

# Forest bird diversity and ski-runs: a case of negative edge effect

Paola Laiolo\* and Antonio Rolando

Dipartimento di Biologia Animale e dell'Uomo, Via Accademia Albertina 17, 10123 Turin, Italy

(Received 24 February 2004; accepted 12 May 2004)

## Abstract

Among tourist activities in the Alps, winter sports have a prominent role because of the large scale of changes they cause at the habitat and landscape level. We have analysed whether ski resorts lead to significant threats to the avian diversity in the coniferous forests of the western Italian Alps, by comparing the bird communities of plots located in (1) the forest interior, (2) forest at the edge of ski-runs and (3) forest at the edge of pastures (the latter two are anthropogenic elements of forest fragmentation). Ski-runs produce a negative edge effect in the study forests: plots at their edges present lower bird species richness and Shannon diversity than those located in the forest interior or at the edges of pastures. In particular, birds typical of ecotone habitats seem to favour forest plots set at the edge of pastures. Ski-run-edges are linear landscape features that create high contrast edges; conversely, vegetation structure is more complex at the edge of pastures, attracting a rich and diverse avifauna. In the study area, pastures tend to be abandoned whereas winter sport resorts are increasing in extent. Accordingly, there is a need for coordinated management and cooperation between sport- and land-management agencies, in order to preserve native biodiversity while simultaneously managing land for sport activities.

## INTRODUCTION

The creation of edges, i.e. transition zones between adjacent habitats, is one of the effects of habitat fragmentation (Murcia, 1995). Historically, land managers considered habitat fragmentation to be beneficial for biodiversity (Leopold, 1933), on the basis of what was later called the 'edge effect', i.e. the hypothesis that species richness and density increase at the border between different habitats (Odum, 1971). Recent investigations, however, have described radical changes in community structure at edges, suggesting problems from a diversity perspective (Matlack & Litvaitis, 1999). These problems increase when anthropogenic intervention determines a proliferation of edges, emphasising the natural physical gradients in topography, hydrology and substrate (Saunders, Hobbs & Margules, 1991; Andrén, 1994; Rochelle, Lehmann & Wisniewski, 1999; Shochat, Abramsky & Pinshow, 2001). It has been shown, for instance, that anthropogenic forest fragmentation might cause local or regional extinction of the most forest-dependent animal species, as a consequence of increased predation rates and brood parasitism at the forest edge

(Andrén & Angelstam, 1988; Andrén, 1992; Faaborg *et al.*, 1995; Kurosawa & Askins, 2003), inhibition of dispersal and reduction of home range (Forman, 1997) and intensification of human disturbance (McGarigal *et al.*, 2001). In Europe, the effects of habitat fragmentation have been severe in lowland forests that have experienced a long history of anthropogenic disturbances (Hanson, 1983; Cushman & McGargal, 2003; Gurdebeke *et al.*, 2003). The impact of human activities in high-elevation environments is more recent and a common form of disturbance comes from the development of winter sport resorts. Ski-runs, in particular, brought about considerable damage both above and below the timberline: forest tracts are abruptly clear-cut, bulldozers and power shovels are used for soil removal (to provide comfortable slopes for skiers) and artificial seeding, if any, is conducted to control for soil erosion (Siniscalco *et al.*, 1997; Urbanska, Erdt & Fattorini, 1998; Tsuyuzaki, 2002). After construction, tree pruning and cutting of shrubs are carried out at regular intervals and large amounts of chemicals are spread for soil stability (Barni, Siniscalco & Montacchini, 2002).

Despite ski-runs becoming a common feature in alpine landscapes, there is a paucity of research on their effects on wildlife (Delmas, 1986; Watson & Moss, 2004). This study was undertaken to provide information on the effects of ski-runs on the bird communities of the coniferous forests of the Alps. We compared bird diversity and community composition in plots located in (1) the

\*All correspondence to: Paola Laiolo. Department of Applied Biology, Estación Biológica de Doñana (CSIC), Avenida M. Luisa s/n, 41013 Sevilla, Spain. Tel: +34 954621125; Fax: +34 954232340; E-mail: paolo@ebd.csic.es

forest interior, (2) forest at the edge of ski-runs and (3) forest at the edge of pastures. In particular, we examined whether avian diversity is greater in forest plots located at the edge of an open space – ski-run or pasture – than in the forest interior (as expected when an edge effect occurs). Like ski-runs, pastures have an anthropogenic nature, but while the former form abrupt edges, pastures tend to create more ragged edges. We also investigated bird–habitat relationships, to determine important floristic and structural components of the habitat of the alpine coniferous forest avifauna.

## METHODS

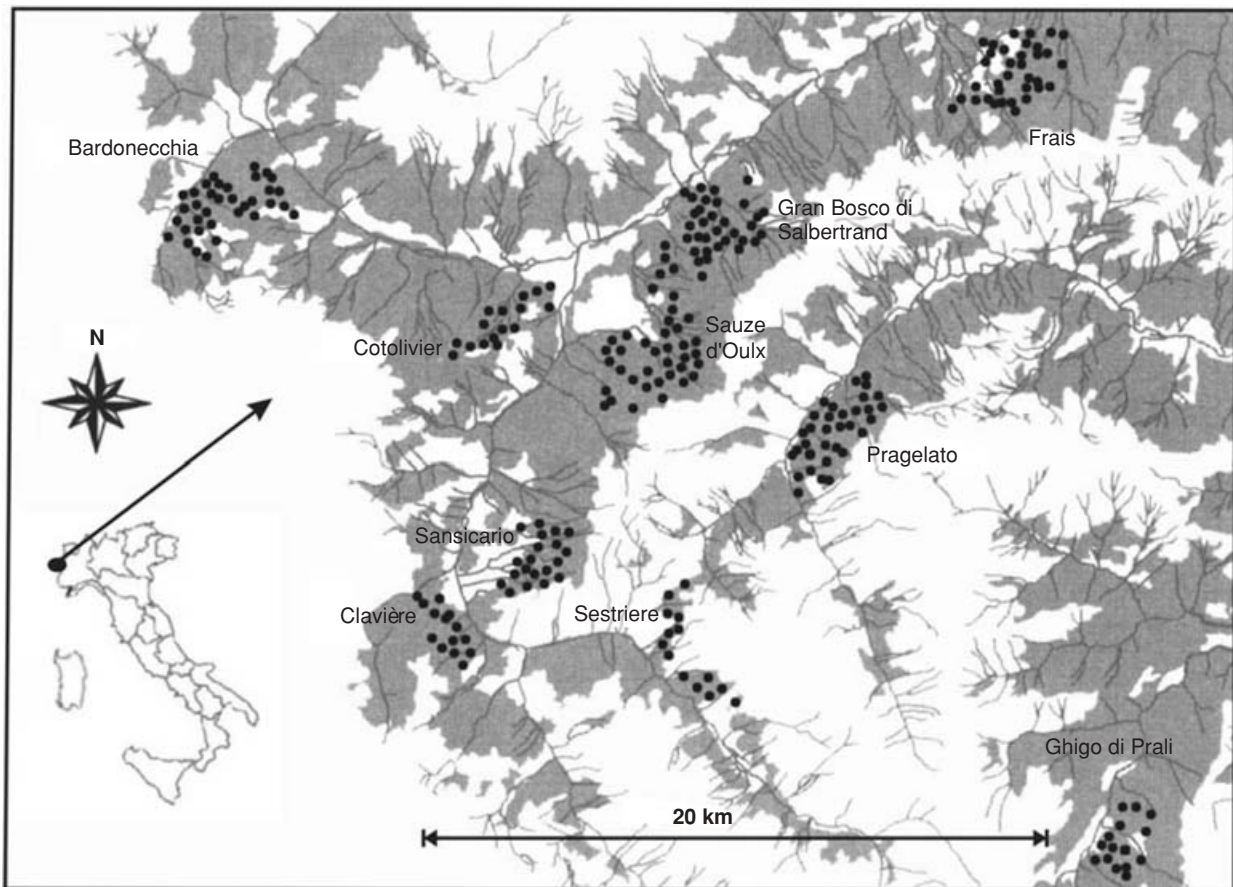
### Study area

The study was carried out in the coniferous forests of the Alta Val Susa, Val Chisone and Val Germanasca, in the western Italian Alps. We surveyed 10 localities comprising ski areas and a Natural Park (Fig. 1). In 2006, the XX Olympic Winter Games will take place in the study area. Since the 1970s, ski-runs have been constructed both on high-elevation grasslands and within coniferous forests; they were established by scraping off the extant vegetation

and the topsoil and by artificially seeding with prevailing native herbs. Coniferous forests of the area are dominated by the larch *Larix decidua*, but the fir *Abies alba*, Norway spruce *Picea abies*, Arolla pine *Pinus cembra* and Scots pine *Pinus sylvestris* also occur. Broadleaved trees (*Fraxinus excelsior*, *Acer pseudoplatanus*, *Betula pendula*, *Alnus viridis*, *Corylus avellana*, *Sorbus spp.*, *Salix spp.*) are found as scattered individuals within the coniferous matrix. The understorey is sparse, mainly composed of *Juniperus*, *Rhododendron*, *Vaccinium* and *Arctostaphylos spp.*

### Bird and habitat sampling design

Field work was carried out in April, May and June 2003. Birds were counted using 50-m fixed radius point-counts, between sunrise and 5 h later in good weather conditions (Bibby *et al.*, 2000). All birds detected during a 7 min period, aurally and/or visually, were recorded. Overall, 252 point-counts were made at 1100–2200 m above sea-level (a.s.l.). The exact location of plots was established in the field by means of a Global Positioning System (GPS) Garmin eTrex® Navigator. Each plot was located at a minimum distance of 200 m from the next nearest sampling plots and we were careful not to record the same



**Fig. 1.** Geographical location and map of the study area. Survey plots (circles), forests (grey areas) and water courses (lines) are shown. Ski-run strips and small pastures (< 5 ha) cannot be distinguished at this detail. The study ski resorts are located in Sestriere, Clavière, Sansicario, Bardonecchia, Fraix, Ghigo di Prali, Pragelato and Sauze d'Oulx. The Gran Bosco di Salbertrand is a Natural Reserve.

individuals on neighbouring points. Three types of plots were defined: forest-interior plots ( $n = 112$ ), ski-run edge plots ( $n = 68$ ) and pasture edge plots ( $n = 72$ ). Ski-run strips were 30–50 m wide and > 500 m long, pastures covered > 1.5 ha. The centre of edge plots was located 50 m from ski-runs and pastures, so that the external perimeter of the plots embraced forest edge on one side. The centre of forest interior plots was located > 200 m from edges (the external perimeter on one side was at a minimum distance of 150 m from edges).

In circular plots of 20 m radius (centred in each census plot), structural parameters of the vegetation were measured. Tree height was measured using a clinometer, tree diameter at breast height was determined using a tape and tree density was established as the inverse of the distance between the nearest trees paced in metres. Ten measurements per plot were taken for tree height, diameter and distance and the averages of these habitat measurements were used in statistical analyses. The variability in canopy profile for each plot was determined through the coefficient of variation of tree height ( $CV = SD/\text{mean height} \times 100$ ). In each point count station of 50 m radius, all trees > 6 cm diameter at breast height were counted and their taxonomic identity recorded, to derive a measure of arboreal diversity per plot (Shannon index:  $H' = -\sum p_i \times \ln p_i$ , where  $p_i$  is the relative frequency of tree species  $i$ ).

Hence, local habitat at each count-station was depicted by means of six parameters: arboreal diversity (AH), relative abundance of larch (the dominant tree, %L), tree height (H), diameter (DBH), density (D) and variability in canopy profile (CVH). Avian community was described in terms of bird species richness (S), diversity (Shannon index, BH) and the density of three ecological groups of birds: woodland species (birds typical of forest and open forest habitats), ecotone-shrub species (species that use grassland and woodland alternatively or dwell in shrubby areas) and grassland species (birds that require open fields both for breeding and foraging).

## Data analysis

### *Differences between plot types*

We tested for differences in mean bird species richness, diversity and density of woodland, ecotone-shrub and grassland species between the three plot types (forest-interior, ski-run-edge and pasture-edge) by means of nested ANOVAs (plots nested into 10 study localities). The values of Shannon diversity was transformed to logarithms ( $y = \log(x) + 1$ ) and those of species richness and density of the three ecological groups were transformed to square roots ( $y = \sqrt{x + 0.5}$ ) to attain a normal distribution.

### *Relationships between bird community and habitat*

Principal component analysis (PCA: Gaunch, 1984) was chosen to compensate for multicollinearity and to reveal patterns in the data for vegetation structure (DBH, H, D

and CVH variables), using standardised data (zero mean and unit standard deviation).

We used generalised linear models to test for the effects of vegetation structure (three scores of PCA), floristics (arboreal diversity, percent larch cover), elevation, locality and plot type (categorical variable defining forest interior, ski-run- and pasture-edges) on bird species richness, diversity and the abundance of the three ecological groups of birds. Species richness and bird abundance values matched Poisson distribution, whereas species diversity matched a Gaussian distribution. Both Poisson/Gaussian regressions and Akaike's Information Criterion (AIC: Akaike, 1973) were used to select the most appropriate models, i.e. those fitting best the available data set. AIC is based on the principle of parsimony and helps to identify the model that accounts for the most variation with the fewest variables: the model that best explains the data is that with the lowest AIC. This information criterion is one of the most powerful approaches for model selection from a set of alternative plausible models and it solves the problems of stepwise model selection because no sequential statistical test is conducted (Burnham & Anderson, 1998).

Generalised linear models and AIC were calculated using the R Package (Ihaka & Gentleman, 1996).

### *Relationships between bird species and habitat*

Density of bird species at each plot was compared with vegetation characteristics by means of the Canonical Correspondence Analysis (CCA). This is a multivariate technique that ordines plots using both a primary matrix of species densities and a secondary matrix of environmental variation (ter Braak, 1986). The primary matrix included 29 bird species, i.e. those contributing with at least eight individuals to the data set, the secondary matrix included floristic and physiognomic descriptors (AH, %L, H, DBH, D and CVH), elevation and plot type. To assess the significance in the CCA axes, we used Monte Carlo simulations to test the hypothesis that there was no correlation between the primary (bird) and secondary (environment) matrices:  $P$  values were based on the proportion of 1000 Monte Carlo simulations with an eigenvalue greater than the observed eigenvalue. CCA was performed using PC-ORD (McCune & Mefford, 1999).

## RESULTS

### *Differences between plot types*

Overall, 1256 individuals from 42 species were sampled in 252 plots (see Appendix 1 for a complete list of bird species and Appendix 2 for the distribution of points within plot types and localities). Forest-interior, ski-run and pasture-edge stations showed significant differences in terms of bird diversity and species richness and no significant interaction resulted between locality and plot type (Table 1). Plots located at the edge of pastures support

**Table 1.** Mean  $\pm$  SD of bird species richness, diversity and abundance of woodland, ecotone-bush and grassland species per plot type

	(1) Forest interior	(2) Pasture-edge	(3) Ski-run-edge	Inter-plot differences (nested ANOVA)	Significant pair-wise comparisons at $P < 0.05$
Species richness	4.0 $\pm$ 1.7	4.5 $\pm$ 1.7	3.4 $\pm$ 1.7	F <sub>2,225</sub> = 7.6***	(1) vs (3), (1) vs (2), (2) vs (3)
Diversity	1.2 $\pm$ 0.5	1.4 $\pm$ 0.4	1.0 $\pm$ 0.7	F <sub>2,225</sub> = 7.7***	(1) vs (3), (2) vs (3)
Abundance of woodland species	4.5 $\pm$ 2.0	4.7 $\pm$ 2.2	3.6 $\pm$ 2.1	F <sub>2,225</sub> = 5.1**	(1) vs (3), (2) vs (3)
Abundance of ecotone-bush species	0.5 $\pm$ 0.8	1.0 $\pm$ 1.2	0.7 $\pm$ 1.0	F <sub>2,225</sub> = 5.3**	(1) vs (2)
Abundance of grassland species	0.02 $\pm$ 0.2	0.1 $\pm$ 0.4	0.2 $\pm$ 1.2	F <sub>2,225</sub> = 2.2	

Inter-plot differences were tested with nested ANOVAs (plot type nested into locality). Least-squares deviation (LSD) post-hoc tests were used for pair-wise comparisons of means. vs, versus.

\*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

the greatest bird species richness and diversity, whereas those set at the edge of ski-runs presented the lowest values. Woodland species density was greatest in forest interior and pasture-edge plots, numbers of ecotone-shrub birds peaked in plots at the edge of pastures (Table 1). Using one-way ANOVAs, we tested for differences between bird diversity of plots located in the surroundings of ski-runs and diversity of plots located further away (distance classes:  $< 0.5$  km,  $0.5$ – $1$  km and  $> 1$  km). When plots located at the edge of ski-runs were included in the analyses, bird species richness and diversity were significantly lower in forests around ski resorts than in forested areas located at least 1 km apart from them (S:  $F_{2,249} = 4.2$ ,  $P < 0.05$ ; BH:  $F_{2,249} = 3.4$ ,  $P < 0.05$ ). However, when only forest interior and pasture-edge plots were considered, no significant difference was found between distance classes (all  $P > 0.05$ ), suggesting that forest bird diversity only drops in the close proximity of a ski-run.

### Relationships between bird community and habitat

The first three principal components (PC1, PC2, PC3) accounted for 89% of the total variation in the vegetation structure matrix, with eigenvalues  $> 1$ . Tree height and diameter at breast height showed the highest correlation with PC1 scores (suggesting a gradient from young *versus* old stands), the variability in tree height provided the

**Table 2.** Results of principal component analysis carried out on habitat structure data

	Factor loadings		
	PC1	PC2	PC3
Tree diameter (cm)	<b>0.62</b>	0.46	0.34
Tree height (m)	<b>0.95</b>	0.06	0.08
Coefficient of variation of tree height (%)	-0.13	<b>-0.97</b>	-0.04
Tree density (1/distance between trees)	-0.14	-0.06	<b>-0.98</b>
Eigenvalues	1.32	1.15	1.07
% Total variance	0.33	0.29	0.27

The highest loadings are in bold type.

major loading (negative) on PC2, tree density showed a negative correlation with PC3 (Table 2).

Results of generalised linear models of bird species richness, diversity, density of woodland, ecotone-bush and grassland birds on environmental predictors are shown in Table 3. Bird species richness and diversity were best modelled by plot type alone, with the AIC minimised for just this variable (S: AIC = 991, BH: AIC = 345); all other variables and their combinations had greater AIC values (S: AIC  $> 1000$ , BH AIC  $> 360$ ). Poisson/Gaussian regressions confirmed these results, since they were significant only when plot type was entered, although

**Table 3.** Generalised linear models of bird species richness, diversity, density of woodland, ecotone-bush and grassland birds on environmental predictors (arboreal diversity, larch cover, elevation, plot type, locality, PCA scores for structural variables)

Predictor	$\beta$	SE	$P$
Species richness			
Plot type pasture-edge	0.29	0.09	$< 0.001$
Plot type forest interior	0.16	0.08	$< 0.05$
AIC = 991			
Diversity			
Plot type pasture-edge	0.32	0.08	$< 0.001$
Plot type forest interior	0.18	0.07	$< 0.01$
AIC = 345			
Abundance of woodland birds			
Plot type pasture-edge	0.21	0.08	$< 0.05$
Plot type forest interior	0.12	0.08	= 0.1
Elevation	-0.53	0.23	$< 0.05$
Larch cover	-0.07	0.03	$< 0.05$
AIC = 1076			
Abundance of ecotone-scrub birds			
Plot type pasture-edge	0.56	0.19	$< 0.01$
Elevation	-0.13	0.67	$< 0.001$
AIC = 573			
Abundance of grassland birds			
PC1	-0.39	0.20	$< 0.05$
PC3	-0.56	0.19	$< 0.01$
Plot type forest interior	-2.61	0.76	$< 0.001$
AIC = 173			

PC1 is an indicator of stand age, PC3 of tree density. Only variables included in the best model (i.e. that minimising AIC) are shown; variables were added sequentially. SE, standard error.

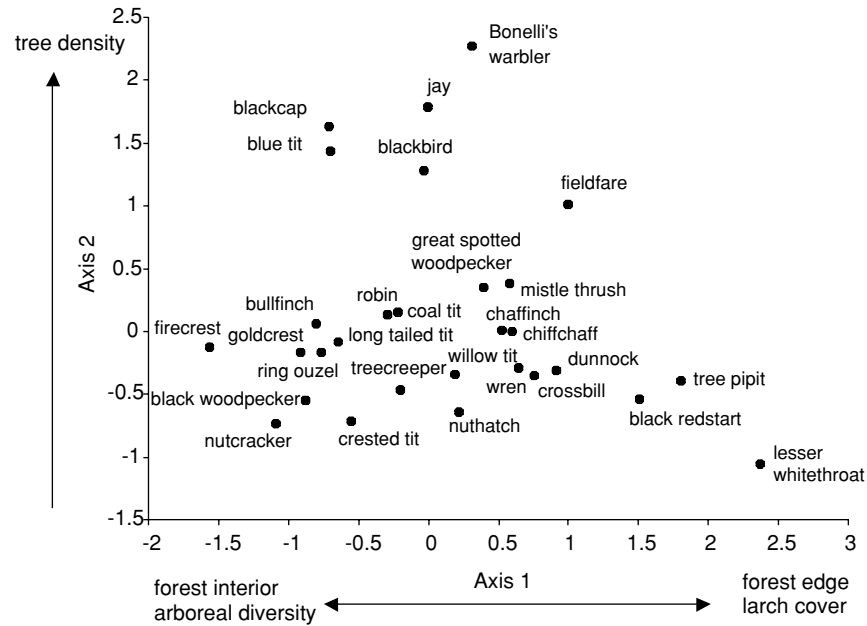


Fig. 2. Scatterplot of the bird community along the first two axes of Canonical Correspondence Ordination (CCA).

the model only explained 5% of the total variation. The density of woodland species decreased with elevation and larch cover and increased in forest interior and pasture-edge plots; birds of the ecotone and shrubs were associated with pasture-edge and high elevation plots, while grassland species only inhabited young woodlots with sparse tree cover at the margin of forest (Table 3).

#### Relationships between bird species and habitat

In canonical correspondence analysis (CCA), the first CCA axis represented a gradient from high tree diversity plots located in forest interior to larch-rich sites of forest margin (AH:  $r = -0.514$ ; forest-interior:  $r = -0.401$ ; pasture-edge:  $r = 0.24$ ; ski-run-edge:  $r = 0.22$ ; %L:  $r = 0.39$ ), the second axis represented increasing tree density (D:  $r = 0.343$ ). Black woodpecker, treecreeper, nutcracker, firecrest, goldcrest and tits were associated with high arboreal diversity and forest interior plots, whereas lesser whitethroat, tree pipit, black redstart, dunnock and mistle thrush occurred at forest edges dominated by larches (Fig. 2). The first two ordination axes of CCA had significant canonical eigenvalues ( $< 0.005$ ), as determined by the Monte Carlo test.

#### DISCUSSION

Among tourist activities in mountains, winter sports have a prominent role because of the large scale of changes they cause at the landscape level and the large demand on energy supply. In particular, the construction of ski-runs in the study area requires the destruction of the pre-existing ecosystems through the removal of topsoil and extant native vegetation (both herbaceous and arboreal) in strips typically 30–50 m wide (Siniscalco & Montacchini, 1990).

Several studies have shown that plant diversity in ski-runs is lower than that of nearby grasslands (Urbanska *et al.*, 1998); vegetation successional stages are also disrupted (Tsuyuzaki, 2002). The effects on the faunal components are less studied and more varied: Shine, Barrott & Elphick (2002), for instance, found that artificial corridors in mountainous forests enable reptiles to penetrate higher into the forest, as these species take advantage of higher solar radiation in anthropogenic clearcuts. On the other hand, Watson & Moss (2004) found out that the breeding success of ptarmigan *Lagopus mutus* can drop as a consequence of ski-development in Scotland. The results of this study show that bird species richness and diversity of forests perforated by ski-runs are significantly lower than those of undisturbed forests. This could be ascribed to the negative edge effect that ski-runs produce in the forest: plots at their edges present lower bird diversity and species richness than those far from edges; conversely, species richness is enhanced when the forest grades into a pasture, suggesting that the latter element causes a local positive edge effect in the forest. We hypothesise that the factors that are responsible for the observed differences are related to the different structure and resource availability of these two types of forest edges. First, ski-runs are linear landscape features that create high contrast edges and bisect patches: the forest ends abruptly and shrub and tree encroachment is prevented by regular pruning and cutting. Second, several ski-runs, especially the steepest ones, have a high proportion of bare ground, due to soil erosion, compaction and the use of chemicals in artificial snow; these factors might limit, in turn, the resources available to forest birds in nearby open habitats. Conversely, at the edge of pastures the shrub layer is denser (due to extra light) and it is not removed as in ski-runs. Furthermore, the shrubs at forest edges may flower more regularly than in the heavily shaded forest interior and the light,

warm conditions at the edge may increase insect density and, in turn, insectivorous bird density. Several studies in temperate forests have shown that the presence of bushes and grassy headlands in forest margins can increase bird diversity (Kroodsma, 1984; Fuller & Warren, 1991; Fautsch, Delvingt & Paquet, 2003). In addition, pasture-edges may offer more suitable habitats for birds because they are older than ski-run edges: both the structure and the plant composition are generally thought to be more complex along old, established edges where there has been a constancy of light penetration (Fuller, 1995). Eventually, grazed patches and their surrounding forest edges may be richer in particular invertebrates that are important prey items for birds, such as bionids and leatherjackets (flies), which depend upon the availability of organic matter (dung) (McCracken, Foster & Kelly, 1995; Vickery *et al.*, 2001).

Typical ecotone bird species preferentially dwell in plots at the edges of pastures and at high elevations, whereas woodland birds are more abundant in forest interior or at the edge of pastures and tend to avoid pure larch sites and high altitude. The fact that forest interior and pasture edge support similar overall abundance of woodland species probably depends on the relative paucity of true forest specialists, which make up a minor share of woodland birds in the study area. Grassland birds are found only close to the edges and prefer young forests where trees are very sparse. All in all, forest plots at ski-run edges are avoided by both typical forest birds and by ecotone birds, which constitute the bulk of the species sampled. Although this study concentrated on forest habitats, it is worth noting that several open-habitat species were more abundant, or occurred only, in pastures and avoided ski-runs: woodlark *Lullula arborea*, rock bunting *Emberiza cia*, yellowhammer *Emberiza citrinella*, red-backed shrike *Lanius collurio*, whinchat *Saxicola rubetra* and rock sparrow *Petronia petronia* (pers. obs.).

Although bird diversity peaks in forest plots at the edges of pastures, CCA shows that forest interior habitats are important for several species, such as the treecreeper, bullfinch, *Regulus* spp., black woodpecker, nutcracker and most tits; these species are also associated with plots with great tree diversity. Conversely, the lesser whitethroat, tree pipit, black redstart, crossbill and dunnock seem to prefer larch-rich habitats at forest edges. Stand age, as indicated by tree height and diameter, is a poor predictor of individual species distribution and this contradicts a widely held general view that forest age is important to the distribution of birds in temperate woodlands (Lack, 1939; Lack & Lack, 1951; Moss, 1978; Helle & Mönkkönen, 1990).

A possible caveat of this research concerns the assessment of habitat quality from measures of bird densities, rather than directly estimating bird breeding success. However, the aim of this study was to investigate the value of different forest plots for the bird community on the whole. Ski-runs do negatively affect bird diversity *per se* and this has to be viewed as detrimental, irrespective of the effects on breeding success.

Despite its short-term nature, this study shows that the occurrence of ski-runs in the forested landscapes of

the Italian Alps lowers bird diversity, since a negative edge effect seems to occur. Plots at the edge of pastures have the greatest diversity, but they are avoided by some forest specialists, such as treecreeper and some *Parus* species. The latter species are priority species for forest-conservation (*sensu* Tucker & Evans, 1997) and their dependence upon forest interior emphasises the role of continuous habitat in the conservation of forest specialists. At present, forest clearing for winter sport activities is the major force driving the fragmentation of the coniferous forests, since there is a generalised trend towards pastoral abandonment in several alpine valleys and most grazed fields in the montane belt turned (or are turning) into forests (Laiolo *et al.*, 2004). In view of this, the only way to preserve the biodiversity of the area seems to be that of restoring the gradual transition from forest to the open habitat created by ski-runs. This could be achieved without compromising the safety of the ski-runs, by managing edge vegetation and encouraging side canopies, because physical gradients are much less pronounced behind close edges (Matlack & Litvaitis, 1999). The value of these measures in promoting natural diversity should be tested experimentally, through coordinated management and improved cooperation between sport- and land-management agencies, which should have the mandate to maintain native biodiversity while simultaneously managing land for commodity production, recreation and other objectives. Eventually, studies on the ecological impacts of alpine sport resorts on wildlife should also be encouraged outside the winter period, to understand whether disturbed ecosystems have already moved outside of their natural range of variation and to identify threshold levels within which human activities can be sustainable.

#### Acknowledgements

We are very grateful to Alessia Formica, Davide Nasi, Simona Caffo and Stefania Cagliari for help in data collection. We also thank Jack Backer for providing useful comments on the manuscript. This research was funded by TOROC, the Organizing Committee of the XX Olympic Winter Games in Turin.

#### REFERENCES

- Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In *International symposium on information theory*: 267–281. 2nd edn. Petran, B. N. & Csari, F. (Eds). Budapest: Akademiai Kiado.
- Andrén, H. (1992). Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* **73**:794–804.
- Andrén, H. (1994). Effects of habitat fragmentation on birds and mammals in landscape with different proportions of suitable habitat: a review. *Oikos* **71**: 355–366.
- Andrén, H. & Angelstam, P. (1988). Elevated predation rates as an edge effect in habitat islands. *Ecology* **69**: 544–547.
- Barni, E., Siniscalco, C. & Montacchini, F. (2002). Vegetation dynamics on restored ski runs (North-western Italian Alps) and the relation

- to soil stability. Interdisciplinary Mountain Research, Europäische Akademie Bozen. London: Blackwell, Verlag.
- Bibby, C. J., Burgess, N. D., Hill, D. A. & Mustoe, S. H. (2000). *Bird census techniques*. 2nd edn. London: Academic Press, UK.
- Burnham, K. P. & Anderson, D. R., (1998). *Model selection and inference: a practical information – theoretic approach*. New York: Springer.
- Cushman, S. A. & McGargal, K. (2003). Landscape-level patterns of avian diversity in the Oregon Coast Range. *Ecol. Monogr.* **73**: 259–281
- Delmas, M. (1986). Tétrasyre et stations de ski; I: résultats de six années de dénombrement de Tétrasyre au chant en Haute-Tarentaise (Savoie). *Boll. Mensuel de l'Office National de la Chasse* **99**: 17–21.
- Faaborg, F., Brittingham, M., Donovan, T. & Blake, J. (1995). Habitat fragmentation in the temperate zone. In *Ecology and management of Neotropical migratory birds*: 357–380. Martin, T. E., Finch, D. M. (Eds). New York: Oxford University Press.
- Fautsch, M., Delvingt, W. & Paquet, J. Y. (2003). L'influence de la structure des lisières forestières sur leur capacité d'accueil pour l'avifaune dans l'Ardenne Belge. *Aulauda* **71**: 253–260.
- Forman, R. T. (1997). *Land mosaics: the ecology of landscapes and regions*. Cambridge: Cambridge University Press.
- Fuller, R. J. (1995). *Bird life of woodland and forest*. Cambridge: Cambridge University Press.
- Fuller, R. J. & Warren, M. S. (1991). Conservation management in ancient and modern woodlands: responses of fauna to edges and rotations. In *The scientific management of temperate communities for conservation*: 445–471. Spellerberg, I. F., Goldsmith, F. B. & Morris, M. G. (Eds). British Ecological Society Symposium No. 31. Oxford: Blackwell Scientific Publications.
- Gauch, H. G. Jr. (1984). *Multivariate analysis in community ecology*. Cambridge: Cambridge University Press.
- Gurdebeke, S., De Bakker, D., Vanlanduyt, N. & Maelfait, J. P. (2003). Plans for a large regional forest in eastern Flanders (Belgium): assessment of spider diversity and community structure in the current forest remnants. *Biodiver. Conserv.* **12**: 1883–1900.
- Hanson, L. (1983). Bird numbers across edges between mature conifer forest and clearcuts in Central Sweden. *Ornis Scandinavica* **14**: 97–103.
- Helle, P. & Mönkkönen, M. (1990). Forest succession and bird communities: theoretical aspects and practical implications. In *Biogeography and ecology of forest bird communities*: 299–318. Keast, A. (Ed.). The Hague: SPB Academic Publishing.
- Ihaka, R. & Gentleman, R. (1996). R: a language for data analysis and graphics. *J. Computat. Graph. Stat.* **5**: 299–314.
- Kroodsma, R. L. (1984). Effect of edge on breeding forest bird species. *Wilson Bull.* **96**: 426–436.
- Kurosawa, R. & Askins, R. (2003). Effects of habitat fragmentation on birds in deciduous forests in Japan. *Conserv. Biol.* **17**: 695–707.
- Lack, D. (1939). Further changes in the Breckland avifauna caused by afforestation. *J. Anim. Ecol.* **8**: 277–285.
- Lack, D. & Lack, E. (1951). Further changes in birdlife caused by afforestation. *J. Anim. Ecol.* **20**: 173–179.
- Laiolo, P., Dondero, F., Ciliento, E. & Rolando, A. (2004). Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. *J. Appl. Ecol.* **41**: 294–304.
- Leopold, A. (1933). *Game management*. New York: Charles Scribners.
- Matlack, G. R. & Litvaitis, J. A. (1999). Forest edges. In *Maintaining biodiversity in forest ecosystems*: 210–234. Hunter, M. L., Jr (Ed.). Cambridge: Cambridge University Press.
- McCracken, D. I., Foster, G. N. & Kelly, A. (1995). Factors affecting the size of leatherjacket (Diptera: Tipulidae) populations in pastures in the west of Scotland. *Appl. Soil Ecol.* **2**: 203–213.
- McCune, B. & Mefford, M. J. (1999). *PC-ORD. Multivariate analysis of ecological data*. Version 4. Gleneden Beach, Oregon: MJM Software Design.
- McGarigal, K., Romme, W. H., Crist, M. & Roworth, E. (2001). Cumulative effects of roads and logging on landscape structure in the San Juan Mountains, Colorado (USA). *Landsc. Ecol.* **16**: 327–349.
- Moss, D. (1978). Diversity of woodland song-bird populations. *J. Anim. Ecol.* **47**: 521–527.
- Murcia, C. (1995). Edge effects in fragmented forests: implications for conservation. *Trends Ecol. Evol.* **10**: 58–62.
- Odum, E. P. (1971). *Fundamentals of ecology*. Philadelphia: Saunders.
- Rochelle, J. A., Lehmann, L. A. & Wisniewski, J. (1999). *Forest fragmentation: wildlife and management implications*. Leiden: Brill.
- Saunders, D. A., Hobbs, R. J. & Margules, C. R. (1991). Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* **5**: 18–32.
- Shine, R., Barrott, E. G. & Elphick, M. J. (2002). Some like it hot: effects of forest clearing on nest temperatures of montane reptiles. *Ecology* **83**: 2808–2815.
- Shochat E., Abramsky Z. & Pinshov B. (2001). Breeding bird species diversity in the Negev: effects of scrub fragmentation by planted forests. *J. Appl. Ecol.* **38**: 1135–1147.
- Siniscalco, C. & Montacchini, F. (1990). Relazioni tra popolamenti vegetali e antropizzazione in ambiente alpino: il caso delle piste da sci nel Parco Nazionale del Gran Paradiso. *Rev. Valdotaïne d'Hist. Nat.* **48**: 307–315.
- Siniscalco, C., Barni, E., Rosa, A. & Montacchini, F. (1997). Vegetation dynamics after seeding in Susa Valley ski runs (W-Italian Alps). *Rev. Valdotaïne d'Hist. Nat.* **48**: 307–315.
- ter Braak, C. J. F. (1986). Canonical Correspondence Analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**: 1167–1179.
- Tsuyuzaki, S. (2002). Vegetation development patterns on skiruns in lowland Hokkaido, northern Japan. *Biol. Conserv.* **108**: 239–246.
- Tucker, G. M. & Evans, M. I. (1997). *Habitat for birds in Europe. A Conservation Strategy for the Wider Environment*. (BirdLife Conservation Series No. 6). Cambridge: BirdLife International.
- Urbanska, K. M., Erdt, S. & Fattorini, M. (1998). Seed rain in natural grassland and adjacent ski run in the Swiss Alps: a preliminary report. *Restor. Ecol.* **6**: 159–165.
- Vickery, J. A., Tallwin, J. R., Feber, R. E., Asteraki, E. J., Atkinson, P. W., Fuller, R. J. & Brown, V. K. (2001). The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *J. Appl. Ecol.* **38**: 647–664.
- Watson, A. & Moss, R. (2004). Impacts of ski-developments on ptarmigan (*Lagopus mutus*) at Cairn Gorm, Scotland. *Biol. Conserv.* **116**: 267–275.

**APPENDIX 1.** List of the bird species recorded in the 252 plots. Species were classed as grassland, ecotone-shrub and woodland birds according to their ecological preferences

Common name	Scientific name	Ecological group
Black grouse	<i>Tetrao tetrix</i>	Ecotone-shrub
Great spotted woodpecker	<i>Dendrocopos major</i>	Woodland
Black woodpecker	<i>Dryocopus martius</i>	Woodland
Green woodpecker	<i>Picus viridis</i>	Woodland
Tree pipit	<i>Anthus trivialis</i>	Ecotone-shrub
White wagtail	<i>Motacilla alba</i>	Grassland
Wren	<i>Troglodytes troglodytes</i>	Woodland
Duncock	<i>Prunella modularis</i>	Ecotone-shrub
Whinchat	<i>Saxicola rubetra</i>	Grassland
Robin	<i>Erithacus rubecula</i>	Woodland
Black redstart	<i>Phoenicurus ochruros</i>	Grassland
Redstart	<i>Phoenicurus phoenicurus</i>	Woodland
Ring ouzel	<i>Turdus torquatus</i>	Ecotone-shrub
Blackbird	<i>Turdus merula</i>	Woodland
Fieldfare	<i>Turdus pilaris</i>	Ecotone-shrub
Mistle thrush	<i>Turdus viscivorus</i>	Ecotone-shrub
Lesser whitethroat	<i>Sylvia curruca</i>	Ecotone-shrub
Garden Warbler	<i>Sylvia borin</i>	Ecotone-shrub
Blackcap	<i>Sylvia atricapilla</i>	Woodland
Bonelli's warbler	<i>Phylloscopus bonelli</i>	Woodland
Chiffchaff	<i>Phylloscopus collybita</i>	Woodland
Goldcrest	<i>Regulus regulus</i>	Woodland
Firecrest	<i>Regulus ignicapillus</i>	Woodland
Long-tailed tit	<i>Aegithalos caudatus</i>	Woodland
Coal tit	<i>Parus ater</i>	Woodland
Willow tit	<i>Parus montanus</i>	Woodland
Crested tit	<i>Parus cristatus</i>	Woodland
Blue tit	<i>Parus caeruleus</i>	Woodland
Great tit	<i>Parus major</i>	Woodland
Treecreeper	<i>Certhia familiaris</i>	Woodland
Short-toed treecreeper	<i>Certhia brachydactyla</i>	Woodland
Nuthatch	<i>Sitta europaea</i>	Woodland
Jay	<i>Garrulus glandarius</i>	Woodland
Nutcracker	<i>Nucifraga caryocatactes</i>	Woodland
Carrion crow	<i>Corvus corone corone</i>	Ecotone-shrub
Chaffinch	<i>Fringilla coelebs</i>	Woodland
Citrel finch	<i>Serinus citrinella</i>	Woodland
Redpoll	<i>Carduelis flammea</i>	Woodland
Bullfinch	<i>Pyrrhula pyrrhula</i>	Woodland
Crossbill	<i>Loxia curvirostra</i>	Woodland
Rock bunting	<i>Emberiza cia</i>	Grassland
Yellowhammer	<i>Emberiza citrinella</i>	Grassland

**APPENDIX 2.** Number of points sampled in each plot type and locality

Locality	Forest interior	Pasture-edge	Ski-run-edge
Bardonecchia	14	5	16
Cotolivier	10	6	–
Sauze d'Oulx	11	6	17
Gran Bosco di Salbertrand	26	7	–
Frais	9	16	8
Sansicario	3	7	10
Clavière	12	–	3
Sestriere	1	7	6
Pragelato	19	14	3
Ghigo di Prali	7	5	5
Total	112	72	68

# Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna

PAOLA LAIOLO, FRANCESCA DONDERO, ENZA CILIENTO and ANTONIO ROLANDO

Dipartimento di Biologia Animale e dell'Uomo, Via Accademia Albertina 17, 10123, Turin, Italy

## Summary

1. There is a long-term trend of depopulation of rural areas and pasture abandonment throughout the Alps. This trend peaked after the Second World War and is now omnipresent. Its ecological consequences are evident mostly below the timberline, where grassland gradually turns into shrub and, ultimately, to forest. This study addresses the consequences of land abandonment and the decline of pastoral practices on the diversity and structure of the bird communities of the Italian Alps.

2. The breeding birds of Gran Paradiso Natural Park in north-western Italy were surveyed, and bird diversity, abundance of grassland, ecotone, woodland and shrub species were analysed using regression in relation to a set of explanatory variables including elevation, local habitat variables, landscape variables and grazing intensity.

3. Avian diversity increased in abandoned pastures as higher numbers of shrub species followed tree and shrub encroachment. Conversely, open habitat species that benefited from grazing were mostly confined to pure grasslands and high altitudes.

4. The effects of grazing were more evident in the montane belt. Grazing maintained open habitats by limiting tree and scrub encroachment, thereby favouring grassland bird species. At higher altitudes, however, grazing had little effect on typical open habitat alpine species (choughs *Pyrrhocorax* spp., water pipit *Anthus spinoletta*, alpine accentor *Prunella collaris*, wheatear *Oenanthe oenanthe*, snow finch *Montifringilla nivalis*, rock thrush *Monticola saxatilis*) and only skylark *Alauda arvensis* and linnet *Carduelis cannabina* preferred grazed meadows.

5. *Synthesis and applications.* This study shows that the abandonment of grazing in the Alps has significant effects on bird species diversity and abundance, especially below the timberline where pastoral decline leads to significant changes in vegetation structure. However, grazing importance differs markedly depending on whether the focus is avian  $\alpha$ -diversity or grassland bird abundance. Pastoral abandonment leads to an overall increase in avian diversity, but most species invading abandoned pastures are already common, whereas several grassland bird species that are dependent upon grazed pastures have an unfavourable conservation status. Overall, in terms of bird conservation objectives, large-scale abandonment of long-established pastoral habitats and their complete replacement with scrub, or even forest, is likely to be detrimental.

*Key-words:* Alps, birds, endangered species, land abandonment, pastures

*Journal of Applied Ecology* (2004) **41**, 294–304

## Introduction

The farmed landscapes of Europe are very diverse, reflecting an ancient history of human settlement. The intensity of land use, and consequently the composition

and distribution of habitats and wildlife communities, has gradually changed across centuries (Pain & Dixon 1997). In the Alps, pastoral activities have been practised for at least 6000 years (Lichtenberger 1994), thereby shaping the alpine environment: pre-existing shrublands and forests were cleared or burned over large areas to increase the availability of wide open grasslands for livestock. Around and above the timberline, traditional mountain farming mostly consisted of

Correspondence: Paola Laiolo, Dipartimento di Biologia Animale e dell'Uomo, Via Accademia Albertina 17, 10123 Turin, Italy (fax +39 0116704732; e-mail paola.laiolo@unito.it).

the 'alpeggio' system, a sort of transhumance in which pastures were grazed during summer months by non-local livestock, which were moved back to valley bottoms for the rest of the year. Hay for feeding livestock in winter was grown below the timberline, especially on rich valley bottom soils. The development of industry in the alpine valleys made the agricultural management regime of mountainous areas less and less necessary or economically viable. As a consequence, people moved to the valley bottoms and the traditional agropastoral systems collapsed, especially in unproductive and remote mountain valleys (Anthelme *et al.* 2001; Didier 2001). Depopulation of rural areas and reduction of stocking levels is a long-term trend that peaked after the Second World War. Now it is omnipresent throughout the Alps and is one of the major driving forces behind changes in ecosystem function and dynamics (Cernusca, Tappeiner & Bayfield 1999; Dirnböck, Dullinger & Grabherr 2003). The ecological consequences of undergrazing or complete elimination of grazing are evident mostly where conditions are suitable for tree and shrub growth: through processes of natural succession grassland gradually turns into shrub and, ultimately, to forest. In the montane belt, shrubs can cover pasture 6–7 years after abandonment, while the same process takes 10–12 years in the subalpine belt (Reyneri 2001). Tree and shrub encroachment leads to a decrease in open ground habitats and reduces heterogeneity in the landscape. In addition, it can have a considerable impact on vegetation characteristics and animal populations (Beaufoy, Baldock & Clark 1994; Pain & Pienkowski 1997). Birds have served as model organisms in a number of studies investigating the individual-, population- and community-level consequences of changes in agropastoral practices. Farmland habitats are known to hold a rich avifauna, comprising several specialists that are highly dependent upon agriculture and grassland (Pain & Pienkowski 1997). Due to agricultural intensification or to the abandonment of traditional, low-intensity farming systems, many birds typical of agropastoral landscapes have an unfavourable conservation status (Tucker & Evans 1997). In order to prevent or reverse declines in these species, we need a clear idea of their requirements. While much work has been done on the effects of intensification of agriculture on farmland birds (Vickery *et al.* 2001), few researchers have addressed the consequences for birds of land abandonment and the decline of pastoral practices (Blanco, Tella & Torre 1998). Moreover, in Europe most studies have concerned bird communities inhabiting lowland grasslands. Few quantitative data are available on the avifauna of montane and alpine pastures, ranging from the lower limit of 1000–1200 m to an upper limit of 3000 m a.s.l.

The aim of this study was to assess the consequences of land-use changes on the diversity and community structure of alpine birds. We focused on the montane belt, where abandoned pastures have been altered through invasion by trees and shrubs, and on the alpine

belt, where structural changes driven by pastoral abandonment are less evident. We analysed the responses of bird communities in terms of their diversity and abundance to a set of variables (elevation, local habitat and landscape variables, plus a descriptor of grazing intensity), in order to highlight important factors for the avifauna of high altitude environments.

## Methods

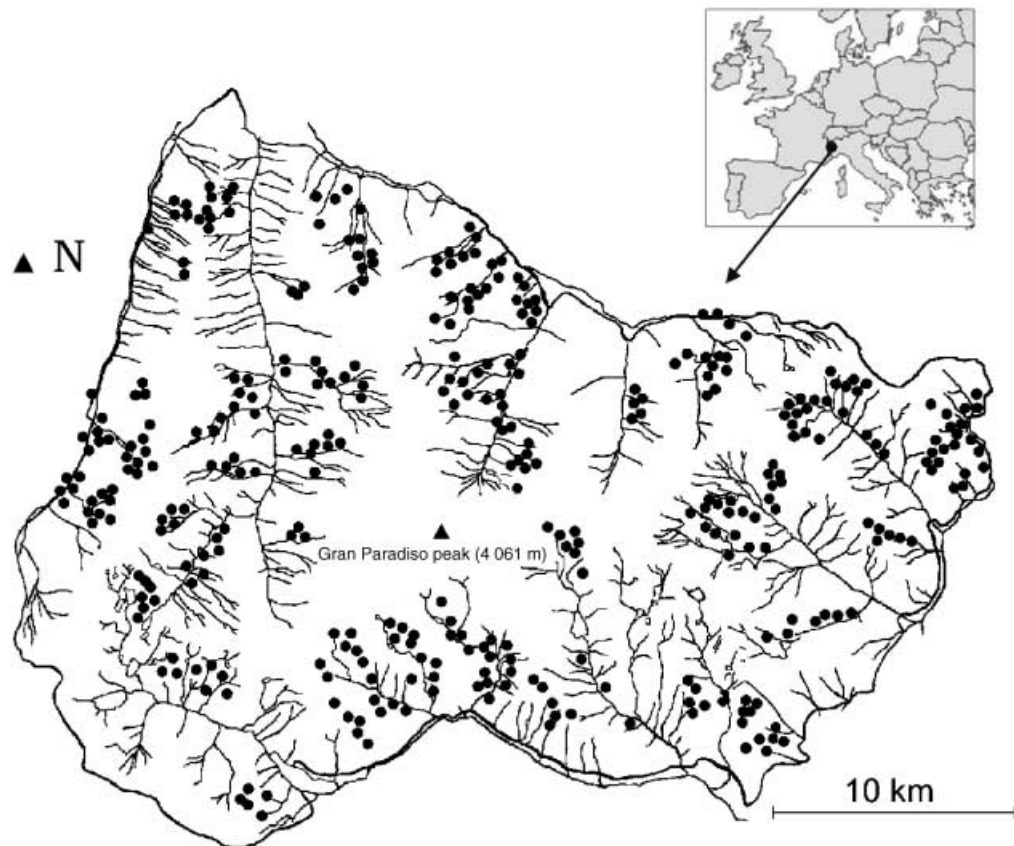
### STUDY AREA

The study was carried out in Gran Paradiso National Park (45°31' N, 7°16' E, north-western Italian Alps; Fig. 1) in June–July 2001 and 2002. The park area extends for about 70 000 ha. The bottom of the valleys is covered by mixed-broadleaved woods (*Castanea sativa*, *Quercus* spp., *Betula alba*, *Populus* spp., *Fraxinus* spp., *Acer* spp.), whereas coniferous woods of European larch *Larix decidua* mixed with Norway spruce *Picea abies*, arrolla pine *Pinus cembra* and, occasionally, silver fir *Abies alba* dominate from around 1000 m a.s.l. to the treeline (1600–2200 m a.s.l.). Progressing up the slopes, trees are replaced by a shrub belt (*Juniperus*, *Rhododendron*, *Vaccinium*, *Arctostaphylos*, *Salix* spp.), wide alpine pastures and natural grassland dominated by *Festuca* and *Nardus* spp. Above 3000 m a.s.l., rocks, screes and snowbeds dominate the alpine landscape, up to the highest peaks and glaciers of Gran Paradiso massif (4061 m a.s.l.). Non-woody vegetation below the timberline consists mainly of semi-natural grasslands dominated by grasses (Gramineae) and green alder *Alnus viridis* shrub growing on disturbed sites (wet and steep slopes, avalanche tracks).

In the study area the decline of stocking levels and summer transhumance activities has precipitated a marked reduction in the extent of grassland below the treeline (Fleury *et al.* 2001). In abandoned pastures, shrubs such as *Berberis*, *Rhododendron*, *Juniperus*, *Alnus*, *Salix* spp., bracken *Pteridium aquilinum* and European larch are encroaching rapidly from field borders and colonizing previously open habitats (Cavallero *et al.* 1997). In pastures that are still exploited, grazing pressure is normally weak, as it occurs for very short periods: 1–2 (sometimes 3) months in July–September

### BIRD SURVEY AND QUANTIFICATION OF LOCAL HABITAT STRUCTURE, GRAZING PRESSURE AND LANDSCAPE PARAMETERS

The grasslands used in this study covered a wide range of altitudes (1000–2800 m a.s.l.) and differed greatly in topography, size (from less than 1 to 1200 ha) and degree of shrub and tree cover. In such heterogeneous landscapes, traditional survey methods such as fixed radius point counts or transects are inappropriate, as differences in bird detectability would bias intersite comparisons. We therefore used a standardized area count method (Bibby *et al.* 2000), surveying birds in



**Fig. 1.** Location of the study area and plots (solid circles); water courses are also shown. The distribution of plots matches that of pastures and abandoned pastures (alpeggi) in the study area; the central zone was under-sampled because it includes bare rocks and glaciers above 3000 m a.s.l.

circular plots of radius 50 m. Counts lasted 15 min. During the first 5 min of the recording period the observer stood still and quiet at the centre of the plot, as in a standard point count, while in the latter part of the count the observer moved around and stopped at suitable vantage points to look and listen, recording all birds seen or heard within the plot. This method is particularly useful when comparing community structure of habitats that differ in vegetation density. Each census plot was visited twice (in June and July of the same year) and the largest values from the two censuses were used as a measure of bird species abundance per plot; overall, 350 plots were visited on two occasions (Fig. 1). Each day a 5–18-km long transect was walked, in an ascent of 800–1500 m. Plots along daily transects were located 200–6000 m away from each other; we were very careful not to record the same individuals on neighbouring plots by tracking birds with binoculars if they were flushed off.

For each plot we calculated the following five variables: vegetation (grass and shrub) height ( $H$ , mean value of 40 measurements per plot taken with a wooden dowel subdivided into 1-cm units; in grazed pastures these were taken prior to grazing); heterogeneity of vegetation height [ $CV = H/SD(H) \times 100$ ]; percentage shrub cover; percentage tree cover; and percentage boulder/stone cover (percentages estimated by eye).

Grazing pressure was estimated, after interviewing local people and consulting the archives of the park as: 0, abandoned pasture where grazing no longer occurred; 1, low to moderate grazing intensity (grasslands were either rapidly crossed by sheep/cows or grazed by free-ranging livestock); 2, high grazing intensity (high stocking levels, with cattle kept in fenced pastures until the whole area was grazed); 3, very high utilization (haymaking associated with grazing, so that the herb layer was kept uniformly short). In the interest of clarity, the terms 'high' and 'very high' have a relative value, as the pastoral activities in the study area were largely extensive. Two landscape variables were calculated from land cover data in the Gran Paradiso GIS database (digitized from 1 : 10 000 aerial photographs) using ArcView (version 3.1, ESRI, CA): the amount of contiguous grasslands (total grassland area) around each census plot and the distance between each plot and the nearest woodland (nearest-neighbour distance from woodland).

#### DATA ANALYSIS

Plots on each transect that were close together were more likely to be similar in bird community composition than those far apart. Accordingly, we tested for plot autocorrelation within transects with Moran's  $I$  coefficient (Moran 1950), a weighted correlation coefficient

used to detect departures from spatial randomness. This index varies between  $-1$  and  $1$ , and a high value indicates positive autocorrelation between plots along a transect. The autocorrelation between the study plots was low (mean  $I = -0.02$ , range  $-0.40$ – $0.20$ ,  $n = 70$  daily transects). Monte Carlo tests with 100 permutations of the data set were used to test for the significance of spatial autocorrelation coefficients via randomization, allowing us to determine if the observed coefficients were significantly different from a random pattern. In all cases, probability levels were  $> 0.05$ , suggesting that plots were spatially independent. Moran's  $I$  and Monte Carlo randomization were performed with RookCase Software (Sawada 1999).

We classified bird species into four major ecological groups: open habitat–grassland species (hereafter grassland species, species that require open fields both for breeding and foraging); ecotone species (species that use grassland and woodland alternatively); shrub species (species that dwell in shrubby areas); and woodland species (species typical of forest and open forest habitats) (see the Appendix).

Bird community structure at each individual plot was expressed in terms of diversity (Shannon index:  $H' = -\sum p_i \times \ln p_i$ , where  $p_i$  is the relative frequency of species  $i$ ) and abundance of the four ecological groups. Results obtained by considering species richness per plot were similar to those achieved using Shannon diversity; hence only the latter index was considered here, as a measure of avian  $\alpha$ -diversity.

To reveal patterns in the local habitat structure and compensate for multicollinearity we summarized habitat attributes with a principal components analysis (PCA) on standardized data (zero mean and unit SD). PCA condensed the original information on three derived axes (PC1, PC2 and PC3) having the benefit of being orthogonal and uncorrelated (Jongman, ter Braak & Van Tongeren 1995). This gave three main factors with eigenvalue  $> 1$  that explained 73.5% of the variability of the data set. Percentage shrub cover and vegetation height showed the highest correlation with PC1 scores (factor loadings  $R = 0.87$  and  $0.80$ , respectively); PC2 was positively correlated with percentage stone cover ( $R = 0.78$ ) and negatively correlated with tree cover ( $R = -0.66$ ), whereas heterogeneity of vegetation height provided the major loading on PC3 ( $R = 0.97$ ). Hereafter PC1, PC2 and PC3 are termed SHRUB-HEIGHT, STONE-TREE and VEGHETERO, respectively.

Mean diversity and abundance of ecological groups were used as dependent variables in stepwise multiple regression analyses using (i) local habitat variables (three PCA scores), (ii) landscape variables, (iii) grazing pressure levels and (iv) elevation as quantitative predictors. To attain a normal distribution, these variables were log-transformed ( $y = \log(x + 1)$ ). Because this transformation proved to be ineffective with the variables bird diversity, abundance of shrub species, abundance of ecotone species and abundance of woodland species, in these four cases normality was achieved through

Box–Cox transformation [ $y = (x^\lambda - 1)/\lambda$ , with  $\lambda = 0.92$  for bird diversity and abundance of woodland species,  $\lambda = 0.98$  for the abundance of shrub species and  $\lambda = 0.50$  for the abundance of ecotone species; Box & Cox 1964].

Before carrying out these regressions, we further tested for correlations between the variables. Grazing pressure proved to be negatively correlated with both elevation ( $R = -0.31$ ) and SHRUB-HEIGHT ( $R = -0.30$ ; with 9% of the variability in SHRUB-HEIGHT being explained by grazing). To control for the effects of vegetation structure and topography on grazing, we used the residuals of the regression between grazing levels vs. elevation and SHRUB-HEIGHT rather than raw values in all the regression models.

In keeping with Herrando & Brotons (2002), we used a parsimonious approach assuming that bird diversity and abundance were affected primarily by elevation, local habitat and grazing pressure, and then by the landscape. A stepwise multiple regression analysis was carried out in two steps. First, bird diversity and abundance of the four ecological groups were used as dependent variables and (i) elevation, (ii) SHRUB-HEIGHT, (iii) STONE-TREE, (iv) VEGHETERO and (v) residuals of grazing pressure (partialling out the effects of elevation and SHRUB-HEIGHT) were used as predictors. Secondly, we used the residuals of the former regression as the dependent variable and (i) total grassland area and (ii) nearest-neighbour distance from woodland as the predictors.

Differences in environmental variables (local habitat and landscape) and bird community among the four grazing levels were also tested by means of one-way ANOVAS on log- or Box–Cox-transformed data (in the case of environmental variables, bird diversity, abundance of grassland, edge, shrub and woodland species) and  $\chi^2$  tests of independence (occurrence of the most common species); in this analysis the altitudinal ranges of 1000–1900 (montane belt) and 1900–2800 (subalpine and alpine belt) m a.s.l. were considered separately.

In order to verify the accuracy of our approach, one-sample Kolmogorov–Smirnov tests were always carried out to test whether the residuals of previous models fit a Gaussian distribution: in all the cases Kolmogorov–Smirnov  $d$  was  $< 0.06$ , and  $P > 0.10$ , suggesting that all residuals were still normally distributed.

## Results

In 350 independent plots we recorded the occurrence of 59 species (see the Appendix), of which 18 were grassland, nine ecotone, four shrub and 25 woodland species. Three species were unclassified either because they occurred in all habitats, for example the cuckoo *Cuculus canorus* L., or because they depended on other habitat features, e.g. wallcreeper *Tichodroma muraria* (L.) on cliffs and dipper *Cinclus cinclus* C.L. Brehm on streams. Grasslands supported the greatest number of threatened species (one-third of grassland species were

declining or vulnerable; *sensu* Tucker & Heath 1994), whereas ecotones, woodlands and shrubs, respectively, held 11%, 4% and 0% of birds with an unfavourable conservation status (see the Appendix).

Within the PCA scores of local habitat, bird diversity was positively correlated with SHRUB-HEIGHT and negatively correlated with STONE-TREE, whereas the four ecological groups showed contrasting responses to habitat predictors. Abundance of grassland and ecotone species decreased at increasing SHRUB-HEIGHT, whereas shrub and woodland species did the opposite. On the other hand, the abundance of ecotone and grassland species showed opposite trends with respect to the elevation, as grassland species increased and ecotone species decreased at increasing altitude. Ecotone and woodland species were also negatively affected by stone cover and positively affected by tree cover (as represented by STONE-TREE).

By considering grazing pressure, the species diversity and abundance of shrub and woodland species were all negatively correlated with grazing pressure, whereas

grassland species were significantly more abundant in grazed pastures (Table 1).

Once local habitat factors, elevation and grazing were controlled for using the residuals of the former model, species diversity and the abundance of woodland species peaked in plots close to woodlands. Conversely, grassland species were positively affected by the distance from the forest (Table 1).

When testing for differences in local habitat and landscape variables among the four levels of grazing pressure, below 1900 m, abandoned and slightly grazed fields showed significantly greater cover of shrubs, trees and stones. Vegetation was significantly taller in abandoned pastures and in fields where both haymaking and grazing occurred (level 3 in grazing pressure), whereas the total grassland patch area was larger in pastures undergoing high utilization (level 2). Above 1900 m a.s.l., abandoned pastures contained significantly taller vegetation and greater shrub cover, while highly grazed plots had the largest grassland patch area. With reference to bird community metrics in the altitudinal range

**Table 1.** Multiple regression models on bird species diversity and abundance of four ecological groups (grassland, ecotone, shrubland and woodland species). The models were conducted in two steps. Step 1: bird diversity and abundance of four ecological groups as dependent variables and elevation, local habitat variables (SHRUB-HEIGHT, STONE-TREE and VEGHETERO) and grazing pressure\* as predictors. Step 2: residuals of the former analysis as dependent variables and landscape variables as predictors. At each step, a backwards stepwise procedure was used; only variables that entered in the model are shown

Variable		Coefficient	SE	t-value	P	R <sup>2</sup>	F	P
Step 1: local habitat, elevation and grazing pressure*								
Species diversity	Intercept	-0.10	0.03	3.10	< 0.01	0.09	$F_{3,346} = 11$	< 0.01
	SHRUB-HEIGHT	0.08	0.03	2.63	< 0.01			
	STONE-TREE	-0.11	0.03	3.41	< 0.01			
	Grazing pressure*	-0.11	0.03	3.56	< 0.01			
Abundance of grassland species	Intercept	-4.9	0.81	6.04	< 0.01	0.23	$F_{3,346} = 35$	< 0.001
	Elevation	1.63	0.25	6.62	< 0.01			
	SHRUB-HEIGHT	-0.09	0.02	5.29	< 0.01			
	Grazing pressure*	0.04	0.02	2.34	< 0.05			
Abundance of ecotone species	Intercept	12.9	4.01	3.17	< 0.01	0.10	$F_{3,346} = 12$	< 0.01
	Elevation	-3.63	1.23	2.94	< 0.01			
	SHRUB-HEIGHT	-0.27	0.08	3.51	< 0.01			
	STONE-TREE	-0.23	0.06	2.86	< 0.01			
Abundance of shrub species	Intercept	-0.53	0.04	12.5	< 0.001	0.44	$F_{2,347} = 138$	< 0.001
	SHRUB-HEIGHT	0.67	0.04	15.9	< 0.001			
	Grazing pressure*	-0.20	0.04	4.7	< 0.001			
Abundance of woodland species	Intercept	36.3	6.92	5.24	< 0.01	0.31	$F_{4,345} = 39$	< 0.001
	Elevation	-10.4	2.09	4.95	< 0.01			
	SHRUB-HEIGHT	0.90	0.13	6.83	< 0.01			
	STONE-TREE	-0.46	0.13	3.33	< 0.01			
	Grazing pressure*	-0.50	0.13	4.24	< 0.01			
Step 2: landscape								
Species diversity	Intercept	0.28	0.11	2.60	< 0.01	0.02	$F_{1,348} = 8.6$	< 0.01
	Nearest-neighbour distance from woodland	-0.13	0.05	2.94	< 0.01			
Abundance of grassland species	Intercept	-0.40	0.11	3.60	< 0.01	0.05	$F_{1,348} = 17$	< 0.01
	Nearest-neighbour distance from woodland	0.19	0.05	4.09	< 0.01			
Abundance of ecotone species	Intercept	0.38	0.11	3.46	< 0.01	0.04	$F_{1,348} = 15$	< 0.01
	Nearest-neighbour distance from woodland	-0.18	0.05	3.92	< 0.01			

\*Residuals of grazing pressure vs. elevation and SHRUB-HEIGHT (predictors), in order to partial out the effects of vegetation structure and elevation on grazing intensity.

of 1000–1900 m a.s.l., diversity peaked in abandoned pastures, but this habitat was not attractive to grassland species. Conversely, shrub and woodland species were more abundant in abandoned pastures. At the species level, eight species were significantly more common in abandoned or lightly grazed fields [dunnock *Prunella modularis* (L.), wren *Troglodytes troglodytes* (L.), chiffchaff *Phylloscopus collybita* (Vieillot), lesser whitethroat *Sylvia curruca* (L.), robin *Erithacus rubecula* (L.), garden warbler *Sylvia borin* (Boddaert), coal tit *Parus ater* L. and willow tit *Parus montanus* Conrad], whereas four species preferred grazed or mown fields [fieldfare *Turdus pilaris* L., red-backed shrike *Lanius collurio* L., whinchat *Saxicola rubetra* (L.) and white wagtail *Motacilla alba* L.; Table 2]. Above 1900 m a.s.l., differences were tested only among the first three grazing levels, as haymaking associated with grazing is no longer practised at such elevations. Bird diversity and

abundance of shrub and woodland species were still greater in abandoned pastures; ecotone species were more abundant in slightly grazed pastures, whereas there was no difference in numbers of grassland species in abandoned or grazed pastures. At the species level, dunnock, wren and willow tit *Parus montanus* still preferred abandoned fields, linnet *Carduelis cannabina* (L.) was more common in slightly grazed fields and skylark *Alauda arvensis* L. favoured grasslands under heavier grazing regimes (Table 3). Below 1900 m a.s.l., the bird community of abandoned pastures was dominated by woodland and shrub species (respectively 45.6% and 26.1% of all the individuals observed), that of grazed pastures by grassland and ecotone species (Table 4); above 1900 m, grassland species made up a disproportionate share of the avifauna in both abandoned and grazed pastures (Table 4).

**Table 2.** Mean  $\pm$  SD of habitat variables, landscape variables, bird diversity and abundance of the four ecological groups in plots under different grazing levels below 1900 m a.s.l. The frequency of occurrence (%) of the most common species is also shown. Differences were tested with one-way ANOVAS and  $\chi^2$  test of independence (d.f. = 3). Grazing levels 0, 1, 2 and 3 represent a gradient of increasing sward utilization. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . See the Appendix for the scientific names of the species listed

	Grazing level				Differences
	0 <i>n</i> = 46 plots	1 <i>n</i> = 21 plots	2 <i>n</i> = 27 plots	3 <i>n</i> = 19 plots	
Below 1900 m a.s.l. (montane belt)					
Vegetation height (cm)	37.4 $\pm$ 34.5	13.2 $\pm$ 7.6	21.8 $\pm$ 26.9	37.4 $\pm$ 29.9	$F_{3,109} = 5.90^{***}$
Heterogeneity of vegetation height (CV percentage)	42.0 $\pm$ 26.1	42.1 $\pm$ 15.4	46.9 $\pm$ 27.9	45.7 $\pm$ 33.3	$F_{3,109} = 0.64$
Shrub cover (%)	34.4 $\pm$ 34.1	7.7 $\pm$ 14.9	1.41 $\pm$ 2.4	1.37 $\pm$ 3.5	$F_{3,109} = 5.36^{**}$
Tree cover (%)	6.54 $\pm$ 10.0	3.14 $\pm$ 7.2	0.39 $\pm$ 1.1	2.26 $\pm$ 7.1	$F_{3,109} = 10.7^{***}$
Boulder/stone cover (%)	10.5 $\pm$ 5.5	10.1 $\pm$ 12.0	1.98 $\pm$ 4.8	0.68 $\pm$ 2.4	$F_{3,109} = 5.90^{***}$
Nearest-neighbour distance from woodland (m)	226 $\pm$ 370	181 $\pm$ 285	98 $\pm$ 164	239 $\pm$ 341	$F_{3,109} = 0.17$
Total grassland area (km <sup>2</sup> )	1.03 $\pm$ 2.2	0.84 $\pm$ 1.5	4.14 $\pm$ 4.3	1.85 $\pm$ 2.9	$F_{3,109} = 6.82^{***}$
Bird diversity	1.25 $\pm$ 0.6	0.91 $\pm$ 0.4	0.77 $\pm$ 0.6	0.85 $\pm$ 0.6	$F_{3,109} = 4.50^{**}$
Abundance of grassland species	1.17 $\pm$ 1.8	1.62 $\pm$ 1.6	1.63 $\pm$ 1.7	2.68 $\pm$ 2.5	$F_{3,109} = 3.00^*$
Abundance of ecotone species	0.59 $\pm$ 1.0	1.00 $\pm$ 1.3	1.41 $\pm$ 1.6	1.53 $\pm$ 2.3	$F_{3,109} = 1.95$
Abundance of shrub species	1.63 $\pm$ 1.5	0.43 $\pm$ 0.9	0.04 $\pm$ 0.2	0.00 $\pm$ 0.00	$F_{3,109} = 18.9^{***}$
Abundance of woodland species	2.85 $\pm$ 3.01	1.24 $\pm$ 1.5	0.74 $\pm$ 1.7	0.79 $\pm$ 1.3	$F_{3,109} = 7.51^{***}$
Frequency of occurrence (%)					
Black redstart	21.7	28.6	14.8	0.0	$\chi^2 = 6.5$
Red-baked shrike	4.4	4.8	0.0	21.1	$\chi^2 = 9.3^*$
White wagtail	0.0	0.0	18.5	21.1	$\chi^2 = 14.3^{**}$
Rock bunting	15.2	9.5	0.0	5.3	$\chi^2 = 5.2$
Whinchat	8.7	28.6	55.6	63.2	$\chi^2 = 26.6^{***}$
Tree pipit	15.2	33.3	29.6	15.7	$\chi^2 = 4.1$
Fieldfare	2.2	0.0	11.1	15.8	$\chi^2 = 6.7^*$
Mistle thrush	15.2	19.1	18.5	0.0	$\chi^2 = 4.0$
Ring ouzel	4.4	4.8	14.8	0.0	$\chi^2 = 5.1$
Carrion crow	4.4	4.8	11.1	15.8	$\chi^2 = 3.3$
Redpoll	8.7	0.0	11.1	15.8	$\chi^2 = 3.6$
Dunnock	41.3	14.3	3.7	0.0	$\chi^2 = 22.4^{**}$
Garden warbler	54.4	9.5	0.0	0.0	$\chi^2 = 40.3^{**}$
Lesser whitethroat	15.2	0.0	0.0	0.0	$\chi^2 = 10.9^{**}$
Wren	34.8	4.8	0.0	5.3	$\chi^2 = 20.9^{**}$
Robin	34.8	4.8	7.4	0.0	$\chi^2 = 18.3^{**}$
Willow tit	17.4	9.5	3.7	0.0	$\chi^2 = 6.2^*$
Coal tit	17.4	19.1	0.0	0.0	$\chi^2 = 9.0^{**}$
Chiffchaff	26.1	9.5	7.4	0.0	$\chi^2 = 9.9^*$
Chaffinch	23.9	19.1	18.5	10.5	$\chi^2 = 1.6$
Blackcap	10.8	4.8	0.0	10.5	$\chi^2 = 3.4$

**Table 3.** Mean ± SD of habitat variables, landscape variables, bird diversity and abundance of the four ecological groups in plots under different grazing levels above 1900 m a.s.l. The frequency of occurrence (%) of the most common species is also shown. Differences were tested with one-way ANOVAs and  $\chi^2$  test of independence (d.f. = 2). \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . Plots under grazing level 3 were not recorded above 1900 m. See the Appendix for the scientific names of the species listed

	Grazing level			Differences
	0 <i>n</i> = 119 plots	1 <i>n</i> = 93 plots	2 <i>n</i> = 25 plots	
Above 1900 m a.s.l. (subalpine and alpine belts)				
Vegetation height (cm)	16.5 ± 29.2	6.6 ± 4.3	5.9 ± 2.8	$F_{2,234} = 5.53^{***}$
Heterogeneity of vegetation height (CV percentage)	51.3 ± 63.4	41.0 ± 17.2	46.1 ± 13.5	$F_{2,234} = 1.57$
Shrub cover (%)	21.4 ± 35.1	8.21 ± 19.7	2.0 ± 6.2	$F_{2,234} = 5.00^{**}$
Tree cover (%)	0.5 ± 2.5	0.19 ± 0.8	0.08 ± 0.3	$F_{2,234} = 0.43$
Boulder/stone cover (%)	16.7 ± 18.5	17.0 ± 19.4	12.7 ± 13.2	$F_{2,234} = 0.01$
Nearest-neighbour distance from woodland (m)	765 ± 781	830 ± 1148	483 ± 291	$F_{2,234} = 0.00$
Total grassland area (km <sup>2</sup> )	2.30 ± 2.5	2.34 ± 3.1	5.37 ± 4.8	$F_{2,234} = 3.85^*$
Bird diversity	0.98 ± 0.5	0.79 ± 0.6	0.79 ± 0.6	$F_{2,234} = 3.69^*$
Abundance of grassland species	3.7 ± 4.3	4.09 ± 6.1	4.72 ± 3.5	$F_{2,234} = 1.59$
Abundance of ecotone species	0.44 ± 1.1	0.88 ± 1.5	0.40 ± 1.0	$F_{2,234} = 3.71^*$
Abundance of shrub species	0.57 ± 1.2	0.12 ± 0.4	0.16 ± 0.6	$F_{2,234} = 7.47^{***}$
Abundance of woodland species	0.75 ± 1.55	0.40 ± 1.0	0.20 ± 0.8	$F_{2,234} = 3.70^*$
Frequency of occurrence (%)				
Black redstart	54.6	50.5	32.0	$\chi^2 = 4.2$
Wheatear	41.2	45.2	56.0	$\chi^2 = 1.9$
Rock thrush	3.4	2.2	4.0	$\chi^2 = 0.3$
Whinchat	1.7	4.3	8.0	$\chi^2 = 2.9$
Water pipit	57.1	47.3	68.0	$\chi^2 = 4.1$
Alpine accentor	10.1	3.2	12.0	$\chi^2 = 4.3$
Skylark	0.8	6.5	12.0	$\chi^2 = 8.3^*$
Snowfinch	4.2	1.1	0.0	$\chi^2 = 2.8$
Red-billed chough	4.2	3.2	4.0	$\chi^2 = 0.1$
Alpine chough	15.1	18.3	16.0	$\chi^2 = 0.4$
Linnet	4.2	14.0	8.0	$\chi^2 = 6.5^*$
Tree pipit	7.6	9.7	0.0	$\chi^2 = 2.6$
Mistle thrush	8.4	17.2	4.0	$\chi^2 = 2.6$
Ring ouzel	8.4	9.7	0.0	$\chi^2 = 5.1$
Dunnock	23.5	8.6	8.0	$\chi^2 = 10.0^{**}$
Lesser whitethroat	9.2	2.2	4.0	$\chi^2 = 4.0$
Wren	15.1	4.3	4.0	$\chi^2 = 8.1^*$
Willow tit	5.9	0.0	0.0	$\chi^2 = 7.2^*$
Nutcracker	3.4	3.2	0.0	$\chi^2 = 0.9$
Chaffinch	10.9	8.6	4.0	$\chi^2 = 1.3$
Redpoll	5.9	4.3	0.0	$\chi^2 = 1.7$

**Table 4.** Percentage relative abundance of the ecological groups (*n*, individuals of the four groups in turn divided by the total number of individuals observed) in plots under different grazing pressure below and above 1900 m a.s.l. Differences among the four groups were tested with  $\chi^2$  goodness-of-fit tests. Grazing levels 0, 1, 2, 3 represent a gradient of increasing sward utilization

	Grazing level			
	0	1	2	3
Below 1900 m a.s.l. (montane belt)				
Grassland species (%)	18.8	37.8	42.7	53.7
Ecotone species (%)	9.4	23.3	36.9	30.5
Shrub species (%)	26.1	10.0	1.0	0.0
Woodland species (%)	45.6	28.9	19.4	15.8
<i>P</i>	< 0.001	< 0.001	< 0.001	< 0.001
Above 1900 m a.s.l. (subalpine and alpine belts)				
Grassland species (%)	67.5	74.5	86.1	
Ecotone species (%)	8.2	16.1	7.3	
Shrub species (%)	10.5	2.2	2.9	
Woodland species (%)	13.8	7.3	3.7	
<i>P</i>	< 0.001	< 0.001	< 0.001	

## Discussion

Ecologists face the complex task of identifying pertinent predictors of community structure within a plethora of environmental characteristics at different scales. The dependence of species–habitat relationships on many factors, ranging from local vegetation structure to landscape features, suggests that several processes operate simultaneously at different scales to influence the community (Pearman 2002). In this study, we developed a conservative model to analyse the relationships between species and environment, supposing that birds are primarily affected by the environmental conditions in their immediate surroundings and only secondarily by the landscape matrix. We believe that such an approach is appropriate for many of the small passerines that are considered here. Individuals often present a restricted range (compared with larger birds), and we hypothesize that they respond primarily to the habitat within their

territories, and then secondarily to the conditions outside. By using this approach and exploiting residuals, we attempted to reduce multicollinearity among predictors.

#### THE EFFECT OF ELEVATION, LOCAL HABITAT AND LANDSCAPE VARIABLES

Bird  $\alpha$ -diversity in the study grasslands increased with shrub and tree cover. By increasing heterogeneity in habitat structure at the local scale, viable populations of more species can be supported. Trees and shrubs increase the available resources and fulfil the habitat requirements of more species. In addition, trees and shrub provide important foraging and nesting substrates, as well as microclimatic refuges during periods of environmental stress (Söderström *et al.* 2001). Considering the four ecological groups of birds, we conclude that the peak of diversity in shrub- and tree-rich patches is determined by the invasion of shrubland and woodland species. Woodland species also tend to prefer pastures as close as possible to the forest. Conversely, open habitat species are mostly confined to higher altitudes, far from wooded areas. Ecotone species show intermediate preferences: they are abundant in pastures with scattered trees, as woodland species, but concurrently prefer shrub-free habitats, as grassland species. These species [tree pipit *Anthus trivialis* (L.), carrion crow *Corvus corone* L., several thrushes *Turdus* spp. and finches *Carduelis* spp.] utilize multiple habitat types and therefore depend on combinations of open grassland for feeding and scattered trees for nesting or singing.

#### THE EFFECT OF GRAZING

In contrast with several centuries of overgrazing elsewhere, the grazing regime in the study area has been declining to a great extent over the last 50 years (Cavallero *et al.* 1997; Fleury *et al.* 2001). Stocking levels have been gradually reduced and the grazing period is now mostly restricted to 1–3 summer months. As grazing and hay-making usually take place from July onwards, the direct effects of grazing (e.g. deterioration of the sward as nesting and sheltering habitat, nest and young destruction through trampling and mowing, decrease in flowering and seed set) are less conspicuous than indirect ones (increase in particular invertebrate prey, long-term changes in sward structure, vegetation and habitat). The most striking effect of grazing on habitat below and around the timberline seems to be the maintenance of large open habitats through the limitation of tree and scrub encroachment: percentage tree and scrub cover increases significantly from heavily grazed through slightly grazed to abandoned pastures. Abandoned fields below 1900 m also show greater stone cover, either because human management involves the removal of stones to increase grassland surface or because the first pastures that were actually abandoned were the less productive ones, with larger proportions of boulders and stones.

Pastoral abandonment temporarily increases habitat heterogeneity, and creates circumstances favoured by more bird species, especially by those of forest origin that follow tree and scrub encroachment. It should be noted, however, that while forest and shrub species are negatively affected by grazing (they represent 70% of the individuals in abandoned pastures below 1900 m, with eight species occurring preferentially in this grassland type), the abundance of grassland species is positively associated with grazing intensity. This is particularly true below 1900 m, where the abundance of grassland species in grazed/mown plots is more than twice that in abandoned fields, and where four species are significantly more common in pastures undergoing heavier grazing or mowing (red-backed shrike, whinchat, fieldfare and white wagtail). The importance of grazing in maintaining an open habitat is much reduced in the alpine belt, where the effects of pastoral abandonment on grassland species are less conspicuous. Above 1900 m a.s.l., ecotone species are more abundant in slightly grazed fields, whereas shrub and woodland species still prefer abandoned pastures. These three groups, however, constitute a minor share of the overall avifauna of high altitude areas (ranging from 32% of all individuals in abandoned fields to 14% in highly grazed plots). At the species level, only two species preferentially dwell in grazed pastures: the linnet, which is mostly found in slightly grazed pastures, and the skylark, which prefers highly grazed pastures.

In conclusion, open habitat species of the montane belt benefit from grazing to a large extent. At higher altitudes only linnet and skylark seem to prefer grazed meadows, whereas for most other species grazing makes no difference. Unfortunately, this study lacks detailed analyses of vegetation composition, which might provide a better indicator of land-use changes at high altitude. It should be stressed, however, that grazing intensity is negatively correlated with elevation, and above 1900–2000 m a.s.l. it is generally modest compared with that at lower elevations (Table 3). Red-billed chough *Pyrrhocorax pyrrhocorax* L. and rock thrush *Monticola saxatilis* (L.), whose decline in Europe has been related to the loss of extensive grazing systems (Sanchez 1994; McCracken & Bignal 1998), show no preference for grazed (either slightly or heavily) fields. However, these species are quite rare in our study area.

#### CONSERVATION IMPLICATIONS

According to the European Union (EU) Habitat Directive, more than 50% of the biotopes in Europe warranting special conservation measures occur in low-intensity farmland landscapes (Bignal & McCracken 1996). Habitat loss of semi-natural grasslands is recognized as a serious threat to many rare and declining animal and plant species (Fuller 1987; Beaufoy, Baldock & Clark 1994; Labaune & Magnin 2002). This study shows that abandonment of upland pastures in the Italian Alps has profound effects on bird assemblages,

but the assessment of grazing importance can differ markedly depending on whether the focus is  $\alpha$ -bird diversity or grassland bird abundance. Avian diversity responds positively to pastoral abandonment because forest species invade abandoned meadows, whereas grassland and ecotone species (to a lesser extent) benefit from grazing. While pastoral abandonment leads to an overall increase in avian  $\alpha$ -diversity, not all species have equal conservation value. Most woodland species that are now invading abandoned pastures need no special assistance, as only 4% have unfavourable status. Furthermore, forest species with unfavourable conservation status need ancient climax forest, which would require centuries to develop from these abandoned pastures; we do not even know if true forest is able to recover fully because the soil has eroded after forest clearance and grazing. Conversely, one-third (33%) of the grassland species recorded in this study are threatened, and some of them are dependent upon grazing. Skylark and red-backed shrike are, respectively, vulnerable and declining species, and the whinchat, despite being secure, is becoming rare in western Europe (populations are declining in 54% of countries), while the linnet is showing a negative population trend in Britain (Tucker & Heath 1994; Chamberlain & Crick 1999; Henderson, Vickery & Fuller 2000). Thus, in terms of bird conservation objectives, large-scale abandonment of semi-natural pastoral habitats and their replacement with scrub, or even forest, is likely to be detrimental, taking into account that upland grasslands are becoming important refuges for grassland species that extend their ranges down to lowlands, where suitable meadows are rapidly diminishing in extent. Moreover, although anthropogenic in nature, semi-natural grasslands are long-established habitats with a complex structure and plant composition, a crucial factor for most wildlife.

Based on the results of this study, bird diversity seems to reflect habitat heterogeneity rather than its quality. We suggest that the occurrence and abundance of some sensitive species (i.e. those listed as priority species for grassland conservation; *sensu* Tucker & Evans 1997) should be investigated in relation to habitat, landscape and grazing regimes before conservation plans are made in the alpine environments. Moreover, if a larger scale is considered, the landscape mosaic created by grazing may be of considerable importance in meeting the diverse habitat requirements of several species, thus contributing to  $\alpha$ -diversity. Overall, semi-natural alpine grasslands need appropriate sustainable management for the benefit of birds, biological diversity and the sustainability and quality of life of rural communities. The latter is particularly important, as social factors cannot be divorced from nature conservation issues, and rural poverty and low standards of living cannot be encouraged just because they are associated with high nature conservation-value farmland (McCracken *et al.* 1997). An integrated approach to agricultural, environmental and social policies for such areas is therefore highly recommended.

## Acknowledgements

This research was funded by Gran Paradiso National Park. We wish to thank Bruno Bassano, Michele Ottino, Patrizia Vaschetto and all the staff of the park for encouraging our study and for logistic support. We are also very grateful to the park guards and local farmers for kindly tolerating our never-ending interviews on the agropastoral activities in the study area. Sergi Herrando, Davy McCracken, Steve Rushton, Gillian Kerby, Luca Borghesio, and an anonymous referee provided valuable suggestions and comments that greatly improved the manuscript.

## References

- Anthelme, F., Grossi, J.L., Brun, J.J. & Didier, L. (2001) Consequences of green alder expansion on vegetation changes and arthropod communities removal in the northern French Alps. *Forest Ecology and Management*, **145**, 57–65.
- Beaufoy, G., Baldock, D. & Clark, J. (1994) *The Nature of Farming*. Joint Nature Conservation Committee, Peterborough, UK.
- Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S.H. (2000) *Bird Census Techniques*, 2nd edn. Academic Press, London.
- Signal, E.M. & McCracken, D.I. (1996) Low-intensity farming systems in the conservation of the countryside. *Journal of Applied Ecology*, **33**, 413–424.
- Blanco, G., Tella, J.L. & Torre, I. (1998) Traditional farming and key foraging habitats for chough *Pyrrhocorax pyrrhocorax* conservation in a Spanish pseudosteppe landscape. *Journal of Applied Ecology*, **35**, 232–239.
- Box, G.E.P. & Cox, D.R. (1964) An analysis of transformations. *Journal of the Royal Statistical Society*, **26**, 211–243.
- Cavallero, A., Bassignana, M., Juliano, G. & Reyneri, A. (1997) Sistemi foraggeri semi-intensivi e pastorali per l'Italia settentrionale: analisi di risultanze sperimentali e stato attuale dell'alpicoltura. *Rivista di Agronomia*, **31**, 482–504.
- Cernusca, A., Tappeiner, U. & Bayfield, N. (1999) *Land-Use Changes in European Mountain Ecosystems*. Blackwell Wissenschafts-Verlag, Berlin, Germany.
- Chamberlain, D.E. & Crick, H.Q.P. (1999) Population decline and reproductive performance of skylarks *Alauda arvensis* in different region and habitats of the United Kingdom. *Ibis*, **141**, 38–51.
- Didier, L. (2001) Invasion patterns of European larch and Swiss stone pine in subalpine pastures in the French Alps. *Forest Ecology and Management*, **145**, 67–77.
- Dirnböck, T., Dullinger, S. & Grabherr, G. (2003) A regional impact assessment of climate and land-use change on alpine vegetation. *Journal of Biogeography*, **30**, 401–407.
- Fleury, P., Curtenaz, D., Bassignana, M., Francesia, C., Jacquemod, C., Stucki, E., Rognon, P., Charretton, P., Barbut, L. & Sauvain, P. (2001) Relations agriculture/environnement dans les Alpes Occidentale: impact des politiques publiques européennes et suisses et propositions d'adoptions. *Studio Euromontana*, pp. 10. Assessorato Territorio, Ambiente e Opere pubbliche, Regione Autonoma Valle d'Aosta, Aosta, Italy.
- Fuller, R.M. (1987) The changing extent and conservation interest of lowland grasslands in England and Wales: a review of grassland surveys 1930–1984. *Biological Conservation*, **40**, 281–300.
- Henderson, I.G., Vickery, J.A. & Fuller, R.J. (2000) Summer abundance and distribution on set aside fields on intensive arable farms in England. *Ecography*, **2**, 50–59.
- Herrando, S. & Brotons, L. (2002) Forest bird diversity in Mediterranean areas affected by wildfires: a multi-scale approach. *Ecography*, **25**, 161–172.

- Jongman, R.H.G., ter Braak, C.J.F. & Van Tongeren, O.F.R. (1995) *Data Analysis in Community and Landscape Ecology*. Cambridge University Press, Cambridge, UK.
- Labauane, C. & Magnin, F. (2002) Pastoral management vs. land abandonment in Mediterranean uplands: impact on land snail communities. *Global Ecology and Biogeography*, **11**, 237–245.
- Lichtenberger, E. (1994) Die Alpen in Europa. *Österreichische Akademie der Wissenschaften. Veröffentlichungen der Kommission für Humanökologie*, **5**, 53–86.
- McCracken, D.I. & Bignal, E.M. (1998) Applying the results of ecological studies to land-use policies and practices. *Journal of Applied Ecology*, **35**, 961–967.
- McCracken, D.I., Pienkowski, M., Bignal, E., Baldock, D., Tubbs, C., Yellachich, N., Corrie, H. & van Dijk, G. (1997) The importance of livestock farming for nature conservation. *Mountain Livestock Farming and EU Policy Development* (eds A. Poole, M. Pienkowski, D.I. McCracken, F. Petretti, C. Brédy & C. Deffeyes), pp. 19–28. Proceedings of the Fifth European Forum on Nature Conservation and Pastoralism, Cogne, Italy.
- Moran, P.A.P. (1950) Notes on continuous stochastic phenomena. *Biometrika*, **37**, 17–23.
- Pain, D.J. & Dixon, J. (1997) Why farming and birds in Europe? *Farming and Birds in Europe* (eds D.J. Pain & M.W. Pienkowski), pp. 1–24. Academic Press, London, UK.
- Pain, D.J. & Pienkowski, M.W. (1997) *Farming and Birds in Europe*. Academic Press, London, UK.
- Pearman, P.B. (2002) The scale of community structure: habitat variation and avian guilds in tropical forest understorey. *Ecological Monographs*, **72**, 19–39.
- Reyneri, A. (2001) Integrazione tra attività agricola e ricreativa nelle vallate alpine. *Le aree a verde per i centri turistici dell'ambiente alpino*. Assessorato Agricoltura e Risorse Naturali, Regione Autonoma Valle d'Aosta, Aosta, Italy. Relazione Eecnica.
- Sanchez, A. (1994) Rock thrush *Monticola saxatilis*. *Birds in Europe: Their Conservation Status* (eds G.M. Tucker & M.F. Heath), pp. 390–391. BirdLife Conservation Series No. 3. BirdLife International, Cambridge, UK.
- Sawada, M. (1999) ROOKCASE: an Excel 97/2000 visual basic (VB) add-in for exploring global and local spatial autocorrelation. *Bulletin of the Ecological Society of America*, **80**, 231–234.
- Söderström, B., Svensson, B., Vessby, K. & Glimskär, A. (2001) Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodiversity and Conservation*, **10**, 1839–1863.
- Tucker, G.M. & Evans, M.I. (1997) *Habitat for Birds in Europe. A Conservation Strategy for the Wider Environment*. BirdLife Conservation Series No. 6. BirdLife International, Cambridge, UK.
- Tucker, G.M. & Heath, M.F. (1994) *Birds in Europe: Their Conservation Status*. BirdLife Conservation Series No. 3. BirdLife International, Cambridge, UK.
- Vickery, J.A., Tallowin, J.R., Feber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J. & Brown, V.K. (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology*, **38**, 647–664.

Received 7 May 2003; final copy received 4 December 2003

## Appendix

List of the bird species recorded in the 350 plots of Gran Paradiso National Park. Species were classed as grassland, shrub, ecotone and woodland according to their ecological preferences. The frequency of occurrence (%) and the conservation status (Tucker & Heath 1994) are also shown. SPEC = Species of European Conservation Concern

Common name	Scientific name	Ecological group	Frequency of occurrence (%)	Conservation status
Black grouse	<i>Tetrao tetrix</i>	Ecotone	0.9	SPEC 3
Tree pipit*	<i>Anthus trivialis</i>	Ecotone	12.3	–
Ring ouzel*	<i>Turdus torquatus</i>	Ecotone	7.4	SPEC 4
Fieldfare*	<i>Turdus pilaris</i>	Ecotone	2.9	SPEC 4
Mistle thrush*	<i>Turdus viscivorus</i>	Ecotone	12.3	SPEC 4
Carrion crow*	<i>Corvus corone</i>	Ecotone	2.9	–
Serin	<i>Serinus serinus</i>	Ecotone	1.4	SPEC 4
Goldfinch	<i>Carduelis carduelis</i>	Ecotone	1.4	–
Linnet*	<i>Carduelis cannabina</i>	Ecotone	7.1	SPEC 4
Ptarmigan	<i>Lagopus mutus</i>	Grassland	0.3	–
Rock partridge	<i>Alectoris graeca</i>	Grassland	2.0	SPEC 2
Skylark*	<i>Alauda arvensis</i>	Grassland	3.4	SPEC 3
Water pipit*	<i>Anthus spinoletta</i>	Grassland	39.1	–
Grey wagtail	<i>Motacilla cinerea</i>	Grassland	2.6	–
White wagtail*	<i>Motacilla alba</i>	Grassland	2.9	–
Alpine accentor*	<i>Prunella collaris</i>	Grassland	5.1	–
Black redstart*	<i>Phoenicurus ochruros</i>	Grassland	40.0	–
Whinchat*	<i>Saxicola rubetra</i>	Grassland	12.9	SPEC 4
Rock Thrush*	<i>Monticola saxatilis</i>	Grassland	2.0	SPEC 3
Wheatear*	<i>Oenanthe oenanthe</i>	Grassland	31.1	–
Red-backed shrike*	<i>Lanius collurio</i>	Grassland	2.3	SPEC 3
Alpine chough*	<i>Pyrrhocorax graculus</i>	Grassland	11.4	–
Red-billed chough*	<i>Pyrrhocorax pyrrhocorax</i>	Grassland	2.9	SPEC 3
Raven	<i>Corvus corax</i>	Grassland	0.3	–
Snowfinch*	<i>Montifringilla nivalis</i>	Grassland	1.7	–
Italian sparrow	<i>Passer italiae</i>	Grassland	0.6	–
Rock bunting*	<i>Emberiza cia</i>	Grassland	4.3	SPEC 3
Dunnock*	<i>Prunella modularis</i>	Shrub	17.4	SPEC 4
Lesser whitethroat*	<i>Sylvia curruca</i>	Shrub	6.0	–
Whitethroat	<i>Sylvia communis</i>	Shrub	0.3	SPEC 4
Garden Warbler*	<i>Sylvia borin</i>	Shrub	9.1	SPEC 4
Great spotted woodpecker	<i>Dendrocopos major</i>	Woodland	0.3	–
Green woodpecker	<i>Picus viridis</i>	Woodland	0.3	SPEC 2
Wren*	<i>Troglodytes troglodytes</i>	Woodland	11.7	–
Robin*	<i>Erithacus rubecula</i>	Woodland	6.3	SPEC 4
Blackbird	<i>Turdus merula</i>	Woodland	0.9	SPEC 4
Song thrush	<i>Turdus philomelos</i>	Woodland	0.9	SPEC 4
Blackcap*	<i>Sylvia atricapilla</i>	Woodland	2.3	SPEC 4
Bonelli's warbler	<i>Phylloscopus bonelli</i>	Woodland	0.6	SPEC 4
Chiffchaff	<i>Phylloscopus collybita</i>	Woodland	6	–
Goldcrest	<i>Regulus regulus</i>	Woodland	0.9	SPEC 4
Long-tailed tit	<i>Aegithalos caudatus</i>	Woodland	0.9	–
Coal tit*	<i>Parus ater</i>	Woodland	4.3	–
Willow tit*	<i>Parus montanus</i>	Woodland	5.1	–
Marsh tit	<i>Parus palustris</i>	Woodland	0.3	–
Crested tit	<i>Parus cristatus</i>	Woodland	1.1	SPEC 4
Blue tit	<i>Parus caeruleus</i>	Woodland	0.3	SPEC 4
Great tit	<i>Parus major</i>	Woodland	0.3	–
Treecreeper	<i>Certhia familiaris</i>	Woodland	0.3	–
Jay	<i>Garrulus glandarius</i>	Woodland	1.7	–
Nutcracker*	<i>Nucifraga caryocatactes</i>	Woodland	3.4	–
Chaffinch*	<i>Fringilla coelebs</i>	Woodland	12.6	SPEC 4
Citril finch	<i>Serinus citrinella</i>	Woodland	0.9	SPEC 4
Redpoll*	<i>Carduelis flammea</i>	Woodland	6.0	–
Bullfinch	<i>Pyrrhula pyrrhula</i>	Woodland	1.7	–
Crossbill	<i>Loxia curvirostra</i>	Woodland	0.3	–
Wallcreeper	<i>Tichodroma muraria</i>	–	0.3	–
Dipper	<i>Cinclus cinclus</i>	–	0.6	–
Cuckoo	<i>Cuculus canorus</i>	–	0.9	–

\*Birds included in comparisons at the species level (Tables 2 and 3).