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Predicting the effects of agricultural changes in central Spanish croplands on seed-eating overwintering birds

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Abstract

The application of the European Common Agricultural Policy is causing traditional crop cultivations to be abandoned over large areas of central Spain. This study tries to assess the effects of these changes on overwintering seed-eating birds by examining how changes in land use could affect winter seed abundances and vegetation structure. Bird densities were measured in the winters of 1985 and 1989, and seed densities and vegetation structure were measured in 1989, in five major habitat types (grasslands, old fields, growing crops, stubble and ploughed fields). The food requirements of birds and the abundances of seeds were transformed to a common energy currency (kJ 10 ha^{-1}) to allow direct comparisons. Estimated winter food requirements were on average an order of magnitude smaller than seed abundances across the five habitat types, and the between-habitat distribution patterns of seed abundance and food requirements of birds did not match at all. Bird abundances tended to be inversely related to herb biomass and shrub cover, which were much larger in uncultivated habitats. From the results obtained, we would expect a decrease of the overwintering seed-eating bird populations in the area if the decrease in cereal crop is maintained. This decrease appears to be due to the increasingly constraining role of vegetation structure (which probably affects food accessibility and perceived predation risk) that would outweigh the larger seed abundance offered by uncultivated habitats relative to croplands.

1. Introduction

Until recently, farming policies in many Mediterranean areas have been based on traditional extensive exploitations that survived within closed, protectionist economic systems (Baldock and Long, 1987). These exploitations usually have a low environmental impact, allowing the preservation of much of the biological diversity in this region. The entry of some Mediterranean countries into the European Economic Community (EEC) is now producing a crisis in most of these systems because of their low commercial competitiveness (Baldock and Long, 1987). Hence, a change of land use in many Mediterranean areas is only to be expected.

The northern half of central Spain is a large plateau (around 95 000 km^2), with a cold, inland Mediterranean climate. Its traditional agriculture is extensive cereal growing, whose productivity is two to three times lower than in non-Mediterranean European countries (Tió, 1991). The application of the Common Agricultural Policy in this area has resulted in a decline in cereal cultivation, further stimulated by EEC funding (Commission of the European Com-

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munities, 1990). Abandoned fields can have two possible uses: cheap wood production, or extensive livestock rearing on the old fields and grasslands. These changes in land use will produce strong modifications in the structure of the vegetation (i.e. permanent herb cover, increase of shrub and tree covers, decrease of bare ground, etc.) and in the abundance of seed resources for birds (seed banks usually are much larger in arable land than in grasslands or forests; see Roberts, 1981), so that changes in the bird populations inhabiting Spanish croplands are to be expected. Despite the interest in the use of these croplands for the conservation of steppe bird species (de Juana, 1990), and their role as overwintering grounds for many granivorous birds (Tellería et al., 1988), little work has been done to ascertain the consequences of the outlined agricultural changes on the bird populations inhabiting Spanish croplands.

In this paper we analyze the distribution patterns of seed-eating birds overwintering in central Spain as related to the distribution of their main food resource, i.e. the seeds of wild and cultivated plants, which varies according to the use of agricultural land (Díaz, 1991, 1992a). The study was carried out in an agricultural landscape composed of a mosaic of the five major habitat types found in the open landscapes of the area, thus providing the conditions for a 'natural experiment' that could reveal the effects of seed abundance on the distribution patterns of overwintering seed-eating birds. Vegetation structure (herb biomass, shrub cover) also differs between habitat types (Díaz, 1992a), so we can also assess whether bird abundance correlates with these resource-independent factors.

2. Material and methods

2.1. Study area

Field work was carried out near Sepúlveda (central Spain; 41°15′N, 3°51′W). The study area (1000 m a.s.l.) has a Mediterranean inland climate, with hot summers (20°C on average in July and August) and cold winters (averaging 1–2°C in January). Annual rainfall averages 610 mm and is evenly distributed throughout the year except for a marked summer drought (Ministerio de Agricultura, 1987).

The landscape is dominated by croplands of barley and wheat (70% of the study area). The general appearance and floristic composition of croplands change during the year mainly as a result of human use, defining three main temporal habitats: growing crops, stubble and ploughed fields. Between agricultural fields, two types of uncultivated habitats can be found: (a) old fields (8% of the study area), located on poorly developed and dry soils; they present shrubby patches (0, 25–0, 5 m tall; mainly *Thymus* spp., *Astragalus granatensis* Lam., and *Helianthemum* spp.) covering around 10% of their surface; (b) grasslands (15% of the study area), growing on well developed and wet soils; they are densely covered by herbaceous plants 10–20 cm tall, and present some isolated (cover less than 2%) *Rosa* spp. shrubs 2–3 m tall. The remaining land area is occupied by poplars (*Populus nigra* L.) along the rivers (3%) and small villages (4%). A more detailed description can be found in Tellería et al. (1988) and Díaz (1991, 1992a).

2.2. Seed abundance and energy contents

Twelve square plots (400 m×400 m), scattered over an area of approximately 200 km^2, were established, reflecting different combinations of the three main habitats (croplands, grasslands, and old fields). On each plot, 22 seed samples were taken in January 1989 to cover the five habitat types (growing crops, stubble and ploughed, and old fields and grasslands). Sampling occurred at 20-pace (approximately 18 m) intervals along a transect (Díaz, 1992a). Vegetation was sampled by cutting all the seed-bearing plants within a 20 cm×20 cm wooden frame placed on the ground, and counting all the seeds and fruits in the laboratory (Díaz, 1991). Two contiguous soil samples 3.8 cm×3.8 cm, 1 cm deep, were taken 15 cm away from the wooden

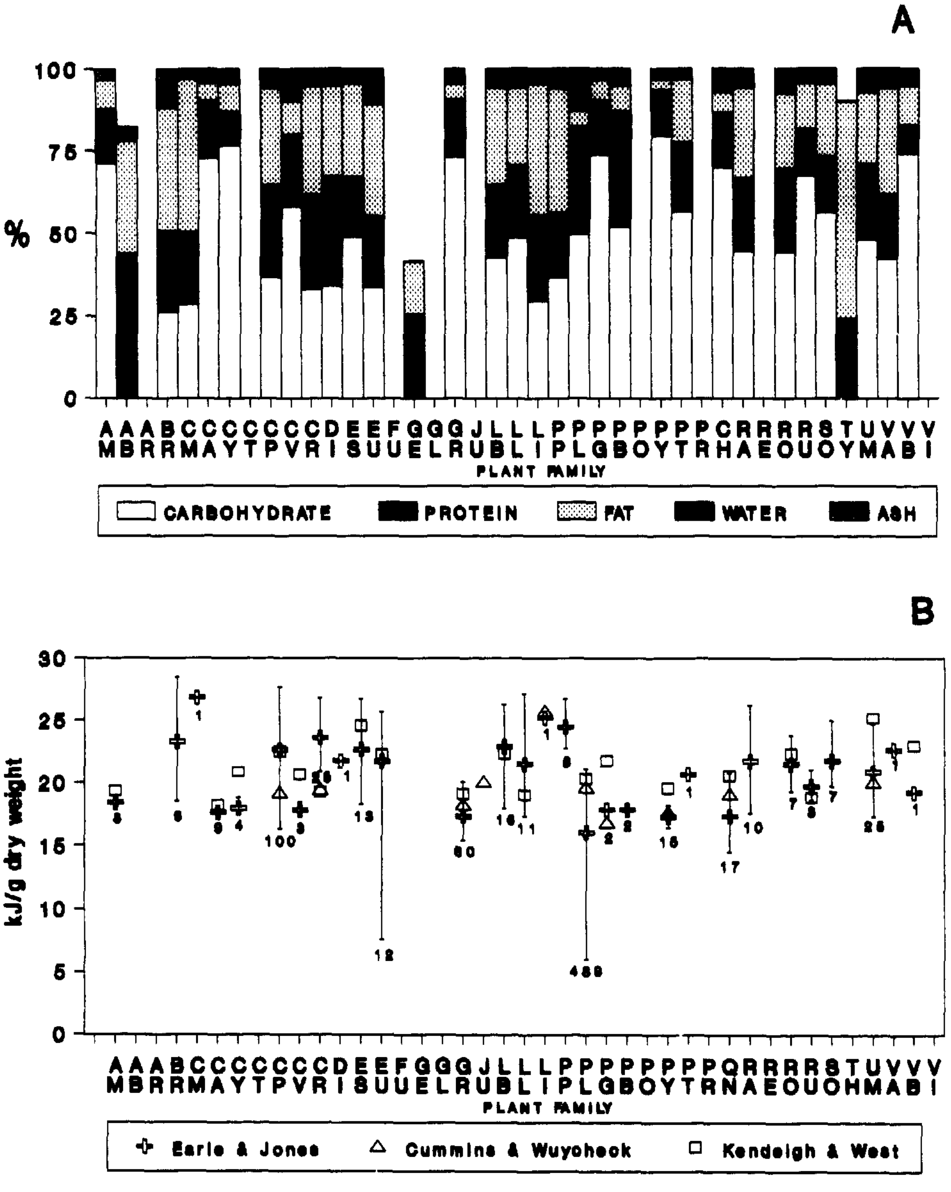

Fig. 1. Average nutrient composition (A) and energy contents (B) of the seeds of the plant families present in the study area (E. Pangua, unpublished data, 1986). Vertical lines and figures represent the range of values obtained and the number of seed samples for each family provided by Earle and Jones (1962), respectively. Plant families: AM, Amaranthaceae; AB, Ambrosianaceae; AR, Aristolochiaceae; BR, Borraginaceae; CM, Campanulaceae; CA, Caryophyllaceae; CY, Cyperaceae; CT, Cistaceae; CP, Compositae; CV, Convolvulaceae; CR, Cruciferae; DI, Dipsacaceae; ES, Scrophulariaceae; EU, Euphorbiaceae; FU, Fumariaceae; GE, Geraniaceae; GL, Globulariaceae; GR, Graminae; JU, Juncaceae; LB, Labiatae; LL, Liliaceae; LI, Linaceae; PP, Papaveraceae; PL, Papilionaceae (Leguminosae); PG, Plantaginaceae; PB, Plumbaginaceae; PO, Polygalaceae; PY, Polygonaceae; PT, Portulacaceae; PR, Primulaceae; CH, Chenopodiaceae; RA, Ranunculaceae; RE, Resedaceae; RO, Rosaceae; RU, Rubiaceae; SO, Solanaceae; TY, Thymeledaceae; UM, Umbelliferae; VA, Valerianaceae; VB, Verbenaceae; VI, Violaceae. For further details, see text.

frame in the transect direction. The soil from these two samples was pooled, air-dried in the laboratory for at least 1 month, and washed through 4, 2, 1 and 0, 6 mm sieves after treatment with a soil disperser (5 g sodium bicarbonate, 10 g sodium hexametaphosphate and 200 cc water per 100 g soil; Díaz, 1991, 1992a). Seeds and fruits retained were counted under a dissecting microscope.

The same sampling points were used to measure vegetation structure by estimating the values of eight physiognomic variables within a 1 m^2 circle around them. A Principal Component Analysis of these variables revealed two main multivariate gradients of vegetation structure, namely herb biomass (33% of the variance explained) and degree of land use by man (25% of the variance). Shrub cover was among these variables, but it was uncorrelated to any Principal Component so that it was used as an independent variable (see Díaz 1992a, for further details).

Most soil and vegetation seeds were identified to species using a reference collection from the study area. Air-dried, intact seeds picked at random from the soil and vegetation samples were measured to estimate average fresh seed weights. Whenever possible, at least ten seeds of each species were weighed, individually or in groups of five to ten, using an electronic balance (intrinsic error = 0.1 mg), after removing heavy seed coats (as in *Sanguisorba minor* Scopoli or *Xanthium spinosum* L.) and ancillary structures (hairs, awns, etc.). Average seed composition and energy value for each plant family were obtained from the literature. Water, ash, protein and fat were derived from Earle and Jones (1962), carbohydrate being calculated as 100% minus water, ash, protein and fat (Becker, 1961; Díaz, 1990). Energy value was calculated using the values: fat 38.94 kJ g^{-1}; protein and carbohydrate: 17.17 kJ g^{-1} (Glück, 1985; Díaz, 1990). Calculations were made for each seed sample and then averaged per plant family (Figs. 1a, b). Figures obtained were similar to those provided by two independent studies of seed caloric values (Kendeigh and West, 1965; Cummins and Wuycheck, 1971; see Fig. 1b), data provided by Cummins and Wuycheck (1971) for the energy contents of the Juncaceae were also used.

Average energy abundance per unit area was obtained by multiplying average soil and vegetation numbers of each seed species by their mean fresh weights, adding the values obtained across families, then multiplying by the average energy values of each family after correcting for its mean water content, and finally summing the values obtained for each habitat type and seed location (soil or vegetation).

2.3. Bird abundance and energy requirements

A census of 23 400 m × 400 m plots was made twice during winter 1985 (January and February), and 12 plots (those studied for seed abundance and vegetation structure) five times in January–February 1989. All plots represented a wide range of combinations of the five open habitat types studied (Tellería et al., 1988; Díaz, 1991). In each census a zig-zag transect was walked across the entire plot to flush out all the birds occupying it. The number of birds observed and the habitat type they occupied were recorded. Care was taken to avoid double contacts. From these data, we evaluated the bird assemblages exploiting each habitat type by means of the following algorithm

$$d_a = \Sigma n_{ai} / \Sigma s_{ai}$$

where d_a is the density (no. birds 10 ha^{-1}) of each bird species in the habitat type a, n_{ai} the number of individuals recorded on habitat a in the ith plot, and s_{ai} the surface of habitat a in the ith plot.

The density of each species in each habitat type was multiplied by its daily field metabolic rate (FMR), calculated from Nagy's (1987) allometric equation

$$\log(\mathrm{FMR}) = 0.949 + 0.749 \times \log(\text{body weight})$$

where FMR is expressed in kJ day^{-1} and body weight in g (data from Perrins, 1987). This equation was computed from measurements obtained during the breeding season by means of the Double Labelled Water technique (it is nearly impossible to recapture individual birds at other times of the annual cycle within the 24–48 h period required). The FMR of breeding birds seems to be, however, extremely high, and probably at the limit of the sustained energy mobilization because of the reproductive effort (Paladino, 1989). Results were multiplied by 120 days to obtain an estimate of the energy requirements of each species during winter (1 December – 31 March). The energy requirements of the bird assemblages exploiting each habitat type, were obtained by summing the calculated values across the whole seed-eating bird species set.

Table 1
Seed and bird densities in winters 1985 (birds) and 1989 (both birds and seeds). Sample sizes (number of seed sampling points, and surface censused for birds), are also shown. See text for details

	Seed abundance (mean no. m^{-2})									
	Shrubland ($N=71$)		Grassland ($N=65$)		Growing ($N=45$)		Stubble ($N=33$)		Ploughed ($N=50$)	
	Soil	Veg.	Soil	Veg.	Soil	Veg.	Soil	Veg.	Soil	Veg.
Leguminosae	1872	442	4879	1559	46	0	483	27	14	0
Gramineae	1292	789	2343	1551	7	0	923	0	131	0
Compositae	999	333	777	551	15	0	1773	1214	13	0
Polygonaceae	39	1	1656	0	469	0	1468	49	415	0
Caryophyllaceae	229	97	1816	110	0	0	1049	240	228	0
Borraginaceae	126	0	111	4	200	0	356	74	124	0
Portulacaceae	24	0	346	0	100	0	304	0	0	0
Others	2126	890	916	325	130	0	2046	183	547	0
Unknown	107	34	47	66	100	0	230	1	110	0
Total	6817	2591	12896	4167	1069	0	8635	1790	1585	0

	Bird abundance (mean no. 10 ha^{-1})									
	Shrubland Study year		Grassland Study year		Growing Study year		Stubble Study year		Ploughed Study year	
	1985	1989	1985	1989	1985	1989	1985	1989	1985	1989
Surface censused (ha)	135.0	52.3	54.6	48.8	41.0	30.7	69.0	21.8	47.2	38.4
Alectoris rufa	0.6	1.1	0.1	0.3	0.4	0.7	1.1	1.4	0.0	0.1
Alauda arvensis	2.4	1.5	10.2	4.2	24.9	19.9	23.6	23.7	2.7	8.4
Melanocorypha calandra	0.4	0.0	0.5	0.2	12.6	25.8	15.4	15.1	3.7	16.6
Galerida cristata	0.0	0.0	0.0	0.0	0.2	0.0	1.5	0.1	0.6	0.1
Galerida theklae	0.9	0.5	0.0	0.0	0.0	0.0	0.3	0.0	0.1	0.4
Fringilla coelebs	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.1	0.0	0.0
Carduelis carduelis	0.0	0.0	0.0	0.2	0.0	0.0	0.0	1.2	0.0	0.0
Carduelis cannabina	1.2	3.1	4.5	0.0	0.0	1.6	9.6	39.6	0.9	18.4
Passer montanus	0.1	0.0	0.0	3.0	0.0	0.6	2.2	4.3	0.0	0.3
Petronia petronia	0.0	0.0	0.1	0.0	0.0	0.0	0.0	16.4	0.0	0.0
Emberiza schoeniclus	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Miliaria calandra	0.6	0.2	0.7	0.7	0.0	1.5	0.8	6.3	0.1	1.5
Total	6.1	6.5	16.0	9.1	38.0	50.1	54.6	108.1	8.1	45.7

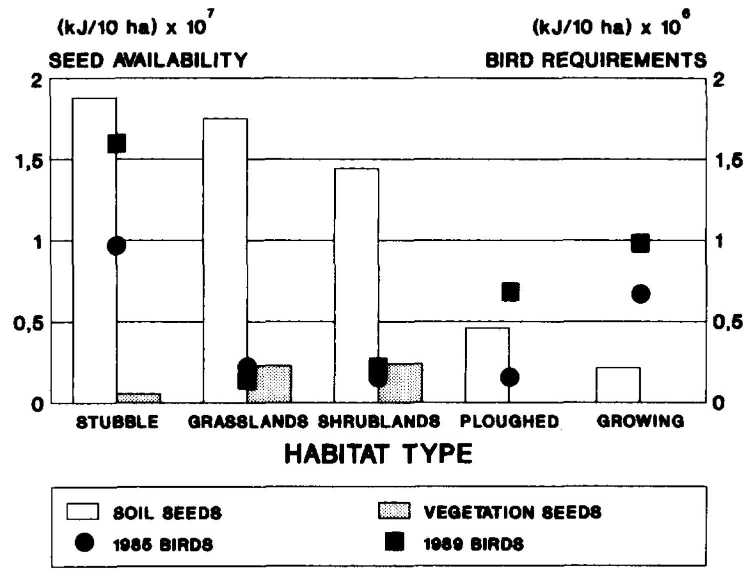

Fig. 2. Seed abundance in winter 1989, and whole winter bird requirements in both 1985 and 1989, according to habitat type (ordered in decreasing soil seed abundance). The values presented were obtained by transforming bird and seed numbers to a common energy currency (see text for the methodology employed). The different scales used for bird and seed data should be noted.

3. Results

3.1. Seed abundance

Table 1 summarizes the results obtained in both the seed and bird surveys. Seed numbers in the top soil layer varied between 1100 and 12 900 seeds m^{-2} for growing fields and grasslands, and between 0 and 4200 seeds m^{-2} in the vegetation for ploughed or growing fields, and grasslands. We found seeds from 197 species in 29 plant families, plus 19 species that remain unidentified. These unidentified seeds, together with those of families for which no data on energy contents were available (Ambrosianaceae, Cistaceae, Geraniaceae, Polygalaceae, and Primulaceae; see Fig. 1), comprised between 4% (grasslands) and 22% (old fields) of the seeds found. The weights of these seeds were transformed to energy units by multiplying them by the average water and energy contents of five families present in the area but not recorded in the winter seed samples (Amaranthaceae, Campanulaceae, Dipsacaceae, Liliaceae and Verbenaceae; see Fig. 1). The seven commonest seed families (listed in Table 1) comprised between 92% (grasslands) and 59% (ploughed fields) of the seeds found, their nutritional quality being extensively documented in the literature (Fig. 1).

3.2. Bird abundance

Twelve species of overwintering seed-eating birds were found in the two study years (Table 1). Three species, skylark (*Alauda arvensis*), calandra lark (*Melanocorypha calandra*) and linnet (*Carduelis cannabina*), were the commonest in both years. Winter bird abundance was highest in stubble fields in both years, followed by growing fields. Old fields had the lowest bird numbers, followed by ploughed fields in 1985 and grasslands in 1989. Bird abundance was fairly similar between years in old fields, but not in the remaining habitat types: grassland bird densities were 1.7 times higher in 1985 than in 1989, 1.3 to 5.6 times lower in the cultivated habitats. Despite these differences, the general order of preference for habitats by overwintering seed-eating birds was consistent between study years ($r_S = 0.90$, $p = 0.072$; bird densities in each habitat type in 1985 vs. those in 1989; $n=5$).

Figure 2 shows the results obtained when these data were transformed to a common energy currency (kJ 10 ha^{-1}). Whole winter energy requirements of birds were an order of magnitude smaller on average than seed resources across the five habitat types. Between-habitats patterns of seed abundance and bird requirements did not match at all ($r_S=-0.40, p=0.424$, and $r_S=0.20$, $p=0.689$; soil and vegetation seed abundances vs. bird requirements in 1989 and 1985, respectively; $n=5$), the uncultivated habitats being greatly under-exploited (seed resources nearly 100 times larger than bird requirements), growing and ploughed fields less so (seed resources two to seven times the overwintering bird requirements).

4. Discussion

Many authors have argued that spatial and temporal differences in bird abundance are largely determined by fluctuations in the abundance of their food resources (Newton, 1980). Other approaches have questioned this view by suggesting that the relationship between bird abundance and food resources is weak except during infrequent periods or situations when resources are particularly scarce (Wiens, 1989). Seed-eating birds have been increasingly studied to test the above-mentioned hypothesis. Direct and indirect evidence of the positive correlation between summer seed crops and winter seed-eating bird abundances was obtained (Pulliam and Brand, 1975; Pulliam and Parker, 1979; Dunning and Brown, 1982) to support the view of a role played by food in determining the number of overwintering birds. The lack of relationship between food and bird abundances, however, was demonstrated by Wiens and Dyer (1975), Laurance and Yensen (1985), and Pulliam and Dunning (1987). This apparent contradiction might be explained by setting alternative hypotheses which consider the incidence of resource-independent factors such as vegetation structure.

Despite the limited geographical and temporal scale covered in this study, results obtained seem representative both of the usual size of the seed bank in each habitat type, and of the pattern of abundance and species composition of the seed-eating bird communities overwintering in southwestern Europe. Soil seed abundance reported from the top 1 cm soil layer of cereal croplands ranged from 320 to 4890 seeds m^{-2}, whereas grassland seed abundances ranged from 406 to 31 344 seeds m^{-2} (Roberts, 1981; Cavers and Benoit, 1989; Rice, 1989). European shrub-steppes tend to support very few seed-eating birds during winter (0.5–9.4 birds 10 ha^{-1}; Tellería et al., 1988; Curcó and Estrada, 1987), as well as deforested grasslands (28.6 birds 10 ha^{-1}; Tellería, unpublished data, 1986). Cereal fields, however, have high densities of overwintering seed-eating birds (30–120 birds 10 ha^{-1}; Santos and Tellería, 1985; Tellería and Santos, 1985; Potti and Garrido, 1986; Zúñiga et al., 1987). Birds tend to prefer stubble fields to ploughed and growing ones (Curcó and Estrada, 1987; Møller, 1984), larks (mainly *Alauda arvensis*, *Melanocorypha calandra* and *Galerida* spp.), finches (mainly *Carduelis cannabina*) and buntings (mainly *Miliaria calandra*) being the dominant species recorded in all these studies.

Bird requirements in the study area were on average an order of magnitude smaller than seed resources when both variables were expressed in a common energy currency (Fig. 2). This large difference would overcompensate possible biases due to the methodology used to transform numbers of birds and seeds into energy (see Wiens, 1989). It also suggests that food abundance was not a limiting factor for seed-eating birds overwintering in the study area.

Bird densities did not track the spatial variations in seed abundance observed in this study (Fig. 2). Three processes could possibly explain the low bird densities found in old fields and grasslands. Birds could have been excluded from unploughed habitats by competition with mice and ants, the other important seed-eating animals inhabiting open habitats (Tellería et al., 1988; Brown et al., 1979). This hypothesis is based on a shortage of seed resources which did not occur in our mid-winter seed survey (Fig. 2). Moreover, former studies in this area (Díaz

1991, 1992a,b) demonstrated that both ants and mice were constrained by the availability of shrub cover for nesting so that large patches of these stable habitats were left free from their foraging activities.

Alternative hypothesis are based on the incidence of resource-independent factors such as food accessibility or predation risk, both apparently mediated by vegetation structure at least in open habitats. Ground-foraging birds apparently prefer bare ground and short vegetation to forage (Bowden, 1990; Thompson et al., 1991), which results in an inverse relationship between foraging efficiency (number of preys captured per unit time) and standing vegetation biomass (Brownsmith, 1977; Thompson et al., 1991). Grasslands and old fields were the habitats with the highest winter herb biomass, followed by growing crops, stubble and ploughed fields (Fig. 3), whereas herb biomass and bird density tended to be inversely correlated ($r_S = -0.60$, $p = 0.230$, and $r_S = -0.70$, $p = 0.161$; herb biomass index vs. bird densities (birds 10 ha^{-1}) and bird requirements (kJ 10 ha^{-1}), respectively, in the winter of 1989; $n = 5$; see Fig. 3). The likely decrease in foraging efficiency in these habitats would have outweighed higher food abundance.

The importance of predation risk in determining patterns of habitat use has been considered especially when food is plentiful (Lima et al., 1987; Brown, 1988; Holbrook and Schmitt, 1988; Lindström, 1990). Lark-like North American buntings were shown to perceive shrubs as a potential source of attack so that they never seek shrubs when attacked by raptors (Lima, 1990). Larks being the main components of the overwintering bird communities studied, bird density and shrub cover being inversely correlated ($r_S = -0.89$, $p = 0.074$, and $r_S = -0.78$, $p = 0.117$; shrub cover vs. bird densities (birds 10 ha^{-1}) and bird requirements (kJ 10 ha^{-1}), respectively, in winter 1989; $n = 5$; see Fig. 3). Shrub avoidance associated with the perceived risk of predation could be another resource-independent process explaining the observed patterns.

Results obtained show that the desertion of croplands and its substitution by grasslands and old fields in the Spanish central plateau may increase seed resources for seed-eating overwintering birds. However, land-use changes may also produce a decrease in the attractiveness of the area for birds because of their effect on resource-independent factors (food accessibility, predation risk), a situation which may paradoxically reduce the number of overwintering seed-eating birds in central Spain. This conclusion, although

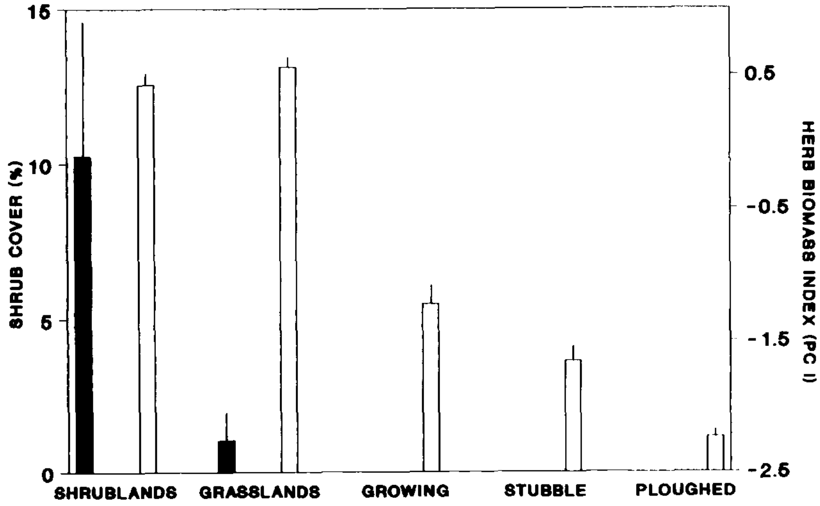

Fig. 3. Mean (+ SE) herb biomass indices (open bars) and shrub covers (filled bars) for five habitat types in winter 1989 (data from Díaz, 1992a). Sample sizes as in Table 1. For further details, see text and Díaz (1992a).

based on the differential preferences showed by birds at a local scale, can be generalized to larger spatial scales as the observed bird densities in each habitat type were largely coincident with previous censuses carried out over large, isolated tracts of these habitats types (see above, and Santos and Tellería, 1985; Tellería and Santos, 1985; Potti and Garrido, 1986; Curcó and Estrada, 1987; Zúñiga et al., 1987; Tellería et al., 1988; Tellería, unpublished data, 1986). Finally, results obtained emphasize the need for considering not only the obvious, proximate factors affecting bird abundance, but also the potential effects of other aspects of the ecology and behaviour of the species involved which have been scarcely explored to date.

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References

Baldock, D. and Long, T., 1987. The Mediterranean Environment under Pressure: The Influence of CAP in Spain and Portugal and the "IMPs" in France and Italy. Institute for European Policy, Bonn, 91 pp.

Becker, M., 1961. Análisis y Valoración de Piensos y Forrajes. Acribia, Zaragoza, 250 pp.

Bowden, C.G.R., 1990. Selection of foraging habitats by Woodlarks (*Lullula arborea*) nesting in pine plantations. J. Appl. Ecol., 27: 410-419.

Brown, J.H., Reichman, O.J. and Davidson, D.W., 1979. Granivory in desert ecosystems. Ann. Rev. Ecol. Syst., 10: 201-227.

Brown, J.S., 1988. Patch use as an indicator of patch preference, predation risk, and competition. Behav. Ecol. Sociobiol., 22: 37-47.

Brownsmith, C.B., 1977. Foraging rates of starlings in two habitats. Condor, 79: 386-387.

Cavers, P.B. and Benoit, D.L., 1989. Seed banks in arable land. In: M.A. Leck, V.T. Parker and R.L. Simpson (Editors), Ecology of Soil Seed Banks. Academic Press, San Diego, CA, pp. 309-328.

Commission of the European Communities, 1990. EEC Council Regulation No. 2078/92 on the introduction and maintenance of agricultural production methods compatible with the requirement of the protection of the environment and the maintenance of the countryside. Official Journal of the European Communities, No. L 215/85.

Cummins, K.W. and Wuycheck, J.C., 1971. Caloric equivalents for investigations in ecological energetics. Mitt. Int. Ver. Limmnol., 18: 1-158.

Curcó, A. and Estrada, J., 1987. Estudio comparativo de la ornitofauna invernante en las principales comunidades vegetales. In: Junta de Castilla y León (Editor), Actas I Congreso Internacional sobre Aves Esteparias. Junta de Castilla y León, León, pp. 406-419.

De Juana, E. (Editor), 1990. Areas importantes para las aves en España. Sociedad Española de Ornitología, Madrid, 183 pp.

Díaz, M., 1990. Interspecific patterns of seed selection among granivorous passerines: effects of seed size, seed nutritive value, and bird morphology. Ibis, 132: 467-476.

Díaz, M., 1991. Spatial patterns of granivorous ant nest abundance and nest site selection in agricultural landscapes of central Spain. Insect. Soc., 38: 351-363.

Díaz, M., 1992a. Rodent seed predation in cereal crop areas of central Spain: effects of physiognomy, food availability, and predation risk. Ecography, 15: 77-85.

Díaz, M., 1992b. Spatial and temporal patterns of granivorous ant seed predation in patchy cereal crop areas of central Spain. Oecologia, 91: 561-568.

Dunning, Jr., J.B. and Brown, J.H., 1982. Summer rainfall and winter sparrow densities: a test of the food limitation hypothesis. Auk, 99: 123-129.

Earle, F.R. and Jones, Q., 1962. Analyses of seed samples from 113 plant families. Econ. Bot., 16: 221-250.

Glück, E.E., 1985. Seed preference and energy intake of Goldfinches *Carduelis carduelis* in the breeding season. Ibis, 127: 421-429.

Holbrook, S.J. and Schmitt, R.J., 1988. The combined effects of predation risk and food reward on patch selection. Ecology, 69: 125-134.

Kendeigh, S.C. and West, G.C., 1965. Caloric values of plant seeds eaten by birds. Ecology, 46: 553-555.

Laurance, W.F. and Yensen, E., 1985. Rainfall and winter sparrow densities: a view from the northern Great Basin. Auk, 102: 152-158.

Lima, S.L., 1990. Protective cover and the use of space: different strategies in finches. Oikos, 58: 151–158.

Lima, S.L., Wiebe, K.L. and Dill, L.M., 1987. Protective cover and the use of space by finches: is closer better? Oikos, 50: 225–230.

Lindström, A., 1990. The role of predation risk in stopover habitat selection in migrating bramblings, *Fringilla montifringilla*. Behav. Ecol., 1: 102–106.

Ministerio de Agricultura, 1987. Caracterización Agroclimáticade la Provincia de Segovia. Ministerio de Agricultura, Madrid, 173 pp.

Møller, A.P., 1984. Community structure of birds in agricultural areas in summer and winter in Denmark. Holarct. Ecol., 7: 413–418.

Nagy, K.A., 1987. Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr., 57: 111–128.

Newton, I., 1980. The role of food in limiting bird numbers. Ardea, 68: 11–30.

Paladino, F.V., 1989. Constraints of bioenergetics on avian population dynamics. Physiol. Zool., 62: 410–428.

Perrins, C., 1987. Birds of Britain and Europe. Collins, London, 319 pp.

Potti, J. and Garrido, G., 1986. Dinámica estacional de una ornitocenosis agrícola en el centro de España. Alytes, 4: 29–48.

Pulliam, H.R. and Brand, M.R., 1975. The production and utilization of seeds in plain grasslands of southeastern Arizona. Ecology, 56: 1158–1166.

Pulliam, H.R. and Dunning, J.B., 1987. The influence of food supply on local density and diversity of sparrows. Ecology, 68: 1009–1014.

Pulliam, H.R. and Parker, T.H., 1979. Population regulation of sparrows. Fortschr. Zool., 25: 137–147.

Rice, K.J., 1989. Impacts of seed banks on grassland community structure and population dynamics. In: M.A. Leck, V.T. Parker and R.L. Simpson (Editors), Ecology of Soil Seed Banks. Academic Press, San Diego, CA, pp. 211–230.

Roberts, H.A., 1981. Seed banks in soils. Adv. Appl. Biol., 4:1–55.

Santos, T. and Tellería, J.L., 1985. Patrones generales de distribución invernal de passeriformes en la Península Ibérica. Ardeola, 32: 17–30.

Tellería, J.L. and Santos, T., 1985. Avifauna invernante de los medios agrícolas del norte de España. I. Caracterización biogeográfica. Ardeola, 32: 203–225.

Tellería, J.L., Santos, T., Alvarez, G. and Sáez-Royuela, C., 1988. Avifauna de los campos de cereales del interior de España. In: F. Bernis (Editor), Aves de los Medios Urbano y Agricola. Sociedad Española de Ornitología, Madrid, pp. 173–319.

Tellería, J.L., Santos, T. and Carrrascal, L.M., 1988. La invernada de los paseriformes (*O. Passeriformes*) en la Península Ibérica. In: J.L. Tellería (Editor), Invernada de Aves en la Península Ibérica. Sociedad Española de Ornitología, Madrid, pp. 153–166.

Tellería, J.L., Suárez, F. and Santos, T., 1988. Bird communities of the Iberian shrubsteppes. Holarct. Ecol., 11: 171–177.

Thompson, D.B., Brown, J.H. and Spencer, W.D., 1991. Indirect facilitation of granivorous birds by desert rodents: experimental evidence from foraging patterns. Ecology, 72: 852–863.

Tió, C., 1991. Los cereales y la nueva política agrariacomunitaria. El Campo, 122: 25–28.

Wiens, J.A., 1989. The Ecology of Bird Communities, 2 vols. Cambridge University Press, Cambridge, MA, 855 pp.

Wiens, J.A. and Dyer, M.I., 1975. Simulation modelling of Red-Winged Blackbird impact on grain crops. J. Appl. Ecol., 12: 63–82.

Zúñiga, J.M., Zamora, R. and Hernández, M.L., 1987. Dinámica temporal de las comunidades de aves de dos medios semiáridos: la estepa cerealista y la sabana de *Quercus rotundifolia* en la depresión de Guadix (SE de España). In: Junta de Castilla y León (Editor), Actas I Congreso Internacional sobre Aves Esteparias. Junta de Castilla y León, León, pp. 369–377.