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Source: *Ecological Applications*, Vol. 11, No. 4 (Aug., 2001), pp. 1141-1150

Published by: Ecological Society of America

Stable URL: <http://www.jstor.org/stable/3061018>

Accessed: 14/02/2009 14:58

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## GRAZING EFFECTS ON BETWEEN-YEAR VARIATION OF FARMLAND BIRD COMMUNITIES

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**Abstract.** Livestock grazing is the dominant land use in the remaining seminatural grasslands in Europe. Abandonment of grasslands and, conversely, intensified grazing by livestock have been suggested as possible causes for the widespread population declines of many farmland birds, although the direct impact of grazing on farmland birds is poorly known. Here, we use a comprehensive, long-term data set (20 pastures surveyed over five years) to test the effects of changes in grazing intensities in seminatural dry pastures on between-year variation of the farmland bird community, functional groups of species, and individual species. Bird communities in all 20 seminatural pastures showed a low degree of temporal variability (Kendall's coefficient of concordance on ranked abundances: mean  $W = 0.72$ , range = 0.58–0.89). Community variability was not significantly related to site area, grazing pressure, vegetation structure, or adjacent habitat composition. However, analyses of functional groups of species categorized according to body mass and breeding diet showed that different species subsets had differential responses to between-year changes in grazing pressure (as reflected by changes in grass height). Local extinction and recolonization of ground-feeding insectivorous bird species were affected by yearly changes in grazing pressure, but there was no effect of grazing on ground-feeding species that fed on a mixed diet or on species that foraged in trees and shrubs. In general, large insectivores (>30 g) preferred moderately grazed pastures, and small insectivores ( $\leq 30$  g) preferred pastures with intensive grazing pressure. We propose that current intensive grazing should be relaxed (i.e., by reducing the number of stock per hectare or by within-season rotational grazing) so that with a given stock size, larger areas of seminatural dry pastures could be grazed. This would decrease the rate of habitat loss and conserve a larger part of the farmland bird community breeding in this habitat.

**Key words:** farmland bird communities; functional groups; grazing pressure; habitat loss; insect abundance; seminatural pastures; Sweden; temporal variability; turnover.

### INTRODUCTION

Acquiring knowledge of the extent to which different communities vary over time is an important issue for many applied ecological problems. Conservation and management policies, for example, are often based on the results of short-term surveys, which may be misleading if communities vary greatly over time (Wiens 1981). Furthermore, the usefulness of indicator communities for detecting environmental change would be limited if communities were to vary over time in the absence of environmental changes (Milchunas et al. 1998). However, few studies have assessed the temporal variability (or conversely, stability or predictability) of communities, or the environmental factors that may affect community variability (but see Rotenberry and Wiens 1980, Bellamy et al. 1996, Bengtsson et al. 1997, Boulinier et al. 1998).

Intensification and specialization of agricultural

practices have drastically altered farmland landscapes in North America and Europe. Small farms have been consolidated into larger units and non-crop habitats such as seminatural and natural grasslands have dramatically decreased in area (Best et al. 1995, McLaughlin and Mineau 1995, Pain and Pienkowski 1997). Today, grasslands occur only as small, scattered fragments of their former distribution. Fragmentation and loss of grassland habitats are most likely major factors causing the declines in range and abundance of many animal and plant species associated with these habitats (Beaufoy et al. 1994, Herkert 1994, Fuller et al. 1995, Tucker 1997).

In addition to negative fragmentation effects, agricultural policies have indirectly, and agricultural practices have directly, disrupted traditional disturbance regimes in many fragmented grasslands, to the detriment of native flora and fauna. Seminatural and natural grasslands are dynamic systems dependent on regular disturbance such as grazing or fire for maintaining vegetation structure (Knopf and Samson 1997). Abandonment of financially nonviable seminatural grasslands grazed by livestock, or, conversely, more intensive grassland management with intense grazing and high

Manuscript received 15 November 1999; revised 12 June 2000; accepted 15 June 2000.

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applications of fertilizers, are thought to be important factors contributing to the rapid population declines of many farmland birds across Europe (Tucker 1997, Newton 1998). However, previous attempts to study the impact of grazing on grassland birds have been restricted by short study duration (one to two years), few replicates, and difficulties in separating effects of different levels of grazing pressure from those of general habitat succession (Brown and McDonald 1995, Saab et al. 1995, Herkert and Knopf 1998). Conservation strategies for farmland bird communities in managed grasslands thus call for replicated long-term data to (1) establish the extent to which different levels of grazing pressure affect the temporal variability of farmland birds, and (2) identify species or ecological groups of species particularly prone to be affected by changes in grazing regimes.

In Sweden, seminatural pastures have evolved under grazing pressure for centuries, and native flora and fauna may thus tolerate, or even require, grazing (Ekstam and Forshed 1992). About 60% of the vascular plants, 50% of the invertebrates, and 60% of the vertebrates red-listed in Sweden are found on farmland (Ehnström et al. 1993, Aronsson et al. 1995, Ahlén and Tjernberg 1996). The majority of these species inhabit traditional grasslands such as grazed seminatural pastures (Berg and Tjernberg 1996). For example, many of the farmland birds that have shown sharp declines in abundance during the last 25 yr have very high breeding densities in seminatural pastures (Pärt and Söderström 1999a). Recent shifts in agricultural policies have caused many farmers to convert pastures to crop fields or tree plantations; about 35% of total pasture area has been lost since the late 1950s (Statistics Sweden 1990a, b). In addition, 20% of the remaining pastures are currently abandoned and thus are rapidly regenerating into scrub or forest. Similarly, this important habitat for many plants and animals has almost disappeared in central and western Europe (Fuller 1987, Tucker 1997). In Sweden and other northern and eastern European countries, however, seminatural dry pastures are still a fairly common farmland habitat (Sweden has ~3500 km<sup>2</sup> distributed in >25 000 patches; Statistics Sweden 1990a).

To counteract the loss of old managed grasslands, the Swedish government started a large-scale subsidy scheme for the management and restoration of seminatural pastures (Swedish Environmental Protection Agency 1991). Management is mainly aimed at protecting the high diversity of vascular plants, typical of old seminatural pastures, by prescribing intense grazing throughout the grazing season. However, the explicit aim is to protect and promote overall biodiversity associated with grasslands (Board of Agriculture 1996, Swedish Environmental Protection Agency 1997). Studies on grassland invertebrate taxa suggest that species abundance and richness may be negatively affected by such intensive grazing (Morris 1967, Dennis et al. 1997, Zulka et al. 1997), in contrast to the intended

goals. Previous bird-habitat association studies suggest that the diversity and abundance of farmland birds breeding in seminatural pastures are associated with different management regimes as well as with surrounding landscape composition (Pärt and Söderström 1999a, b, Söderström and Pärt 2000). Ground-foraging bird species feeding on invertebrates, in particular, seem to respond positively to management regimes with moderate to high levels of grazing pressure (Pärt and Söderström 1999a). However, these correlative studies do not provide cause and effect knowledge of the importance of different grazing intensities to farmland birds.

In this paper, we used a comprehensive, long-term data set (20 pastures surveyed over five years) to test the effects of changing grazing intensities in seminatural dry pastures on between-year variation of the farmland bird community, functional groups of species, and individual species. Grass height (reflecting grazing pressure) within pastures varied considerably between consecutive years, whereas changes in the tree and shrub layers and in the surrounding landscape composition were negligible. First, we indexed temporal variability in the relative abundances of farmland birds by using Kendall's coefficient of concordance (see, e.g., Rahel 1990). Second, we tested whether differences among pastures in the temporal variability of bird communities are linked to pasture area, grazing pressure, vegetation structure, and adjacent habitat composition. Third, we tested the independent effects of between-year changes in grazing pressure on between-year changes of species subsets and individual species within farmland bird communities.

## METHODS

### *Description of seminatural dry pastures in Sweden*

Grazed seminatural dry pastures are an integral part of traditional farmland landscapes in Sweden, where a continuous grazing regime sometimes has been maintained for centuries (Swedish Environmental Protection Agency 1997). The high species diversity of native grasses and herbs is probably a result of low soil nutrient levels that result from the continuous biomass removal through grazing and restricted use of artificial fertilizers, although most pastures are partly affected by fertilizers. About half of all seminatural dry pastures have at least some tree cover, either solitary trees or small tree groups, and ~30% have shrubs that occur scattered within the pastures (Statistics Sweden 1990b). The pastures are fenced with barbed wire fences or traditional stone walls, and no boundary hedges exist. Boulders occur frequently within the pastures, and bare rock sometimes occurs as well, which makes the ground unsuitable for plowing. In short, a Swedish seminatural pasture is usually a fine-scaled mosaic of open ground, shrubs, trees, and boulders.

### Study sites

Our study was conducted in 20 seminatural dry pastures located in an agriculturally dominated landscape within 30 km of Uppsala (59°52' N, 17°39' E), in south-central Sweden. Pasture size was  $6.5 \pm 0.9$  ha (mean  $\pm 1$  SE, range 2–15.3 ha). Juniper (*Juniperus communis*) covered  $11.9 \pm 3.2\%$  of the area, and thorny shrubs, i.e., sloe (*Prunus spinosa*) and roses (*Rosa* spp.), covered  $4.0 \pm 0.2\%$ . Isolated trees or tree groups, mostly Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), birch (*Betula pendula*), and aspen (*Populus tremula*), covered  $14.8 \pm 2.1\%$  of the area. Signs of artificial fertilization were observed in  $40.3 \pm 7.7\%$  of the field layer. Habitats adjacent to the pastures were agricultural crop field ( $34.3 \pm 6.3\%$  of the pastures' circumference), forest ( $29.2 \pm 5.2\%$ ), cultivated grassland plowed on a regular basis ( $13.6 \pm 6.1\%$ ), fenced seminatural pasture ( $10.0 \pm 3.5\%$ ), and other habitats such as farmyard, garden, or clearcut ( $12.9 \pm 1.9\%$ ).

The pastures were selected to cover the variation in management regimes and habitat characteristics of pastures in this region. Selected pastures did not differ from unselected ones in area, grass height, amount of shrubs, amount of tree groups, or adjacent habitats (*t* tests, selected vs. unselected pastures; *df* = 86, all *P* > 0.20). However, our pastures were not a random sample with respect to artificial fertilizer use; instead, we unwittingly selected a higher proportion of unfertilized pastures (*t* = 2.33, *df* = 86, *P* = 0.02). This is not likely to present bias because we previously have found small effects of fertilization on abundance and species richness of farmland birds breeding in pastures (Pärt and Söderström 1999a, b).

### Grazing pressure

Grazing pressure is often expressed as livestock unit days of grazing per hectare (i.e., stocking rates). Here, however we use estimated grass height as a measure of grazing pressure for two reasons. First, food resources available for birds are probably more affected by changes in grass height than by the grazing animals per se (Bock and Webb 1984). Second, depending on the date of livestock release (not exactly known for all pastures) and type of livestock (i.e., cattle, sheep, and horses), it was only possible to estimate the preceding and current grazing pressure by using grass height. Admittedly, climatological factors (e.g., precipitation and temperature during spring), soil type, and nutrient level potentially could have slightly influenced grass height, independent of grazing pressure. However, mean grass height over all pastures in early June was not significantly associated with different years and their specific weather conditions (one-way ANOVA, main effect of year;  $F_{3,76} = 2.04$ , *P* = 0.12). We accounted for the effect of year on bird responses to changes in grazing pressure by including year as a covariate in all analyses.

The main reason for the observed between-year var-

iation in grass height within pastures was a corresponding variation in grazing pressure caused by different dates of livestock release onto the seminatural dry pastures. Livestock release generally occurred following spring tillage, and the timing of spring tillage differed among years and farms. Furthermore, repair of fences enclosing the pastures delayed release in particular pastures in some years, and livestock were sometimes rotated between pastures within the grazing season. All of these factors contributed to a stochastic within-pasture variation in grazing pressure in May and June. In our study area, the grazing period typically lasted from mid-May to early October. Twelve pastures were grazed by cattle, two by sheep, and one each by cattle with sheep, cattle with horses, and sheep with horses. In addition, three pastures that were abandoned around 1990 were included. There were no changes in livestock types in any of the pastures during the study period, and effects of non-stock grazers on grass height were negligible.

Grass height was estimated visually on 1–10 May, 1–10 June, and 20–30 June as the proportion of the field layer where the height of the grass was <5, 5–15 cm, or >15 cm (in 0.10 increments). This was done in 1-ha quadrats in a grid covering the whole pasture. Repeatability of visual estimates among different field recorders was tested each year. In no case did the visual estimates of any of the grass height categories differ more than  $\pm 0.10$  among recorders. The grass height estimates taken in May, early June, and late June were highly correlated (Pearson correlation coefficient, 1–10 May vs. 1–10 June, 1–10 May vs. 20–30 June, 1–10 June vs. 20–30 June each year; all *r* > 0.78, *P* < 0.0001). We evaluated the reliability of the visual estimates of grass height by taking eight random sward-stick measurements per hectare in 18 pastures. The person taking the sward-stick measurements had no prior knowledge of the results of the visual estimates of grass height. These two independent estimates of grass height were closely correlated (*r* = 0.88, *P* < 0.0001). In statistical analyses, we used the yearly changes in the proportion of the field layer that was grazed (i.e.,  $\leq 15$  cm) in early June because this is the time when most breeding birds have established their territories. The rationale for combining the grass height categories <5 cm and 5–15 cm was that, in early June, it was often difficult to tell these two categories apart. Although this sacrifices some data, grass height <15 cm best reflects whether the pasture was grazed or not during the current or preceding season.

For each 1-ha quadrat, or the part that was situated within the pasture, a grass height heterogeneity index was calculated that described the distribution of grazed vegetation ( $\leq 15$  cm). A heterogeneity value (*H*) of 1 was given to 1-ha quadrats where the proportion of grazed area was  $\leq 0.10$  or  $\geq 0.90$ , a value of 2 where the proportion of grazed area was 0.20 or 0.80, and so forth. A maximum heterogeneity value of 5 thus oc-

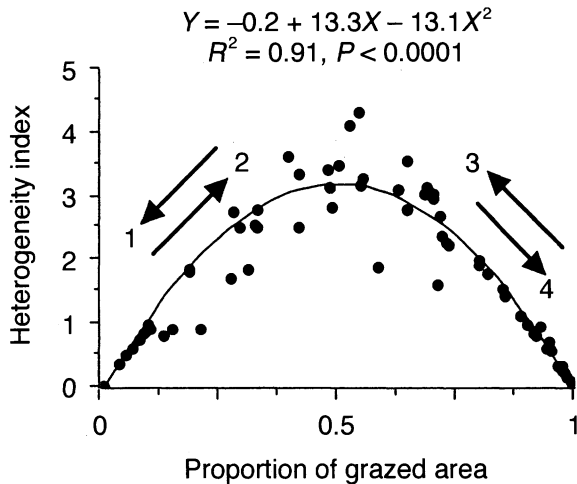


FIG. 1. The relationship between the heterogeneity index (the distribution of grazed vegetation) and the proportion of grazed area (i.e., grass height  $\leq 15$  cm) in 20 seminatural pastures between 1994 and 1997. Arrows denote four possible pathways of changes in grazing pressure (see Table 1).

curred when 0.50 of the quadrat was grazed (Fig. 1). Subsequently, all quadrats were weighted for their respective area and summed to give an index for the whole pasture according to the formula

$$\sum_{i=1}^n H_i(A_i/A_p)$$

where  $n$  is the total number of 1-ha quadrats;  $H_i$  and  $A_i$  are the heterogeneity value and area, respectively, for the  $i$ th 1-ha quadrat; and  $A_p$  is the total area of the pasture. The quadratic relationship between the heterogeneity index and the proportion of grazed area (Fig. 1) suggests that livestock did not preferentially graze only one part of the pasture at moderate grazing levels, but that grazed areas were distributed over the whole pasture.

#### Other habitat variables

The number, area, and length of tree groups, juniper shrubs, and thorny shrubs were recorded in the field on maps (scale 1:2500) with the help of land use maps (scale 1:10 000) and aerial photographs taken in June 1992 (scale 1:20 000). Area and length measurements were done by computer-digitizing the maps. Only the area measurements were retained in analyses, because of high correlations between different estimates. Bordering habitats were classified into eight categories (e.g., crop field, forest, farmyard, and gardens; see Pärt and Söderström 1999a). All within-pasture variables were expressed as proportions of the total area of the pasture, and border habitats were expressed as proportions of the circumference. For detailed information on the methods of habitat mapping, see Pärt and Söderström (1999a, b).

Each year, we repeated the habitat mapping to doc-

ument possible changes in the amount of tree groups, juniper shrubs, or thorny shrubs within pastures, land use of adjacent habitats, or changes in other factors of potential importance for the abundance and distribution of farmland birds (e.g., construction of new fences or application of artificial fertilizers).

#### Bird censuses

The breeding birds were censused yearly between 1993 and 1997 by the territory mapping method, in which song and other indications of breeding are used to determine the number and position of territories (Bibby et al. 1992). All pastures were visited seven times between sunrise and 1000 hours, once in each 10-d period between 20 April and 1 July. Several pastures were censused during the same morning, but in a different sequence to avoid bias based on differences in bird activity. Each visit, we spent  $\sim 10$  min/ha in each pasture. Four to five field observers with prior experience with the census technique conducted the bird censuses in each year. To minimize bias due to different observer experience, routes were shifted between the 10-d periods so that each observer censused all pastures an equal number of times. Altogether, 25 farmland bird species for which pastures were judged important as breeding or foraging habitat were censused (Appendix A). For criteria used to determine the number of breeding territories within the pastures, see Pärt and Söderström (1999b).

#### Analyses

We calculated a community variability index for each pasture based on the Kendall's coefficient of concordance,  $W$  (Siegel and Castellan 1988, Rahel 1990). This nonparametric multisample correlation analysis ranks bird abundances for each of the five years, calculates mean rank over all years, and then calculates Kendall's  $W$  and a corresponding chi-square statistic correcting for ties (Norusis 1994). For each pasture, we only included bird species occurring in at least one year.  $W$  varies between 0 and 1, with 0 signifying no agreement in rank abundances between years and 1 signifying complete agreement. High values of  $W$  thus reflect a high degree of synchrony in abundance fluctuations of different bird species, or, less likely, no variation in species' abundances (Rahel 1990). Values of  $W$  may be disproportionately affected by rare species (Rahel et al. 1984); therefore, we also calculated  $W$  after eliminating species that were recorded in  $< 50\%$  ( $\leq 2$ ) of the years. To investigate whether community variability was influenced by environmental variables, we correlated Kendall's  $W$  with pasture area, the proportion (mean  $\pm 1$  SD) of pasture area that was grazed during the 5-yr period; the proportion of pasture area covered by juniper and thorny shrubs, the proportion of pasture area covered by tree groups, and the proportion of the pasture bordering on crop field and forest (i.e., the dominant land uses in the surrounding landscape).

TABLE 1. Changes (mean  $\pm$  1 SE) between consecutive years 1994–1997 in 20 seminatural Swedish pastures in the proportion of grazed pasture area (i.e., grass height  $\leq$  15 cm) and heterogeneity index.

Change in grazing pressure†	n	Proportion of grazed pasture area		Heterogeneity index‡	
		Year x	Year x + 1	Year x	Year x + 1
Moderate to low (1)	7	0.52 $\pm$ 0.07	0.06 $\pm$ 0.01	2.89 $\pm$ 0.30	0.63 $\pm$ 0.13
Low to moderate (2)	13	0.14 $\pm$ 0.04	0.46 $\pm$ 0.05	0.92 $\pm$ 0.29	2.81 $\pm$ 0.95
High to moderate (3)	9	0.85 $\pm$ 0.04	0.60 $\pm$ 0.08	1.28 $\pm$ 0.34	2.41 $\pm$ 0.24
Moderate to high (4)	10	0.56 $\pm$ 0.06	0.83 $\pm$ 0.06	2.58 $\pm$ 0.21	1.04 $\pm$ 0.32
No change	21	0.47 $\pm$ 0.09	0.45 $\pm$ 0.09	1.13 $\pm$ 0.28	1.09 $\pm$ 0.95

† Numbers in parentheses: see Fig. 1.

‡ Calculation of the heterogeneity index, *H*, is described in *Methods: Grazing pressure*.

We investigated effects of year-to-year changes in grazing pressure (as reflected by grass height) on the number of local extinctions and recolonizations of species subsets. Previous studies suggested that ground-foraging insectivorous birds were strongly associated with changes in grazing pressure (Pärt and Söderström 1999a), and that preferences for larger invertebrate prey increased with bird size (Kaspari and Joern 1993). We therefore classified four different subsets according to breeding diet (exclusive insect diet or a mixed diet of plant material and insects) and body mass ( $>30$  g or  $\leq 30$  g; Appendix A). Tree- and shrub-foraging species acted as a fifth, control subset (termed foliage gleaners in Appendix A). We also analyzed changes in species subsets classified according to nesting location (ground-nesting birds with open nest types vs. birds with other types of nesting locations; Appendix A). We hypothesized that bird species with open nests on the ground would be particularly affected by changes in grazing pressure due to the physical disturbance of the field layer caused by grazing (cf. Saab et al. 1995).

A classification of farmland bird species according to foraging method (probing in the ground vs. gleaning from the ground) was not independent of the subsets based on breeding diet and body size. This is because four of five large insectivorous bird species are ground probers, whereas almost all large species with mixed diets, and small species with insect or mixed diets are ground gleaners (chi-square test,  $\chi^2_3 = 12.00$ ,  $P = 0.007$ ; Appendix A). Because of the lack of independence between these subsets, we did not test the effect of changes in grazing pressure on birds classified according to foraging method.

Between-year changes in grazing pressure were classified into five different categories depending on the direction and magnitude of changes in the proportion of grazed area and the heterogeneity index (Table 1, Fig. 1). When changes in the proportion of grazed area were  $<0.10$ , it was referred to as "no change" (Table 1). We did not observe changes from low to high and from high to low grazing pressure between seasons. Grass height was not estimated in a standardized fashion in 1993; therefore, only changes between consecutive years of the period 1994–1997 are included in

analyses. Most farmland birds have higher abundances in pastures located in open farmland than in those located along forest borders (Pärt and Söderström 1999a). It is possible that bird responses to changes in grazing intensities differ depending on pasture location within the landscape, but small sample sizes precluded testing the importance of this factor.

We used Kolmogorov-Smirnov and Levene's tests to examine the normality and equality of variances, respectively. Pasture area was  $\log_{10}$  transformed and proportional variables were arcsine transformed to meet the assumptions required for parametric tests. All but two of the species subsets met the required assumptions; however, the use of nonparametric tests for these two groups did not change the results (i.e., statistically significant or nonsignificant results were not altered). For simplicity, only the results of parametric tests are shown. To investigate whether pasture area or year (i.e., 1994–1995, 1995–1996, 1996–1997) influenced the results, we included these two variables as covariates in all ANCOVA analyses. However, neither main effects nor their interactions with change in grazing pressure were significant (i.e., all  $P > 0.08$ ). Scheffé's post hoc test for unequal sample sizes was used when a significant main effect of change in grazing pressure was found. Results are reported as means  $\pm$  1 SE. Statistical analyses were performed using SPSS version 6.1 (Norris 1994) and SYSTAT version 5.2 (SYSTAT 1992).

## RESULTS

In total, 2380 breeding territories of farmland birds were found during the 5-yr study period, with an average of  $23.80 \pm 0.96$  territories per pasture each year. On average, there were  $10.71 \pm 0.34$  farmland bird species per pasture. Of the 25 farmland bird species included in this study, 84% did not show significant ( $P \geq 0.10$ ) regional population trends over the five years (population densities in Appendix B). Three species, Gray Partridge (*Perdix perdix*), Goldfinch (*Carduelis carduelis*), and Yellowhammer (*Emberiza citrinella*), declined significantly, whereas Magpies (*Pica pica*) showed a tendency to increase (Appendix A). The proportion of grazed area varied within each pasture between years (Table 1), although there were no con-

sistent (unidirectional) changes in grass height over the 5-yr period in the study region as a whole (Spearman correlation,  $r_s = 0.051$ ,  $P = 0.65$ ,  $n = 80$ ), or within different pastures. There were no changes in the amount of shrubs or the amount of tree groups within pastures during the 5-yr study period. Although we did not distinguish between different types of cereal crops in surrounding crop fields, we could not document any major changes in habitats adjacent to the pastures. Hence, we suggest that the only major habitat modification between years that might have influenced farmland bird abundance was a change in grass height.

All 20 farmland bird communities were highly significantly concordant (mean  $W = 0.72 \pm 0.02$ , range = 0.58–0.89, all  $P < 0.001$ ). When we excluded less common species, there were no changes in the main results (mean  $W = 0.76 \pm 0.02$ , range = 0.57–0.94, all  $P < 0.01$ ). In the former analysis, there were 8–23 bird species in different pastures; in the latter, there were 5–17. However, in neither case was species richness correlated with  $W$  (all species,  $r_s = -0.05$ ,  $P = 0.84$ ; excluding rare species,  $r_s = -0.31$ ,  $P = 0.19$ ). A high value of  $W$  can be due to synchrony in abundance fluctuations, but it can also result from constancy in the absolute abundances of species. However, in nine of 20 seminatural pastures, no farmland bird species showed constant abundance over the five years (including only species occurring in  $\geq 1$  yr). Among the remaining 11 pastures, an average of 1.6 species per pasture showed constant abundance (one or two pairs) over the whole period. It therefore seems that the main reason for the low level of variability among communities was synchronous shifts in species' abundances.

We examined whether stability of abundance rankings could be related to environmental variables (see *Methods*). However, none of the environmental variables was significantly related to  $W$  (of all species and rare species), although there was a tendency for pastures with a higher proportion of forest along their borders to show higher community variability ( $W$  of all species;  $r_s = -0.43$ ,  $P = 0.09$ ). Separate species subsets may have shown specific responses to changes in grazing pressure, but such relationships may have been masked at the community level. Indeed, there was a significant interaction term between species subsets, classified according to breeding diet and body mass, and changes in grazing pressure (ANCOVA, interaction term:  $F_{16,272} = 2.51$ ,  $P = 0.001$ ). Numbers of local extinctions and recolonizations of both subsets of ground insectivores were significantly affected by yearly changes in grazing pressure (Fig. 2A, B), whereas species feeding on a mixed diet and species that foraged in trees and shrubs showed no clear pattern (Fig. 2C–E). Furthermore, insectivorous bird species varied, depending on body size, in their response to changes in grazing pressure (ANCOVA, interaction term  $F_{4,107} = 4.44$ ,  $P = 0.002$ ). A change from low to moderate

grazing pressure led to more recolonizations of large insectivores; conversely, a change from moderate to low grazing pressure resulted in more local extinctions (Fig. 2A). In contrast, a change from moderate to high grazing pressure led to more recolonizations of small insectivores, whereas a change from high to moderate grazing pressure resulted in more local extinctions (Fig. 2B). Not all species within the subsets contributed equally to these results. Green Woodpecker (*Picus viridis*), Wryneck (*Jynx torquilla*), and Starling (*Sturnus vulgaris*) contributed most to the pattern among large species, and Meadow Pipit (*Anthus pratensis*), White Wagtail (*Motacilla a. alba*), and Whinchat (*Saxicola rubetra*) contributed most among small species (Table 2).

In contrast to the insectivore foraging guilds, there were no significant effects of changes in grazing pressure on species classified according to nesting location (open ground-nesting species:  $F_{4,52} = 2.04$ ,  $P = 0.10$ ; species with other types of nesting locations:  $F_{4,52} = 2.14$ ,  $P = 0.09$ ).

## DISCUSSION

### *Temporal variability of farmland bird communities*

Our analysis of abundance rankings showed that bird communities of all 20 pastures had a low degree of temporal variability or, conversely, a high degree of temporal predictability (mean  $W = 0.72$ , range = 0.58–0.89). However, in comparison with figures on stability reported for woodland bird communities, they seemed more variable. For example, bird communities in 18 mature woodland plots in Britain had a mean  $W$  of 0.86 over five years, (calculated using the regression equation of Bengtsson et al. [1997]: Fig. 1). It has been suggested that bird community stability is related to habitat stability because successional habitats (e.g., seminatural dry pastures) are more likely to change in vegetation structure and composition over time than are climax habitats (Bengtsson et al. 1997; but see Noon et al. 1985, Wiens 1989). However, in the absence of successional changes, our results suggest that other factors cause the higher temporal variability of bird communities in seminatural dry pastures than in mature woodland. For example, seminatural dry pastures may display more between-year variation in the field layer structure (due to grazing) than do climax habitats. This may, in turn, affect food resource levels in pastures, resulting in higher temporal variability of farmland bird communities.

### *Local turnover in relation to changes in grazing pressure*

There was no significant effect of grazing on species subsets categorized according to nesting location, which suggests that grazing disturbance of the field layer, affecting ground-nesting birds with open nests, may be of less importance. In contrast, species subsets

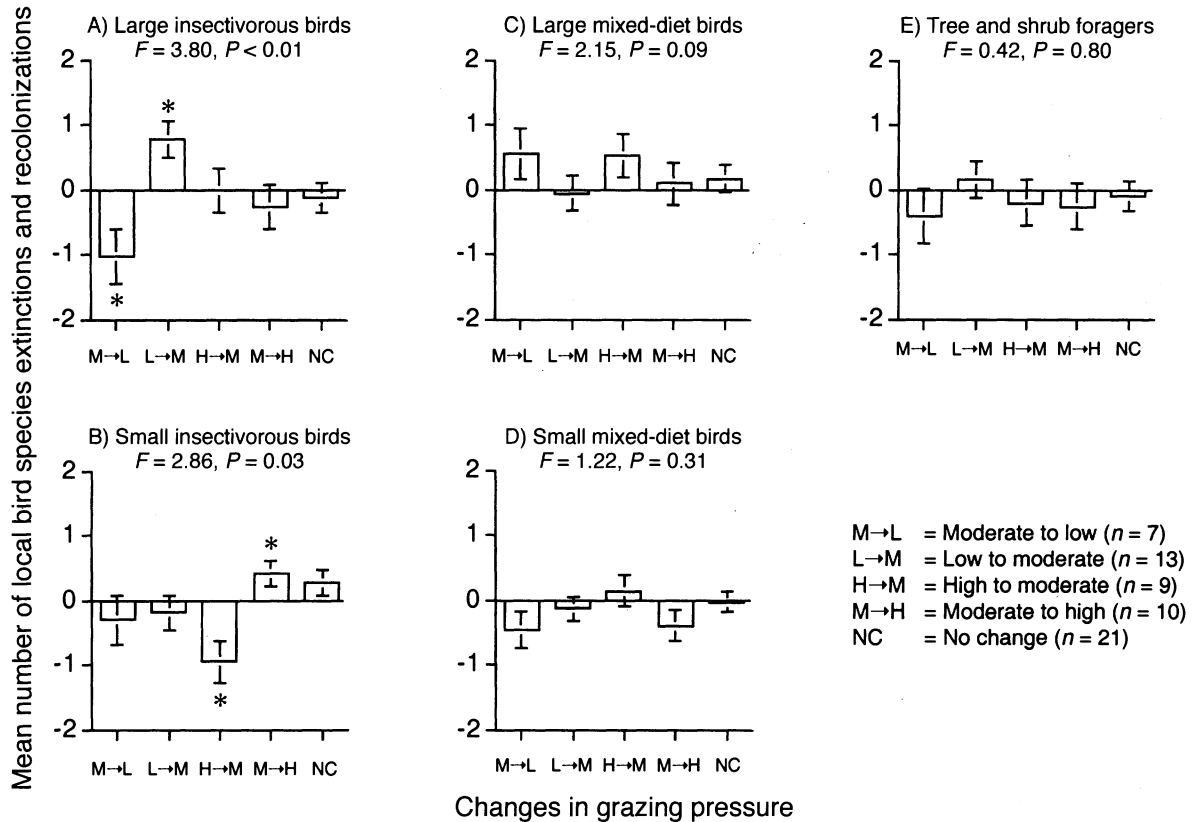


FIG. 2. Relationships between the number of local extinctions and recolonizations of five different species subsets (A–E) and yearly changes in grazing pressure as analyzed by ANCOVA. Adjusted means  $\pm$  1 SE are shown. Asterisks denote significant differences in post hoc tests. Changes in species occurrence are based on five species in all subsets except for (C) and (E), where there were six and four species, respectively. For all analyses,  $df = 4, 52$ .

classified according to breeding diet and body mass had differential responses to changes in grazing pressure. Local extinction and recolonization of both subsets of ground insectivores were significantly affected by yearly changes in grazing pressure (Fig. 2A, B), but

there was no clear pattern for subsets of species feeding on a mixed diet or for tree and shrub foragers (Fig. 2C, D, E). In comparing the abundance of different foraging guilds in riparian habitats in western North America, Saab et al. (1995) similarly reported that only ground

TABLE 2. Number of cases with local extinction (“-” = presence  $\rightarrow$  absence), no change (“0” = presence  $\rightarrow$  presence), and local recolonization (“+” = absence  $\rightarrow$  presence) of ground insectivores relative to changes in grazing pressure between consecutive years.

Species grouped by body mass	Change in grazing pressure				
	Moderate to low -, 0 +	Low to moderate -, 0, +	High to moderate -, 0, +	Moderate to high -, 0, +	No change -, 0, +
<b>Small (<math>\leq 30</math> g)</b>					
Meadow Pipit, <i>Anthus pratensis</i>	0, 1, 1	1, 2, 0	3, 1, 1	0, 3, 2	2, 2, 3
Tree Pipit, <i>Anthus trivialis</i>	3, 1, 0	2, 3, 1	0, 1, 1	1, 0, 0	1, 5, 3
White Wagtail, <i>Motacilla a. alba</i>	0, 5, 1	2, 4, 1	2, 7, 0	0, 7, 1	0, 17, 1
Wheatear, <i>Oenanthe oenanthe</i>	0, 3, 0	0, 3, 0	1, 5, 1	0, 8, 0	0, 11, 2
Whinchat, <i>Saxicola rubetra</i>	0, 1, 0	0, 2, 0	5, 0, 0	0, 1, 2	3, 4, 2
<b>Large (<math>&gt; 30</math> g)</b>					
Wryneck, <i>Jynx torquata</i>	2, 2, 0	1, 3, 3	1, 2, 0	1, 1, 0	3, 4, 3
Green Woodpecker, <i>Picus viridis</i>	4, 1, 0	1, 0, 5	0, 2, 1	3, 2, 0	1, 9, 2
Fieldfare, <i>Turdus pilaris</i>	1, 5, 1	3, 5, 4	2, 4, 2	0, 4, 3	4, 10, 2
Red-backed Shrike, <i>Lanius collurio</i>	0, 2, 1	1, 3, 2	1, 1, 0	0, 2, 0	5, 4, 2
Starling, <i>Sturnus vulgaris</i>	1, 6, 0	0, 8, 2	0, 8, 1	2, 6, 1	0, 19, 1

insectivores differed in abundance between grazed and ungrazed treatments. Thus, it seems as though ground insectivores are particularly affected by changes in grazing pressure. This is probably due to the effects of grazing on variation in abundance or availability of invertebrate food resources, although the detrimental effect of *intensive* grazing on ground-nesting birds (e.g., trampling of nests or increased exposure to nest predation) should not be overlooked (Busche 1989, Saab et al. 1995). In agreement with the food resource explanation, most studies on different grassland invertebrate taxa have documented rapid changes in abundance and species richness as a result of changes in vegetation structure caused by grazing, e.g., Acrididae (Capinera and Sechrist 1982); Lepidoptera (Erhardt and Thomas 1991); Coleoptera (Siepel et al. 1989, Gardner et al. 1997, Dennis et al. 1997); Arachnida (Zulka et al. 1997); aboveground macroarthropods (Milchunas et al. 1998).

Large insectivorous bird species were more affected by changes from an initially low to a moderate grazing pressure, whereas small insectivores mainly were affected by changes from an initially high to a moderate grazing pressure (Fig. 2A, B). Low grass height may increase foraging efficiency because of higher mobility, particularly of small birds, or increased prey detectability (Tye 1992). An alternative hypothesis, however, is that abundances of the preferred invertebrate prey of small and large birds differ depending on the level of grazing pressure. For example, the size distribution of different ground beetles (Coleoptera: Carabidae), an important prey type for many ground-foraging grassland birds, has been shown to change toward smaller sizes as grazing pressure increases (Blake et al. 1994). Small insectivorous species may therefore benefit from higher prey abundance in intensively grazed pastures. However most invertebrate studies suggest that abundance and richness, especially of large invertebrate species, peak at intermediate grazing pressure and are considerably lower in intensively grazed grasslands (Morris 1967, Tietze 1985, Blake et al. 1994, Dennis et al. 1997, Milchunas et al. 1998). Accordingly, we found that large insectivorous bird species that fed mainly on larger prey (Kaspari and Joern 1993) seemed to prefer moderately grazed pastures (Fig. 2A). The immediate responses to short-term changes in grazing pressure suggest a high mobility of farmland birds when conditions deteriorate or when nearby habitats recover. Site tenacity or philopatry may create time lags in the response of individuals to environmental changes (Wiens and Rotenberry 1985, Wiens et al. 1986). For example, adult Red-backed Shrikes (*Lanius collurio*) that have bred successfully in a given grassland may often return to the same area in the following year (B. Söderström, unpublished results). Thus, site fidelity may delay the response to environmental changes, such as differences between years in grazing intensity. Several pastures were continuously occupied by individual bird species

despite short-term changes in grazing pressure (Table 2).

#### Management implications

Grazing as a management and conservation tool is increasingly used to preserve native biota of the remaining seminatural grasslands in Europe (Andrews and Rebane 1993, Beaufoy et al. 1994), although information on the effects of different grazing intensities on plant and animal communities often is lacking (Bullock and Pakeman 1996). Proper management of the remaining seminatural grasslands in Europe is one of the most important issues in conserving declining farmland bird populations. Our results provide the first reliable evidence that even rather minor changes in grazing level between consecutive years affect the distribution of certain groups of birds breeding in grasslands.

Furthermore, this study demonstrates that ground insectivorous bird species, in particular, are dependent on livestock grazing in seminatural dry pastures. Larger insectivores prefer moderate grazing, whereas small insectivores prefer more intensive grazing. In conjunction with empirical data on invertebrates, these results suggest that farmland birds track variation in the availability and abundance of invertebrate food. In order to benefit many farmland birds of present conservation concern, our results suggest that seminatural dry pastures should be managed under varied moderate and high grazing pressure. Current management demands that seminatural dry pastures within the subsidy scheme be intensively grazed (sward height <3 cm; Swedish Environmental Protection Agency 1997). The poor economics of animal husbandry cause most owners of seminatural dry pastures to apply for the subsidies (Länsstyrelsen Uppsala, *personal communication*). Therefore, livestock will be concentrated on pastures receiving subsidies to meet the prescribed intensive grazing management demands, while other pastures are abandoned, to the disadvantage of many farmland birds. Relaxing the present demands of intense grazing pressure, either by reducing the number of stock per hectare or by within-season rotational grazing, would decrease the loss of managed seminatural pasture habitat, because a given stock size could cover larger areas. In addition, less intense grazing pressure would conserve more farmland birds breeding in this habitat and, most likely, more grassland invertebrates (Erhardt and Thomas 1991, Dennis et al. 1997). Plants may also be favored by less intense grazing, because sexually reproducing plants will not be able to flower under continuous intensive grazing regimes (Howe 1994, Lennartsson 1997). However, some pastures may be better suited for intense grazing management. Most small insectivorous bird species are more abundant in open farmland pastures than in those located along forest borders. This association is probably due to the combined effects of good foraging habitats close to suitable nest sites and avoidance of areas with in-

creased risk of nest predation (Pärt and Söderström 1999a). In contrast, all large invertebrate-feeding species are equally common in both types of pastures, or are more abundant in pastures bordering forest. Hence, results presented here suggest that a higher proportion of pastures located in open farmland than along forest borders should be intensively grazed.

## ACKNOWLEDGMENTS

We thank Åke Berg, Carol Boggs, Erica Fleishman, Lennart Hansson, and John T. Rotenberry for valuable comments on earlier drafts of this paper. Martin Amcoff, Johan Ericsson, Sören Eriksson, Magnus Hellström, Magnus Johansson, Olle Kvarnäck, Robert Lager, Stephen Manktelow, and Staffan Roos helped with the bird censuses. This study was financed by World Wildlife Fund (Sweden) and SLU (Swedish University of Agricultural Sciences), and is part of the faculty program "Pastoral landscapes" at SLU.

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#### APPENDIX A

A table presenting the classification by functional group of farmland bird species breeding in seminatural dry pastures in Sweden is available in ESA's Electronic Data Archive: *Ecological Archives* A011-015-A1.

#### APPENDIX B

A table presenting the mean breeding densities of farmland bird species censused annually in 20 pastures in Sweden during 1993–1997 is available in ESA's Electronic Data Archive: *Ecological Archives* A011-015-A2.