternoon censuses were pooled as there were no statistical differences between these two time periods in the response and predictor variables ($p > 0.1$). The census plots were separated at least 200 m from each other, and located in order to include homogeneous habitat types of the study area. These main habitat types were scots/cluster pine forest (*Pinus sylvestris/pinaster*), Pyrenean oak forest (*Quercus pyrenaica*), Holm oak forest (*Quercus rotundifolia*), narrow-leaved ash grove (*Fraxinus angustifolia*), shrubland (mainly of genus *Cistus* and *Genista*), and pastureland. However, ecotonal habitats were also sampled to attain a better gradient of the environmental diversity of this highly fragmented region. Each sampling plot was georeferenced with a Garmin 12 GPS (precision of 1 m by means of the average location function). Censuses of the different natural environments considered were spanned throughout the study period, avoiding censusing certain habitats in only 1 year. We did not observe any clear interannual variation in bird abundance of the study species, so we pooled all the censuses obtained during all the years.

Habitat structure was sampled within a radius of 25 m centered in each census plot, immediately before the beginning of bird counts. The observer remained quietly in the center of the plot while conducting habitat structure measurements (approx. 2–4 min). The same protocol was used in the 276 plots censused. We estimated by eye, after training, the following features of the habitat: percentage cover of rocky outcrops, of herbaceous, shrub and tree canopy layers, average height of the shrub and tree canopy layers, and number of trees with trunks 5–10, 10–30 and >30 cm wide at breast height, used for calculating mean trunk-diameter of trees. The vegetation of deciduous trees and bushes was fully leafed-out when habitat sampling was carried out. Binomial variables were used to codify the absence (0) or the presence (1) of predominant tree cover (coniferous, sclerophyllous or deciduous), as well as the presence of water (pools or streams). The distances between each sampling plot and the border of the nearest city (established by the perimeter defined by houses) and road were measured on 1:25,000-scale maps. Table 1 shows the mean and range values of the variables across the 276 point-count censuses. These variables were used as predictors in the modelling of the species richness and the bird abundance per sampling plot.

Particular subsets of species were also analyzed separately, to test their tolerance to city/road disturbances. Because recovery actions should prioritize the preservation of taxa of conservation concern, the richness per sampling plot of species with problematic levels of European threat status was modelled (*threatened species*, hereafter, grouping the 22 species with SPEC index = 1, 2 or 3; BirdLife International, 2004). On the basis of the results from a previous study on birds within the urban environments of the study region, the total abun-

Table 1 – Basic descriptive statistics of the variables measured per sampling plot (n = 276)

	Mean ± Std.Err.	Min–Max
<i>Predictor variables</i>		
ALT	1245 (16)	(887–1883)
Presence of deciduous trees	0.42 (0.03)	(0–1)
Presence of sclerophyllous trees	0.16 (0.02)	(0–1)
Presence of coniferous trees	0.46 (0.03)	(0–1)
Presence of water	0.16 (0.02)	(0–1)
ROADdist	1062 (71)	(20–5200)
URBdist	1285 (60)	(60–3900)
%ROC	4.2 (0.5)	(0–65)
%HER	54.5 (1.9)	(0–100)
%SHR	18.5 (1.3)	(0–95)
%TREE	36.0 (1.6)	(0–90)
hSHR	1.1 (0.0)	(0–2.5)
hTREE	10.3 (0.3)	(0–23)
ØTREE	20.4 (0.6)	(0–48)
<i>Response variables</i>		
Species richness	9.1 (0.2)	(1–21)
Total bird abundance	11.6 (0.4)	(1–50)
Urban-exploiter birds	1.1 (0.2)	(0–42)
Urban-avoider birds	8.1 (0.3)	(0–28)
Threatened birds	1.7 (0.1)	(0–6)
Corvid birds	1.1 (0.1)	(0–22)

ALT: altitude a.s.l. (m); ROADdist: distance to nearest road (m); URBdist: distance to nearest city (m); %ROC: amount of rock cover; %HER: amount of herbaceous cover; %SHR: amount of shrub cover; %TREE: amount of tree cover; hSHR: mean height of the shrub layer (m); hTREE: mean height of the tree layer (m); ØTREE: mean diameter at breast height of the tree trunks (cm). All the response variables are expressed in number of individuals, except 'species richness' and 'threatened birds' that are number of species.

dances per sampling plot of *urban-exploiter* and *urban-avoider* species were examined (6 and 36 species, respectively; urban-exploiter and urban-avoider species were defined by Palomino and Carrascal (2006) for the study area according to significant $-p < 0.05$ – differences comparing pooled natural habitats versus urban environments). Finally, the total abundance per sampling plot of *corvids* was also studied (grouping six species: *Corvus corax*, *Corvus corone*, *Corvus monedula*, *Cyanopica cooki*, *Garrulus glandarius* and *Pica pica*). These species are opportunistic birds with an *a priori* large adaptability to human disturbances. The Appendix shows the list of all species censused and the subsets in which they were included.

2.2. Statistical analyzes

Regression trees were used to analyze the influence of habitat features on bird parameters. This kind of analysis allows the interpretation of datasets where there are complex nonlinear relationships between response and predictor variables, and/or high-order interactions among predictor variables (Venables and Ripley, 1994; De'ath and Fabricius, 2000). Instead of defining a unique linear pattern affecting the whole pool of samples, regression trees identify successive critical values of predictors splitting the response variable in a dichotomous hierarchical manner. This is particularly useful for the scope of this work, because regression trees can show the threshold

distances to cities/roads to which birds are sensitive, as well as their relative importance compared to other environmental factors. In order to avoid excessively complex tree models, the following stopping rules were applied in tree growth: (1) models having only six terminal tips (i.e. five splitting criteria), (2) division subsets including 10 or more cases (i.e. sampling plots), and (3) statistically significant reductions in the group heterogeneity after each subdivision (testing residual deviance according to a χ^2 -test).

3. Results

All of the regression trees obtained included the distances to nearest city and/or road as a significant criterion. Hereafter, we make brief descriptions of the patterns shown in Figs. 2–7 for each bird parameter, focusing on the particular influences of both disturbance variables.

The tree model on the total species richness per sampling plot accounted for 31.4% of original variability ($\chi^2 = 882$; d.f. = 5; $p < 0.001$; Fig. 2). The total number of species was negatively influenced by the distance to the nearby roads: the plots with the lowest mean species richness (averaging 5.8 species/0.8 ha) were those lacking deciduous tree cover and located at less than 110 m from roadsides. On the contrary, the highest mean species richness (12.2 species/0.8 ha) was measured in deciduous woodlands located above 1030 m a.s.l., with a well developed shrub layer (shrub height > 1 m).

The tree model analyzing the number of species under European conservation concern accounted for 35.3% of original deviance ($\chi^2 = 195.7$; d.f. = 5; $p < 0.001$; Fig. 3). The sampling plots with the largest number of these species (averaging 3.7 species/0.8 ha) were almost totally treeless (tree cover < 3%). Conversely, the lowest species richness of this group of birds was found in mature woodlands (tree cover > 20%, and aver-

age tree height > 13 m). Distance to the nearest road had a negative influence in open woodland areas (tree cover: 3–20%), as the number of threatened species considerably decreased from 2.2 to 1.2 species/0.8 ha if roads were located at less than 400 m.

The tree model on total bird abundance accounted for 32.2% of original variability ($\chi^2 = 3316$; d.f. = 5; $p < 0.001$; Fig. 4). The highest bird abundance (averaging 24.5 birds/0.8 ha) was recorded in areas with deciduous trees, at intermediate distances from the nearest road (290–540 m), and with shrubs taller than 1.4 m. The negative influence of roads nearer than 290 m on bird abundance was mitigated if distance to urban developments was lower than 350 m. The minimum abundances of the study region were reached closer to roads, but farther from cities (8.9 birds/0.8 ha).

The regression tree describing the variability in abundance of urban-exploiters accounted for 34.4% of original deviance ($\chi^2 = 1034$; d.f. = 5; $p < 0.001$; Fig. 5). The most influential predictor was urban distance: the maximum abundance of these birds (averaging 10.0 birds/0.8 ha) was found in plots located at less than 190 m from a city, with tree cover lower than 17%. Farther than 190 m from cities, these species were almost absent, especially above 1070 m a.s.l. (averaging 0.3 birds/0.8 ha). When distance to the nearest urban development was farther than 390 m, the abundance of urban-exploiters increased if there were roads at less than 510 m.

With regard to the urban-avoider species, the tree regression model accounted for 32.8% of the original variability in their abundance ($\chi^2 = 1749$; d.f. = 5; $p < 0.001$; Fig. 6). The lowest abundances (4.1 birds/0.8 ha) were measured at sites with tree height lower than 5.4 m. Other variables positively affecting the abundance of urban-avoider species were altitude and the cover of the shrub and herbaceous layers. The roads located at less than 60 m had a negative impact on the

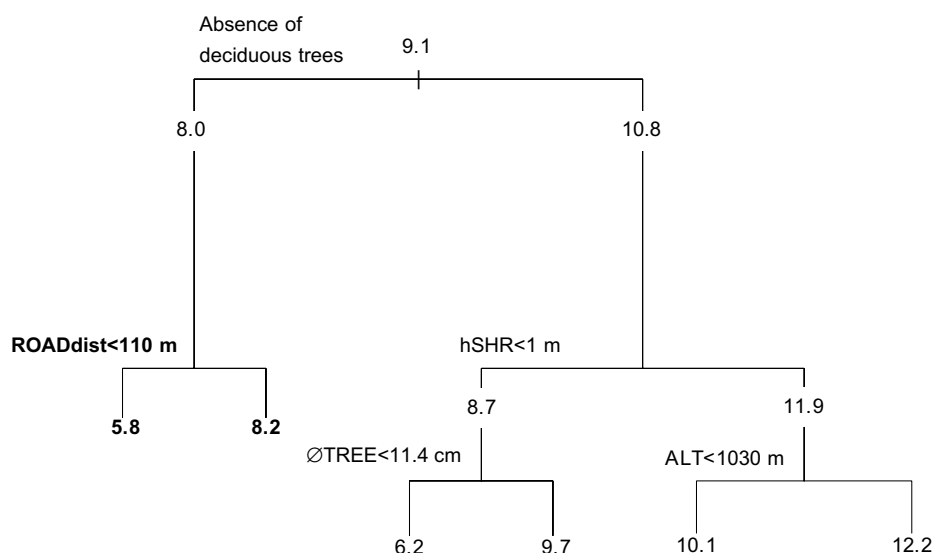


Fig. 2 – Regression tree model analyzing total species richness per census plot (0.8 ha). Splitting criteria indicate the conditions met for the left branches (the opposite applies for the right branches). At the top of the tree is showed the mean richness or abundance of all sites combined. The rest of the numbers are mean richness figures under previous condition. Length of the branches are proportional to deviance explained by each split (minimum of 10 sampling plots at each resulting subdivision). All of the dichotomies are statistically significant ($p < 0.01$). When present, effects of city/road distances are emphasized in bold. See Table 1 for variable names.

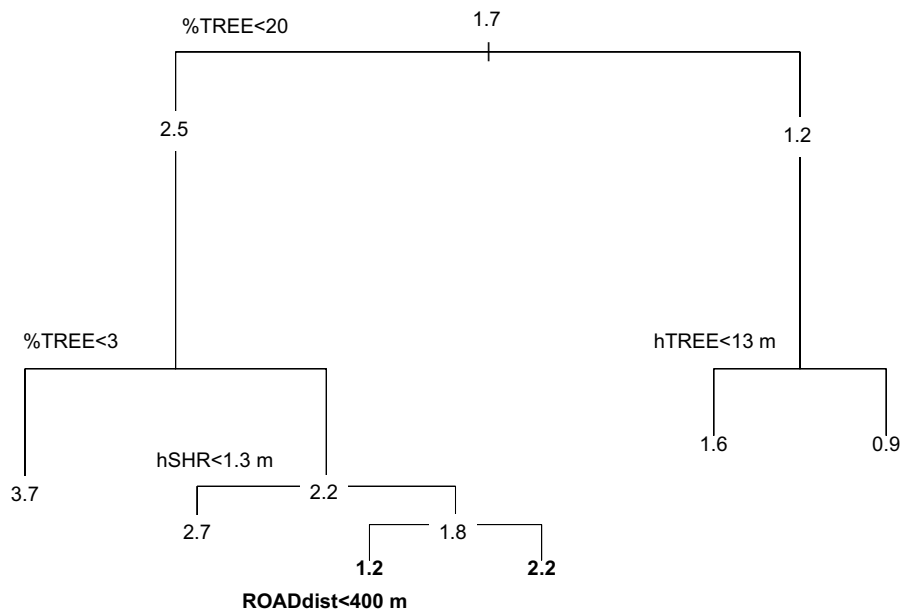


Fig. 3 – Regression tree model analyzing number of threatened species at an European level per census plot (0.8 ha). See Fig. 2 for details.

abundance of urban-avoider species. No threshold distances to cities entered the tree model.

Finally, the regression tree obtained for the abundance of corvids explained 26.1% of the original variability among plots ($\chi^2 = 274$; d.f. = 5; $p < 0.001$; Fig. 7), and showed that these birds were more abundant at shorter distances from cities (<630 m). On the contrary, either in favourable or less optimal conditions for these species (mainly depending on altitude), total corvid abundance was negatively influenced by distance to roads, with threshold distances ranging from 190 to 490 m.

4. Discussion and conclusions

The proximity to cities and roads are important determinants of the native bird diversity in the study area, even though these two simple measures of potential disturbance constitute a minor number of variables with respect to other habitat descriptors of the natural environment. As a general rule, the significant threshold distances in the models averaged 400 m for cities, and 300 m for the roads, although these figures varied among different bird parameters. This paper shows some

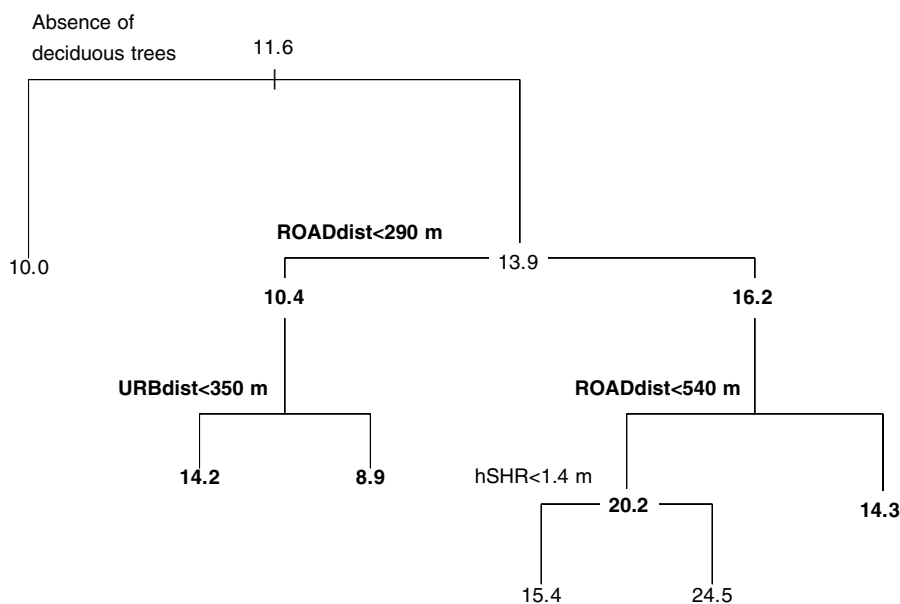


Fig. 4 – Regression tree model analyzing total bird abundance per census plot (0.8 ha). See Fig. 2 for details.

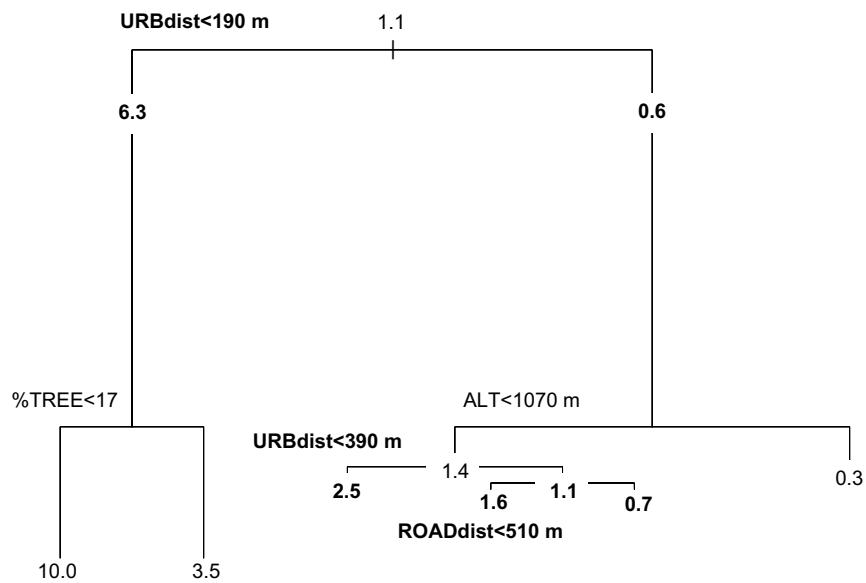


Fig. 5 – Regression tree model analyzing abundance of urban-exploiter birds per census plot (0.8 ha). See Fig. 2 for details.

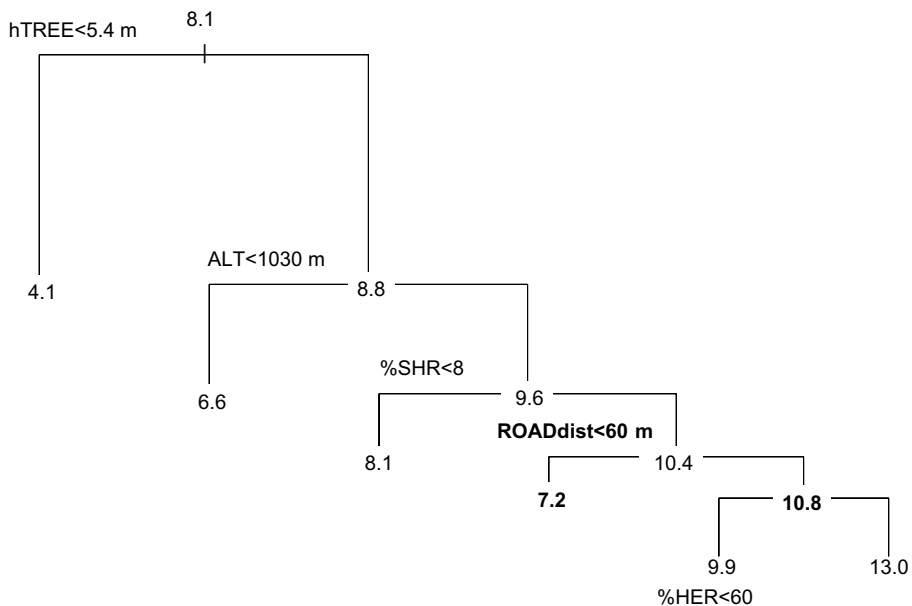


Fig. 6 – Regression tree model analyzing abundance of urban-avoider birds per census plot (0.8 ha). See Fig. 2 for details.

interesting distinctions between the influence of roads and cities on bird diversity and that these effects varied according to the groups of birds considered.

The relatively short threshold distances found in this paper could suggest that impacts are not too severe, since avian disturbances extending outward thousands of meters have been already reported (Reijnen et al., 1996). However, it must be noted that all negative effects detected are highly significant, even though the studied cities are still not too large nor the roads too busy (when compared with nearby regions in the province of Madrid). On the other hand, these buffer distances, in such a densely developed landscape matrix, en-

tail a severe fragmentation of the suitable habitat for the native avifauna.

Nearby cities do not affect the total bird species richness in natural habitats of the study region, but total bird abundance increases with the reduction of the distance to the nearest urban development. Notably, urban surroundings support elevated abundances of urban-exploiters and corvids. The mere presence of a city nearer than 190 m entails a 10-fold increase in bird abundance of the species which are highly adapted to the urban environment, irrespective of habitat type. Although the number of species included in these two groups of species is relatively low (only 12 species out of 70

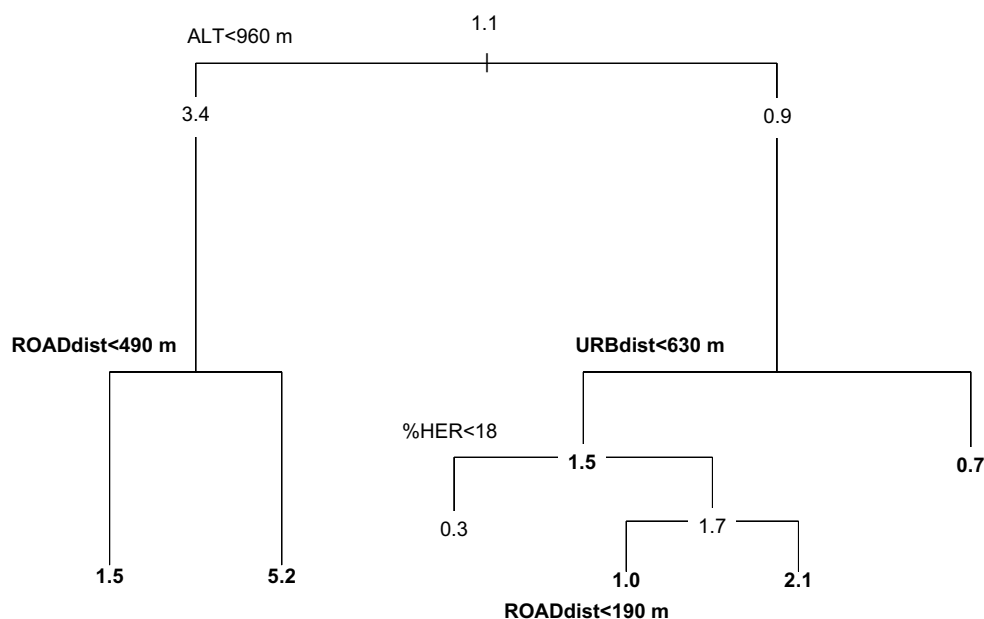


Fig. 7 – Regression tree model analyzing abundance of corvid birds per census plot (0.8 ha). See Fig. 2 for details.

detected in censuses), they constitute an important amount of all individual birds recorded (27%). This peri-urban pattern of increased bird abundance due to the overabundance of just a few species mirrors the effect usually found inside the urban habitats (Beissinger and Osborne, 1982; Blair, 1996; Clergeau et al., 1998; Melles et al., 2003; Crooks et al., 2004; Sandström et al., 2006). Therefore, this study points out that the biotic homogenization, which is a typical threat from the urban developments (McKinney, 2006), spreads over the habitats surrounding the cities hundreds of meters away (see also Odell and Knight, 2001).

With regard to enhanced corvid numbers near the cities, several previous works show similar effects related to other human disturbances (e.g. Gutzwiller et al., 2002; Storch and Leidenberger, 2003; Neatherlin and Marzluff, 2004), and more specifically with urbanization (e.g. Konstantinov et al., 1996; Russo and Young, 1997; Marzluff et al., 2001). Therefore, the higher abundance of corvids in the vicinity of urban developments in the study area, is not surprising. Nonetheless, a previous study in this region (Palomino and Carrascal, 2006) showed that no corvid species was denser inside urban than in natural habitats. Hence, a particular finding from this study is that these birds benefit from the ecotonal conditions surrounding the cities, although apparently they occupy the urban environment itself with a lower intensity. This pattern could entail conservation concerns, as several works have identified that corvids act like opportunistic avian nest predators (e.g. Andrén, 1992; Groom, 1993; Engels and Sexton, 1994; Gutzwiller et al., 2002), and their overabundance around the cities could be another deleterious factor affecting other bird species.

The studies dealing with the effects of roads on bird diversity report either diminished (e.g. Reijnen et al., 1995; Kuitunen et al., 1998; Forman et al., 2002) or enhanced bird values, the latter mostly taking place when road verges support a well-developed vegetation layer increasing local habitat het-

erogeneity (Arnold and Weeldenburg, 1990; Camp and Best, 1993; Leach and Recher, 1993; Meunier et al., 1999). This study shows that the species impoverishment caused by nearby roads is not generalizable to different habitats. Pinewoods, shrublands and pastures support a lower species richness when a road is less than 110 m away. Nevertheless, the areas having deciduous tree cover (oakwoods and ash parklands) are not negatively affected by nearby roadsides. From a perspective of landscape restoration, the observed resilience of bird species in deciduous habitats to impacts from existing roads supports afforestations with oaks and ashes, rather than the currently prevailing pine plantations.

Nevertheless, total bird abundance in deciduous woodlands peaks at intermediate distances from roads (290–540 m; Fig. 3). Many birds may become attracted to roadsides due to edge effects, if the availability of any relevant resource is remarkably higher in the road margins than in sites away from these habitat borders (e.g. Laursen, 1981; Warner, 1992; Meunier et al., 1999). We found there is a higher availability of deciduous tree cover near the roads (Fig. 8), which is the feature with most positive influence on the bird community of the study region. The reason behind this is probably the fact that poplars and ashes are used like natural barriers separating private lots from roads, and/or that environmental conditions next to roadsides are more favourable for the development of woody species (higher soil moisture from drainage ditches, lower slope of the terrain, less livestock). However, because at too short distances from roads the advantages of high tree cover could be counteracted by noise disturbance and/or collision risk during regular movements, total bird abundance raises with the distance to the road (Fig. 8).

Threshold distances to roads vary among different groups of species. The negative effects from road presence vanish at low distances in the urban-avoider species (60 m). Consequently, the road network should not constitute a severe disturbance, particularly for those common urban-avoider

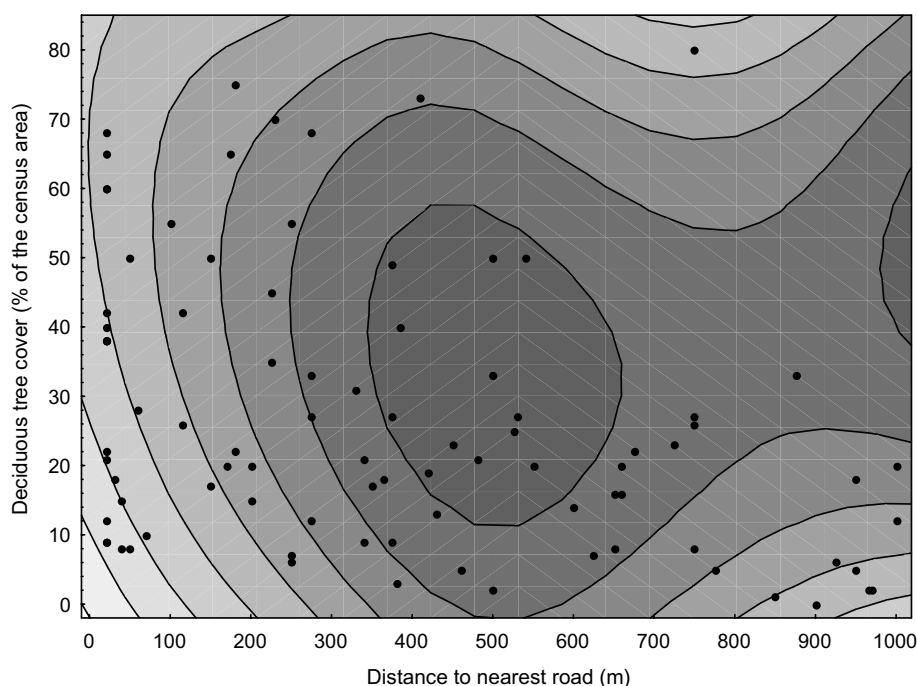


Fig. 8 – Relationship between amount of deciduous tree cover, road distance, and bird abundance at each sampling plot (the higher the abundance of birds per 0.8 ha, the darker the grey colour).

species such as *Certhia brachydactyla*, *Erithacus rubecula*, *Fringilla coelebs*, *Parus ater*, *Parus major* and *Sylvia atricapilla*. On the contrary, the group of species with endangered levels of European conservation status suffers from road presence as far as 400 m. Predominant among these threatened species are those preferring open rather than wooded habitats (e.g. *Carduelis cannabina*, *Coturnix coturnix*, *Emberiza cia*, *Galerida cristata*, *Miliaria calandra*, *Saxicola torquata* or *Sylvia undata*). Reijnen et al. (1996) and Forman et al. (2002) have found that roads have an important impact on determining bird values hundreds of meters away in grasslands and shrublands, probably because of the easier noise propagation in treeless habitats. Hence, our results show that species with higher conservation concern deserve special attention with regard to the potential habitat degradation from excessive road density in open country.

Although some works have shown that corvids are particularly prone to visit road verges, mostly searching for carcasses from collisions with vehicles (e.g. Dean and Milton, 2003; Kristan et al., 2004), this study points out that corvids are more abundant far from roads. Breeding individuals in the study region probably prioritize nesting requirements for choosing their territories, avoiding during this period the threats and disturbances linked to roads, including the presence of opportunistic raptors and carnivores prowling around ditches (Meunier et al., 2000). Moreover, most corvids found dead in roads usually are immature and inexperienced individuals searching for predictable food, but whose risky foraging largely predispose themselves to car collisions (Burger and Gochfield, 1992; Mumme et al., 2000).

The group of urban-exploiter birds is the only one showing a positive relationship with roads, probably because most of

the disturbances linked to roads do not differ from those they regularly bear in cities. Many isolated infrastructures, where these species appear, require road accesses which could cause the subtle relationship observed. Furthermore, some urban species could become attracted to roads because they can be used as dispersal corridors between nearby cities (e.g. Lipp et al., 2004; Peris and Pescador, 2004), a common phenomena in other taxa with invasive characteristics (e.g. Brown et al., 2006).

In summary, the preservation of areas free from deleterious influences of cities/roads is needed to maintain a more diverse assemblage of native species. This is particularly important with regard to deciduous patches of the study area, because they favour the overall avifauna in the region, but also with regard to grasslands and shrublands, which favour the most threatened species. Considering the dense network of roads and the high interspersion of urban areas in this region, it would be desirable not to build new scattered urban developments within the remnant natural areas. The presence in the environment and their connection to the nearby cities by new roads would add 'invisible' negative effects on the native bird fauna living in the heavily fragmented landscape of this region, considering the buffer distances determining most significant impacts (300–400 m).

Acknowledgements

Ana Aranda and Claire Jasinski kindly improved the English of the manuscript with their comments. This paper is a contribution to the project 07M/0080/2002 funded by the Consejería de Educación de la Comunidad de Madrid. David Palomino was supported by an "El Ventorrillo" Field Station-CSIC grant.

Appendix

List of all species censused (in brackets, the number of sampling plots where they were present and the mean density on them – birds/0.8 ha –, respectively) and the subsets in which they were included. uex: urban-exploiter; uav: urban-avoider; thr: threatened species at an European level; cor: corvids.

*Aegithalos caudatus*_{uav} (16; 2.6)
*Alectoris rufa*_{thr} (4; 1.3)
*Anthus trivialis*_{uav} (3; 1.3)
*Carduelis cannabina*_{thr} (5; 3.4)
Carduelis carduelis (9; 1.7)
*Carduelis chloris*_{uex} (16; 1.4)
*Certhia brachydactyla*_{uav} (104; 1.3)
*Cettia cetti*_{uav} (11; 1.1)
*Columba livia*_{uex} (4; 2.5)
Columba oenas (2; 2.0)
*Columba palumbus*_{uav} (33; 1.4)
*Corvus corax*_{cor} (4; 4.0)
*Corvus corone*_{uav cor} (14; 1.4)
*Corvus monedula*_{uav cor} (4; 7.5)
*Coturnix coturnix*_{thr} (3; 1.0)
*Cuculus canorus*_{uav} (15; 1.1)
*Cyanopica cooki*_{uav cor} (25; 2.2)
*Dendrocopos major*_{uav} (19; 1.1)
*Emberiza cia*_{thr} (7; 1.4)
*Emberiza cirulus*_{uav} (10; 1.6)
*Erithacus rubecula*_{uav} (129; 1.4)
*Ficedula hypoleuca*_{uav} (11; 1.1)
*Fringilla coelebs*_{uav} (191; 2.0)
*Galerida cristata*_{thr} (1; 1.0)
*Garrulus glandarius*_{uav cor} (31; 1.3)
*Hippolais polyglota*_{uav} (23; 1.1)
*Hirundo rustica*_{uex thr} (5; 1.6)
*Lanius excubitor*_{thr} (7; 1.3)
*Lanius senator*_{thr} (4; 1.0)
Loxia curvirostra (7; 1.4)
*Lullula arborea*_{uav thr} (23; 1.3)
*Luscinia megarhynchos*_{uav} (62; 1.3)
*Merops apiaster*_{thr} (4; 6.3)
*Miliaria calandra*_{uav thr} (28; 1.5)
Motacilla alba (2; 1.5)
Motacilla cinerea (2; 1.0)
*Muscicapa striata*_{thr} (1; 1.0)
*Oriolus oriolus*_{uav} (26; 1.2)
*Parus ater*_{uav} (94; 2.2)
*Parus caeruleus*_{uav} (54; 1.4)
*Parus cristatus*_{uav thr} (67; 1.3)
*Parus major*_{uav} (85; 1.4)
*Passer domesticus*_{uex thr} (26; 5.3)
*Passer montanus*_{uav thr} (11; 2.2)
Petronia petronia (5; 1.8)
*Phoenicurus ochruros*_{uex} (1; 1.0)
*Phylloscopus bonelli*_{uav thr} (54; 1.7)
Phylloscopus collybita (4; 1.0)
*Pica pica*_{cor} (69; 2.0)
*Picus viridis*_{uav thr} (32; 1.1)
*Regulus ignicapillus*_{uav} (48; 1.3)

Regulus regulus (27; 1.3)
*Saxicola torquata*_{uav thr} (7; 1.5)
Serinus citrinella (10; 1.3)
*Serinus serinus*_{uex} (92; 1.5)
*Sitta europaea*_{uav} (17; 1.2)
Streptopelia decaocto (1; 1.0)
*Streptopelia turtur*_{uav thr} (17; 1.3)
Sturnus unicolor (39; 3.5)
*Sylvia atricapilla*_{uav} (72; 1.3)
Sylvia borin (8; 1.1)
*Sylvia cantillans*_{uav} (28; 1.3)
Sylvia communis (7; 1.3)
*Sylvia hortensis*_{thr} (1; 1.0)
Sylvia melanocephala (5; 1.0)
*Sylvia undata*_{thr} (5; 1.6)
*Troglodytes troglodytes*_{uav} (53; 1.1)
Turdus merula (129; 1.4)
*Turdus viscivorus*_{uav} (16; 1.3)
*Upupa epops*_{uav thr} (14; 1.2)

REFERENCES

- Andrén, H., 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73, 794–804.
- Arnold, G.W., Weeldenburg, J.R., 1990. Factors determining the number and species of birds in road verges in the Wheatbelt of Western Australia. *Biological Conservation* 53, 295–315.
- Beissinger, S.R., Osborne, D.R., 1982. Effects of urbanization on avian community organization. *Condor* 84, 75–83.
- Bélisle, M., St.Clair, C.C., 2001. Cumulative effects of barriers on the movements of forest birds. *Conservation Ecology* 5, 9 <http://www.consecol.org/vol5/iss2/art9/> (online, last access: January 2007).
- Bennett, A.F., 1991. Roads, roadsides and wildlife conservation: a review. In: Saunders, D.A., Hobbs, R.J. (Eds.), *Nature Conservation 2: The Role of Corridors*. Surrey Beatty and Sons, Chipping Norton, pp. 99–117.
- BirdLife International, 2004. *Birds in the European Union: A Status Assessment*. BirdLife, Wageningen.
- Blair, R.B., 1996. Land use and avian species diversity along an urban gradient. *Ecological Applications* 6, 506–519.
- Bolger, D.T., Scott, T.A., Rotenberry, J.T., 1997. Breeding bird abundance in an urbanizing landscape in coastal southern California. *Conservation Biology* 11, 406–421.
- Brown, G.P., Phillips, B.L., Webb, J.K., Shine, R., 2006. Toad on the road: use of roads as dispersal corridors by cane toads (*Bufo marinus*) at an invasion front in tropical Australia. *Biological Conservation* 133, 88–94.
- Burger, J., Gochfield, M., 1992. Vulnerability and mortality of young Australian Magpies on roads. *Wilson Bulletin* 104, 365–367.
- Camp, M., Best, L.B., 1993. Bird abundance and species richness in roadsides adjacent to Iowa rowcrop fields. *Wildlife Society Bulletin* 21, 315–325.
- Chace, J.F., Walsh, J.J., 2006. Urban effects on native avifauna: a review. *Landscape and Urban Planning* 74, 46–69.
- Clergeau, P., Croci, S., Jokimäki, J., Kisanlahti-Jokimäki, M-L., Dinetti, M., 2006. Avifauna homogenisation by urbanisation: analysis at different European latitudes. *Biological Conservation* 127, 336–344.

- Clergeau, P., Savard, J.P.L., Mennechez, G., Falardeau, G., 1998. Bird abundance and diversity along an urban–rural gradient: a comparative study between two cities on different continents. *Condor* 100, 413–425.
- Crooks, K.R., Suarez, A.V., Bolger, D.T., 2004. Avian assemblages along a gradient of urbanization in a highly fragmented landscape. *Biological Conservation* 115, 451–462.
- Dean, W.R.J., Milton, S., 2003. The importance of roads and road verges for raptors and crows in the Succulent and Nama-Karoo, South Africa. *Ostrich* 74, 181–186.
- De'ath, G., Fabricius, K.E., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81, 3178–3192.
- Engels, T.M., Sexton, C.W., 1994. Negative correlation of blue jays and golden-cheeked warblers near an urbanizing area. *Conservation Biology* 8, 286–290.
- Findlay, C.S., Houlahan, J., 1997. Anthropogenic correlates of species richness in south-eastern Ontario wetlands. *Conservation Biology* 11, 1000–1009.
- Forman, R.T.T., Alexander, L.E., 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29, 207–231.
- Forman, R.T.T., Reineking, B., Hersperger, A.M., 2002. Road traffic and nearby grassland bird patterns in a suburbanizing landscape. *Environmental Management* 29, 782–800.
- Fraterrigo, J.M., Wiens, J.A., 2005. Bird communities of the Colorado rocky mountains along a gradient of exurban development. *Landscape and Urban Planning* 71, 263–275.
- Groom, D.W., 1993. Magpie *Pica pica* predation on blackbird *Turdus merula* nests in urban areas. *Bird Study* 40, 55–62.
- Gutzwiller, K.J., Barrow, W.C., 2003. Influences of roads and development on bird communities in protected Chihuahuan Desert landscapes. *Biological Conservation* 113, 225–237.
- Gutzwiller, K.G., Riffell, S.K., Anderson, S.H., 2002. Repeated human intrusion and the potential for nest predation by gray jays. *Journal of Wildlife Management* 66, 372–380.
- Hennings, L.A., Edge, W.D., 2003. Riparian bird community structure in Portland, Oregon: habitat, urbanization, and spatial scale patterns. *Condor* 105, 288–302.
- Konstantinov, V.M., Nowicki, W., Pichurin, A.G., 1996. Recent changes in the avifauna of cities in European Russia and eastern Poland – results of a questionnaire. *Acta Ornithologica* 31, 59–66.
- Kristan, W.B., Boarman, W.I., Crayon, J.J., 2004. Diet composition of common ravens across the urban–wildland interface of the West Mojave Desert. *Wildlife Society Bulletin* 32, 244–253.
- Kuitunen, M., Rossi, E., Stenroos, A., 1998. Do highways influence density of land birds? *Environmental Management* 22, 297–302.
- Laursen, K., 1981. Birds on roadside verges and the effect of mowing on frequency and distribution. *Biological Conservation* 20, 59–68.
- Leach, G.J., Recher, H.F., 1993. Use of roadside remnants of softwood scrub vegetation by birds in south-eastern Queensland. *Wildlife Research* 20, 233–249.
- Lipp, H-P., Vyssotski, A.L., Wolfer, D.P., Renaudineau, S., Savini, M., Tröster, G., Dell'Omo, G., 2004. Pigeon homing along highways and exits. *Current Biology* 14, 1239–1249.
- Marzluff, J.M., 2001. Worldwide urbanization and its effects on birds. In: Marzluff, J.M., Bowman, R., Donnelly, R. (Eds.), *Avian Ecology and Conservation in an Urbanizing World*. Kluwer Academic Publications, Boston, pp. 19–47.
- Marzluff, J.M., McGowan, K.J., Donnelly, R., Knight, R.L., 2001. Causes and consequences of expanding American crow populations. In: Marzluff, J.M., Bowman, R., Donnelly, R. (Eds.), *Avian Ecology and Conservation in an Urbanizing World*. Kluwer Academic Publications, Boston, pp. 331–363.
- McKinney, M.L., 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation* 127, 247–260.
- Melles, S., Glenn, S., Martin, K., 2003. Urban bird diversity and landscape complexity: species–environment associations along a multiscale habitat gradient. *Conservation Ecology* 7, 5 [online, last access: January 2007] <http://www.consecol.org/vol7/iss1/art5/>.
- Meunier, F.D., Verheyden, C., Jouventin, P., 1999. Bird communities of highway verges: influence of adjacent habitat and roadside management. *Acta Oecologica* 20, 1–13.
- Meunier, F.D., Verheyden, C., Jouventin, P., 2000. Use of roadsides by diurnal raptors in agricultural landscapes. *Biological Conservation* 92, 291–298.
- Mumme, R.L., Schoech, S.J., Woolfenden, G.W., Fitzpatrick, J.W., 2000. Life and death in the fast lane: demographic consequences of road mortality in the Florida scrub-jay. *Conservation Biology* 14, 501–512.
- Neatherlin, E.A., Marzluff, J.M., 2004. Responses of American crow populations to campgrounds in remote native forest landscapes. *Journal of Wildlife Management* 68, 708–718.
- Odell, E.A., Knight, R.L., 2001. Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. *Conservation Biology* 15, 1143–1150.
- Palomino, D., Carrascal, L.M., 2006. Urban influence on birds at a regional scale. A case study with the avifauna of northern Madrid province. *Landscape and Urban Planning* 77, 276–290.
- Peris, S.J., Pescador, M., 2004. Effects of traffic noise on passerine populations in Mediterranean wooded pastures. *Applied Acoustics* 65, 357–366.
- Ramp, D., Wilson, V.K., Croft, D.B., 2006. Assessing the impacts of roads in peri-urban reserves: road-based fatalities and road usage by wildlife in the Royal National Park, New South Wales, Australia. *Biological Conservation* 129, 348–359.
- Reijnen, R., Foppen, R., Meeuwssen, H., 1996. The effects of traffic on the density of breeding birds in Dutch agricultural grasslands. *Biological Conservation* 75, 255–260.
- Reijnen, R., Foppen, R., Terbraak, C., Thissen, J., 1995. The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to the proximity of main roads. *Journal of Applied Ecology* 32, 187–202.
- Russo, C., Young, T.P., 1997. Egg and seed removal at urban and suburban forest edges. *Urban Ecosystems* 1, 171–178.
- Sandström, U.G., Angelstam, P., Mikusiński, G., 2006. Ecological diversity of birds in relation to the structure of urban green space. *Landscape and Urban Planning* 77, 39–53.
- Sauvajot, R.M., Buechner, M., Kamradt, D.A., Schonewald, C.M., 1998. Patterns of human disturbance and response by small mammals and birds in chaparral near urban development. *Urban Ecosystems* 2, 279–297.
- Solonen, T., 2001. Breeding of the great tit and blue tit in urban and rural habitats in southern Finland. *Ornis Fennica* 78, 49–60.
- Spellerberg, I.F., 1998. Ecological effects of roads and traffic: a literature review. *Global Ecology and Biogeography Letters* 7, 317–333.
- Storch, I., Leidenberger, C., 2003. Tourism, mountain huts and distribution of corvids in the Bavarian Alps, Germany. *Wildlife Biology* 9, 301–308.
- Venables, W.N., Ripley, B.D., 1994. *Modern Applied Statistics with S-PLUS*. Springer-Verlag, New York.
- Vierling, K.T., 2000. Source and sink habitats of red-winged blackbirds in a rural/suburban landscape. *Ecological Applications* 10, 1211–1218.
- Warner, R.E., 1992. Nest ecology of grassland passerines on road rights-of-way in central Illinois. *Biological Conservation* 59, 1–7.
- Zeng, H., Sui, D.Z., Wu, X.B., 2005. Human disturbances on landscapes in protected areas: a case study of the Wolong Nature Reserve. *Ecological Research* 20, 487–496.