Acta Zoologica Academiae Scientiarum Hungaricae 57(4), pp. 385-395, 2011

# RELATIONSHIP BETWEEN GRAZING INTENSITY, VEGETATION STRUCTURE AND SURVIVAL OF NESTS IN SEMI-NATURAL GRASSLANDS

ERDŐS S.<sup>1,2</sup>, BÁLDI, A.<sup>3,4</sup> and P. BATÁRY, P.<sup>5</sup>

<sup>1</sup>PhD School of Environmental Sciences, Szent István University H-2100 Gödöllő, Páter K. u. 1, Hungary

<sup>2</sup>Current address: Kiskunság National Park Directorate, H-6000 Kecskemét, Liszt u. 19, Hungary

<sup>3</sup>Animal Ecology Research Group of the Hungarian Academy of Sciences

and the Hungarian Natural History Museum, H-1088 Budapest, Baross u. 13, Hungary E-mail: andrasbaldi@gmail.com (corresponding author)

<sup>4</sup>Present address: Institute of Ecology and Botany of the Hungarian Academy of Sciences

H-2163 Vácrátót, Alkotmány u. 2–4, Hungary <sup>5</sup>Agroecology, Georg-August University, Grisebachstr. 6, D-37077 Göttingen, Germany

One of the causes of decline of farmland birds in Europe is the loss of broods. Here, we investigated if region, cattle grazing intensity, habitat edges and vegetation structure around artificial nests influence predation, the major cause of broods' loss. We placed artificial open ground nests (N = 304) resembling the nests of Skylark (*Alauda arvensis*), baited by one plasticine and one Quail egg in inside and edge habitats of extensively and intensively grazed grasslands in three regions in Hungary in 2003. Interestingly, none of the three factors (region, grazing intensity, edge effect) had significant effects on brood loss according to the generalised linear mixed model, however, interactions between region and management and among region, management and edge effect were significant. This suggests that the effect of management is not the same in different regions, and edge effect depends on both region and management. We also found that nest predation rate is lower if nests are placed in tall grass and greater vegetation cover. This pattern indirectly supports the negative effects of intensive grazing, which can remove most of the vegetation. Therefore, we suggest that extensive grazing should be favoured to conserve ground nesting birds, however, it is essential to avoid duplicating management regimes from one region to another, due to regional differences in the pattern of survival probability.

Key words: artificial nest, farmland, Hungary, nest predation, nest visibility, regional differences

# INTRODUCTION

Recent declines of biodiversity are unprecedented in the history of life on Earth. This loss is mainly driven by the intensification of agricultural management, which has been most pronounced in the last few decades (DONALD *et al.* 2006). The best documented example is the collapse of farmland bird populations in European countries characterised by intensive agriculture (WILSON *et al.* 1999, DON-ALD *et al.* 2001, GREGORY *et al.* 2005, DONALD *et al.* 2006). For example, GREG-ORY *et al.* (2004) reported over 85% decline in Grey Partridge *Perdix perdix*, Tree

Acta zool. hung. 57, 2011 Hungarian Natural History Museum, Budapest Sparrow *Passer montanus* and Corn Bunting *Miliaria calandra* populations between 1970 and 2001 in England. The decline, however, greatly varies across countries of Europe, and is usually smaller in Central and Eastern Europe (DON-ALD *et al.* 2001, 2002*a*, GREGORY *et al.* 2005).

The collapse of farmland bird populations may have several mechanisms related to intensive farming, including food shortages due to loss of invertebrates resulting from pesticide and herbicide use (WILSON *et al.* 1999), nest losses due to mechanisation and high grazing pressure (AMMON & STACEY 1997, WILSON *et al.* 1999, HENDERSON *et al.* 2004, PAVEL 2004, KERNS *et al.* 2010, BÁLDI & BATÁRY 2011*a*), loss or change of habitats (FULLER & GOUGH 1999, BENTON *et al.* 2003), and winter food shortage (SIRIWARDENA 2010). Nest predation is an extremely important factor affecting reproductive output in birds (MARTIN 1995). This is especially true for grassland birds. It has been reported that 50–90% of the ground nests of grassland birds suffered predation in semi-natural dry grasslands in Spain (SUAREZ *et al.* 1993) and in Hungary (ERDŐS *et al.* 2009), in lowland grasslands in England (DONALD *et al.* 2002*b*) and in alpine habitats of Italy (SCHERINI *et al.* 2003). Since most grasslands in Europe are managed in some way, nature-friendly agricultural practices might enhance the survival of nests, thus can contribute to the conservation of farmland bird populations.

Farming practices in Central and Eastern Europe since the collapse of the socialist economy is less intensive than in Western Europe; land ownership changed causing legal problems for land users, and the low level of investment prevented large scale intensification (DONALD et al. 2002a, KLEIJN & BÁLDI 2005, STOATE et al. 2009, BÁLDI & BATÁRY 2011a). In Hungary, for example, only 5% of grassland was fertilised (NAGY 1998), and there is no increase due to lack of investment. Contrary, grasslands in countries with intensive agriculture, like the UK or the Netherlands, are heavily chemicalised with inorganic fertilizers and pesticides. The extensively managed farmlands in Hungary harbour a diverse wildlife, like large population of the vulnerable Great Bustard (Otis tarda), European Ground Squirrel (Spermophilus citellus) or the near threatened Red-Footed Falcon (Falco vespertinus) and European Roller (Coracias garrulus), and one third of the protected animal- and plant species in Hungary (ÁNGYÁN et al. 2003). In all new EU member states of Central and Eastern Europe agri-environment programs exist, which might have the potential to become powerful tools to maintain extensive farming. In Hungary the Hungarian Agri-Environment Program (HAEP) was established in 1999, and one of the most popular schemes was the grassland management scheme (ÁNGYÁN et al. 2003). This is promising for nature conservation, since grassland is the most characteristic habitat of Hungary ("puszta"), which covers 12% (1.15 million hectares) of the country.

The most important grassland management in Hungary is grazing; there is almost no fertiliser and other chemical use (NAGY 1998). However, high grazing pressure might affect reproduction of birds via the modification of landscape, vegetation structure and destruction of nests (AMMON & STACEY 1997, FULLER & GOUGH 1999, DONALD *et al.* 2002*b*, PAVEL 2004, EVANS *et al.* 2005, 2006, LOE *et al.* 2007, KERNS *et al.* 2010). One of the most important detrimental factors is that grazing may reduce vegetation height and cover, thus making nests more visible and hence more exposed to predators (MARTIN 1995, AMMON & STACEY 1997). Another important factor of nest predation is the amount of edge habitats. The general understanding is that bird nest predation is higher in edge than in the interior (> 50 m) of habitat patches, thus grassland fragmentation is harmful for bird populations (BATÁRY & BÁLDI 2004). On the other hand, the increase of farmland heterogeneity, thus creating more habitat edges, is thought to be a key contributor to maintain species diversity in farmland (BENTON *et al.* 2003).

In this study we used artificial nests to study the effects of grazing intensity and habitat edges on nest predation. Although the use of artificial nests to study nest predation is often criticised as not reflecting the real predation rate (MOORE & ROBINSON 2004), for comparative purposes (e.g. to compare predation in different areas) artificial nests can be useful, and can even guide restoration efforts (MAJOR & KENDAL 1996, VILLARD & PART 2004, LEWIS *et al.* 2009). In reality, predation of artificial nests indicate the predation pressure in the given location and timeframe, which might be different from the predation of real nests. However, the presence of predators able to predate eggs in artificial nests is an indication of potential threat to real nests. An often overlooked advantage of artificial nests over real nests is that breeding birds are not disturbed. Therefore, the use of artificial nests has limitations, but also advantages.

The aims of this study were (1) to examine if higher grazing pressure increases artificial clutch loss in grasslands; (2) to relate nest losses to the density of ground nesting farmland birds; (3) to study if artificial clutch loss is higher at the edge than 50 m inside the grassland patches and (4) to assess if increased vegetation cover and/or higher vegetation decreases clutch losses.

### MATERIALS AND METHODS

The study was carried out in three regions of Hungary, where different grassland vegetations were present: alkali grasslands and wet meadows in the Kiskunság (Central Hungary), and alkali grasslands in the Heves (northern part of the Great Plain). Most of the study sites were within protected areas (for a map see BÁLDI *et al.* 2005).

The alkali grasslands of the Kiskunság belong to solonchak-solonetz soil type ("alkali region"). These are almost perfect plains, where traditional animal husbandry is responsible for the creation and maintenance of vegetation and landscape structure. Their flora consists mainly of halophyte and salt resistant species due to ground capacity and water provision. An outstanding value of the bird fauna is the large population of the Great Bustard. Further characteristic species are Stone Curlew *Burhinus oedicnemus*, Lapwing *Vanellus vanellus*, Black-tailed Godwit *Limosa limosa* and the Skylark.

The "meadow region" is characterized by marshes, meadows with tree and bush groups, resulting in a more heterogeneous landscape than the former alkali area. Marsh Harrier *Circus aeruginosus*, Sedge Warbler *Acrocephalus schoenobaenus* live in the reed marshes. In the wet meadows Black-tailed Godwit occurs and in the shrubby areas Corn Bunting and Yellow Wagtail *Motacilla flava* are abundant.

The grasslands of the "Heves region" belong to solonetz type of the alkali soils, which is characteristic to Eastern-Hungarian alkali grasslands, like the Hortobágy. Their flora consists mainly of salt resistant species. Important species are for example the Imperial Eagle *Aquila heliaca*, Saker Falcon *Falco cherrug* and the Great Bustard. The Skylark and the Yellow Wagtail are the most frequent passerine birds. More details on the farmland birds of the areas are in BALDI *et al.* (2005) and BATÁRY *et al.* (2007*a*).

All study sites were grazed by cattle. All pastures had the same grazing pressure for at least 5 years, and were categorised as grassland dominated (over 60% grassland cover) landscapes (BATÁRY et al. 2007a). In each region, sites were selected in pairs, where the members of the pair had similar vegetation and landscape context, only the grazing intensity was different: extensive (< 0.5 cattle/ha), or intensive (> 1 cattle/ha). No other management differences were recorded between extensive and intensive fields; there was no fertilizer or other chemical use. We selected 7-7 extensively and intensively grazed pairs in each region (except the "alkali region" in the Kiskunság, where only 5 pairs were used), resulting in 19 pairs (38 sites). In all sites two transects were established (N = 76), one was in the edge and the other was inside, 50 m from the edge. The adjacent habitats at the edges varied (e.g. grassland, tree line), but were similar within each pair of extensive and intensive sites. We used open ground artificial nests intended to resemble the nests of Skylark (Alauda arvensis), which was the most abundant farmland bird in these grasslands (BALDI et al. 2005). We placed 4 nests in each transects ca. 25 m apart from each other (N = 304). We put one plasticine and one Quail Coturnix coturnix japonica egg into the nests (MAJOR & KENDAL 1996). The experiment lasted for 2 weeks from 28 April to 15 May 2003, the main egg laying and hatching season of grassland birds. We checked the nests in 4-8 days intervals. We considered the nest depredated if the plasticine or Quail egg disappeared, or was damaged.

We analysed the effect of region, management, transect (edge *versus* interior) and their interactions on daily probability of nest survival using a generalised linear mixed model (GLMM) with binomial error distribution, logit link function, and involving nest days as denominator. Nest days were rounded up to the nearest day (HAZLER 2004). Pair and transect were random factors. This method is known as Mayfield logistic regression (HAZLER 2004, PASINELLI & SCHIEGG 2006).

The influence of density of ground breeding farmland birds (pooled territory number of the three most abundant species, namely Skylark, Yellow Wagtail and Quail) was evaluated in a separate model, as in our earlier analyses we showed that both management and region have effect on the breeding bird assemblages (BALDI *et al.* 2005, BATÁRY *et al.* 2007*a*). Therefore, we were not able to include breeding bird density data into the above predation model, due to collinearity with these factors (management and region). All models were performed with R version 2.12.1 (R DEVELOPMENT CORE TEAM 2010) using the "glmmPQL" function of the "MASS" package (version 7.3.9, VENABLES & RIPLEY 2002).

We examined the effects of grass height and vegetation cover around the artificial nests on nest success in the Heves alkali grasslands (N = 112 nests). We estimated the height of the grass (in cm) by eye within 1 m radius around the nest. Percentage coverage was estimated in the same circle. Grass height and vegetation cover around depredated and intact artificial nests were compared with t-tests.

#### RESULTS

We found evidence of predation in 136 of the 304 artificial nests (44.7%). Sixty depredated nests were on the extensive, and 76 were on the intensive fields. Regarding edge effect, 67 predated nests were in the edge and 69 in the inside of the grasslands. The predation rates were 35% on the alkaline grasslands of Kiskunság, 47% on the alkali grasslands of Heves and 49% on the wet meadows of Kiskunság. Only a few from the 136 depredated nests had sufficient marks to identify predators, therefore we were not able to proceed with further analysis.

The results for the full model, including all three predictor variables (edge effect, management and region) and their interactions show that no individual variable alone significantly predicts daily predation rate. However, the interactions "region × management" and "region × management × edge effect" were significant, indicating that the effect of management is different in the three regions, while edge effect is significant only if both region and management are considered (Table 1, Fig. 1). The three-way interaction suggests that significant edge effects were apparent under some grazing treatments and in some regions.

If we analyse the regions separately with the GLMM, we found that in one region predation rates were significantly higher on the intensive than on the extensive fields and did not differ in the two other regions (Alkali:  $F_{1,14} = 1.10$ , P = 0.311; Meadow:  $F_{1,20} = 2.72$ , P = 0.115; Heves:  $F_{1,20} = 4.59$ , P = 0.045) (Fig. 1).

Table 1. Generalised linear models on the effects of three regions, two managements (extensive ver-
sus intensive grazing), the location (edge of grassland or inside) and their interactions on the preda-
tion probability of artificial nests in Hungarian grasslands. Num df: numerator degrees of freedom;
Den df: denominator degrees of freedom.

	•			
Effect	Num df	Den df	F value	Р
Region	2	16	0.80	0.465
Management	1	48	3.56	0.065
Edge effect	1	48	0.29	0.593
Region × Management	2	48	3.45	0.040*
Region × Edge effect	2	48	0.63	0.537
Management × Edge effect	1	48	0.37	0.548
Region × Management × Edge effect	2	48	3.25	0.048*

\*P < 0.05



**Fig. 1.** Daily nest survival rate (±SE) for artificial ground nests according to edge *vs*. interior and grazing intensity in three grassland regions of Hungary

We found that the density of ground nesting farmland birds was positively related to survival of artificial nests ( $F_{1.56} = 7.32$ , P = 0.009).

The results on grass height and vegetation cover showed that these local factors significantly influence predation. In the case of the higher grass and higher vegetation cover the predation rate was significantly lower than in short grass and lower cover (grass height: t = 3.122, df = 110, P = 0.002; vegetation cover: t = 4.384, df = 110, P < 0.0001) (Fig. 2).



**Fig. 2.** Grass height and vegetation cover (mean $\pm$ SE) around predated and not predated (intact) artificial ground nests in Hungarian grasslands. (\*\*: *P* < 0.01; \*\*\*: *P* < 0.001)

# DISCUSSION

Using artificial nests we showed that nest losses in Hungarian grasslands are influenced by the interaction of several factors, such as grazing intensity, edge effect and region. At local scale brood survival was higher under larger vegetation height and cover. We recorded the predation of 45% of nests. We used artificial nests, therefore this rate relates only to the egg stage and indicates only the predation pressure in the given locations, not intensity of predation on real nests.

The role of grazing is crucial to maintain the openness of Central European grasslands (STOATE *et al.* 2009), and to provide suitable habitats for a wide range of taxa. These include arthropods, which provide food for grassland birds (DENNIS *et al.* 2008). Low intensity traditional grazing also contributes to local scale vegetation heterogeneity, which improves foraging possibilities and nest placement (EVANS *et al.* 2006, ERDŐS *et al.* 2009). An additional mechanism of how grazing influences nest success is related to vegetation height. Grazing results in short vegetation, where food is abundant and easy to hunt for, however, it less suitable to hide the nests as high vegetation, resulting in larger brood loss (KERNS *et al.* 2010).

An interesting finding was that none of the three factors (region, management, edge effect) alone were significant in the model to explain nest predation, only interactions were significant. For example, management had effect, with higher nest predation on intensively grazed pastures, but only in one out of three regions, resulting in overall lack of management effect, and a significant region x management interaction (Table 1). Therefore, only if region and management were considered together (i.e. evaluating their interaction) effect became obvious (Table 1). Similarly, edge effect was significant if region and management were both considered with edge effect. As we found a positive correlation between density of ground nesting farmland birds and predation of artificial nests, this may mirror patterns and interactions that were observed between grazing and landscape (BATÁRY *et al.* 2007*a*).

A potential source of interaction can be traced back to the different abundance of nest predators in different regions and on fields with different grazing intensity. The potential predator community in the areas was diverse, including Corvidae, and mammalian predators (e.g. Red Fox *Vulpes vulpes*). As far as our data from bird censuses in the same year in the experiment areas indicate (BÁLDI *et al.* 2005), the two main potential avian nest predators, Magpie (*Pica pica*) and Hooded Crow (*Corvus cornix*) had similar observations: 5 in extensive and 7 in intensive pastures, and 4, 3 and 5 in the Alkali, Meadow and Heves regions, respectively. However, the numbers are low, and there is no data for mammals, which are important predators of ground nesting birds (PURGER *et al.* 2008).

The importance of interactions highlights that extrapolating from local scale studies and experiments to another location can be misleading (WHITTINGHAM *et al.* 2007, BÁLDI & BATÁRY 2011*b*). For example, RHODES *et al.* (2008) showed that thresholds in the amount of required habitat by species vary among regions. Here, we showed that nest predation seems to be site-specific, where factors at different spatial scale act, starting from the regional differences through landscape scale (grazing pressure) towards local scales (edge effect and vegetation structure). On the same study fields we found that species richness and abundance of grassland birds were similarly regulated at local and landscape scales (BATÁRY *et al.* 2007*a*).

The lack of edge effect seems to contradict conventional wisdom (BATÁRY & BÁLDI 2004). However, nest predation edge effect is habitat-dependent, being significant in deciduous forests and marshlands, while absent in field edges (BATÁRY & BÁLDI 2004). In addition, most of the studied grasslands were not fenced, and herdsmen keep their herds away from neighbouring arable fields, thus from the grassland edges. This may result in lower grazing pressure, thus denser and higher vegetation at edges, which, in turn, may reduce nest predation. Indeed, grass is slightly higher in the edge than in the inside (9.58 cm in the edge and 8.83 cm in the inside), based on estimations in 840 quadrates (BATÁRY *et al.* 2007*b*).

Dense and high vegetation in grasslands was shown to reduce nest predation risk, probably via reduced visibility (MARTIN 1995, AMMON & STACEY 1997, FLASPOHLER *et al.* 2000). Our results supported this view for Hungarian grasslands, a habitat harbouring large number of threatened bird species. Since grazing influence grassland vegetation structure, it also influences reproductive success via nest visibility. In our study of species abundances we found that true grassland birds, which breed on the ground, had higher number of territories in the extensively than in the intensively grazed grasslands of the same study sites (BATÁRY *et al.* 2007*a*).

In conclusion this study highlights the possibility that intensive grazing may partly be responsible for declines of ground nesting grassland birds in Hungary. Supporting the maintenance of extensive and traditional grazing can enhance protection of these birds. However, applying homogeneous conservation regimes to larger areas should be avoided, notwithstanding that it is attractive to stakeholders. Apparently, there is a limited scope for generalisations about the management of grasslands that is clearly beneficial for the conservation of threatened birds (WHIT-TINGHAM *et al.* 2007, this study). Policy makers should take into account regional differences when programming effective measures to protect farmland biodiversity.

\*

Acknowledgements – We are grateful to GERGELY HEGYI and ROB FIELD for help with statistics and ROB FIELD for his comments on an earlier version of the paper. Staff of the Kiskunság and Bükk National Parks gave valuable help, among others we thank JENŐ FARKAS, ANDRÁS MÁTÉ, LÁSZLÓ MOLNÁR, ISTVÁN NAGY, LÁSZLÓ TÓTH and TIBOR UTASSY. DÉNES VONAH helped with the logistics in the Heves area. We thank the Kiskunság and Bükk National Parks for permissions, and landowners JÁNOS CSAPLÁR, PÁL OLÁH and FERENC PONGRÁCZ for allowing us to work on their fields. The study was supported by the EU-funded project 'EASY' (QLK5-CT-2002-01495). The writing of paper was partly supported by the Hungarian Scientific Research Fund (K81971).

# REFERENCES

- AMMON, E. M. & STACEY, P. B. (1997) Avian nest success in relation to past grazing regimes in a montane riparian system. *Condor* 99: 7–13.
- ÁNGYÁN, J., TARDY, J. & VAJNÁNÉ-MADARASSY, A. (eds) (2003) Essentials of farming on protected and environmentally sensitive areas. Mezőgazda, Budapest, 625 pp. [In Hungarian]
- BÁLDI, A. & BATÁRY, P. (2011a) The past and future of farmland birds in Hungary. Bird Study 58: 365–377.
- BÁLDI, A. & BATÁRY, P. (2011b) Spatial heterogeneity and farmland birds: different perspectives in Western and Eastern Europe. *Ibis* 153: 875–876.
- BÁLDI, A., BATÁRY, P. & ERDŐS, S. (2005) Effects of grazing intensity on bird assemblages and populations of Hungarian grasslands. *Agriculture, Ecosystems & Environment* 108: 251–263.
- BATÁRY, P. & BÁLDI, A. (2004) Evidence of an edge effect on avian nest success: a meta-analysis. Conservation Biology 18: 1–12.
- BATÁRY, P., BÁLDI, A. & ERDŐS, S. (2007a) Grassland versus non-grassland bird abundance and diversity in managed grasslands: local, landscape and regional scale effects. *Biodiversity and Conservation* 16: 871–881.
- BATÁRY, P., ORCI, K. M., BÁLDI, A., KLEIJN, D., KISBENEDEK, T. & ERDŐS, S. (2007b) Effects of local and landscape scale and cattle grazing intensity on Orthoptera assemblages of Hungarian Great Plain. *Basic and Applied Ecology* 8: 280–290.
- BENTON, T. G., VICKERY, J. A. & WILSON, J. D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution* 18: 182-188.
- DENNIS, P., SKARTVEIT, J., MCCRACKEN, D. I., PAKEMAN, R. J., BEATON, K., KUNAVER, A. & EVANS, D. M. (2008) The effects of livestock grazing on foliar arthropods associated with bird diet in upland grasslands of Scotland. *Journal of Applied Ecology* **45**: 279–287.
- DONALD, P. F., GREEN, R. E. & HEATH, M. F. (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London, B* 268: 25–29.
- DONALD, P. F., PISANO, G., RAYMENT, M. D. & PAIN, D. J. (2002a) The Common Agricultural Policy, EU enlargement and the conservation of Europe's farmland birds. *Agriculture, Ecosystems* & Environment 89: 167–182.
- DONALD, P. F., EVANS, A. D., MUIRHEAD, L. B., BUCKINGHAM, D. L., KIRBY, W. B. & SCHMITT, S. I. A. (2002b) Survival rates, causes of failure and productivity of Skylark Alauda arvensis nests on lowland farmland. *Ibis* 144: 652–664.
- DONALD, P. F., SANDERSON, F. J., BURFIELD, I. J. & VAN BOMMEL, F. P. J. (2006) Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. *Agriculture, Ecosystems & Environment* 16: 189–196.

- ERDŐS, S., BÁLDI, A. & BATÁRY, P. (2009) Nest site selection and breeding ecology of Sky Lark (Alauda arvensis) in a Hungarian farmland. *Bird Study* **56**: 259–263.
- EVANS, D. M., REDPATH, S. M., EVANS, S. A., ELSTON, D. A. & DENNIS, P. (2005) Livestock grazing affects the egg size of an insectivorous passerine. *Biology Letters* 1: 322–325.
- EVANS, D. M., REDPATH, S. M., EVANS, S. A., ELSTON, D. A., GARDNER, C. J., DENNIS, P. & PAKEMAN, R. (2006) Low intensity, mixed livestock grazing improves the breeding abundance of a common insectivorous passerine. *Biology Letters* 2: 636–638.
- FLASPOHLER, D. J., TEMPLE, S. A. & ROSENFIELD, R. N. (2000) Relationship between nest success and concealment in two ground-nesting passerines. *Journal of Field Ornithology* 71: 736–747.
- FULLER, R. J. & GOUGH, S. (1999) A major review of sheep grazing impact. *Biological Conserva*tion 91: 73–89.
- GREGORY, R. D., NOBLE, D. G. & CUSTANCE, J. (2004) The state of play of farmland birds: population trends and conservation status of lowland farmland birds in the United Kingdom. *Ibis* **146** *Suppl.* **2**: 1–13.
- GREGORY, R. D., VAN STRIEN, A., VORISEK, P., MEYLING, A. W. G., NOBLE, D. G., FOPPEN, P. B. & GIBBONS, D. W. (2005) Developing indicators for European birds. *Philosophical Transactions of the Royal Society of London, B* 360: 269–288.
- HAZLER, K. R. (2004) Mayfield logistic regression: a practical approach for analysis of nest survival. *Auk* **121**: 707–716.
- HENDERSON, I. G., VICKERY, J. A. & CARTER, N. (2004) The use of winter bird crops by farmland birds in lowland in England. *Biological Conservation* 118: 21–32.
- KERNS, C. K., RYAN, M. R., MURPHY, R. K., THOMPSON, R. F. & RUBIN, C. S. (2010) Factors affecting songbird nest survival in Northern Mixed-Grass Prairie. *Journal of Wildlife Management* 74: 257–264.
- KLEIJN, D. & BÁLDI, A. (2005) Effects of set-aside land on farmland biodiversity: comments on Van Buskirk and Willi. *Conservation Biology* 19: 963–966.
- LEWIS, R. M., ARMSTRONG, D. P., JOY, M. K., RICHARD, Y., RAVINE, D., BERGGREN, A. & BOULTON, R. L. (2009) Using artificial nests to predict nest survival at reintroduction sites. *New Zealand Journal of Ecology* 33: 40–51.
- LOE, L. E., MYSTERUD, A., STIEN, A., STEEN, H., EVANS, D. M. & AUSTRHEIM, G. (2007) Positive short term effects of sheep grazing on the alpine avifauna. *Biology Letters* **3**:109–111.
- MAJOR, R. E. & KENDAL, C. E. (1996) The contribution of artificial nest experiments to understanding avian reproductive success: A review of methods and conclusions. *Ibis* 138: 298–307.
- MARTIN, T. E. (1995) Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65: 101–127.
- MOORE, R. P. & ROBINSON, W. D. (2004) Artificial bird nests, external validity, and bias in ecological field studies. *Ecology* 85: 1562–1567.
- NAGY, G. (1998) Ecological conditions, yield potential and grassland management in Hungary. Pp. 1–13. In: NAGY, G. & PETŐ, K. (eds): Ecological aspects of grassland management. Grassland Science in Europe. Volume 3. European Grassland Federation, Zürich,
- PASINELLI, G. & SCHIEGG, K. (2006) Fragmentation within and between wetland reserves: the importance of spatial scales for nest predation in reed buntings. *Ecography* 29: 721–732.
- PAVEL, V. (2004) The impact of grazing animals on nesting success of grassland passerines in farmland and natural habitats: a field experiment. *Folia Zoologica* 53: 171–178.
- PURGER, J. J., CSUKA, S. & KURUCZ, K. (2008) Predation survival of ground nesting birds in grass and wheat fields: experiment with plasticine eggs and artificial nests. *Polish Journal of Ecology* **56**: 481–486.

394

- R DEVELOPMENT CORE TEAM (2010) R: a language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria. ISBN 3–900051–07–0, URL: http://www.R-project.org
- RHODES, J. R., CALLAGHAN, J. G., MCALPINE, C. A., DE JONG, C., BOWEN, M. E., MITCHELL, D. L., LUNNEY, D. & POSSINGHAM, H. P. (2008) Regional variation in habitat–occupancy thresholds: a warning for conservation planning. *Journal of Applied Ecology* **45**: 549–557.
- SCHERINI, G. C., TOSI, G. & WAUTERS, L. A. (2003) Social behaviour, reproductive biology and breeding success of Alpine Rock Ptarmigan Lagopus mutus helveticus in northern Italy. *Ardea* 91: 11–23.
- SIRIWARDENA, G. (2010) The importance of spatial and temporal scale for agri-environment scheme delivery. *Ibis* 152: 515–529.
- STOATE, C., BÁLDI, A., BEJA, P., BOATMAN, N. D., HERZON, I., VAN DOORNG, A., DE SNOO, G. R. & RAKOSY, L. (2009) Ecological impacts of early 21st century agricultural change in Europe. *Journal of Environmental Management* 91: 22–46.
- SUAREZ, F., YANES, M. & HERRANZ, J. (1993) Nature reserves and the conservation of Iberian shrubsteppe passerines: the paradox of nest predation. *Biological Conservation* 64: 77–81.
- VENABLES, W. N. & RIPLEY, B. D. (2002) Modern Applied Statistics with S. Fourth Edition. Springer, New York. 512 pp.
- VILLARD, M. A. & PART, T. (2004) Don't put all your eggs in real nests: a Sequel to Faaborg. Conservation Biology 18: 371–372.
- WHITTINGHAM, M. J., KREBS, J. R., SWETNAM, R. D., VICKERY, J. A., WILSON, J. D. & FRECKLE-TON, R. P. (2007) Should conservation strategies consider spatial generality? Farmland birds show regional not national patterns of habitat association. *Ecology Letters* **10**: 25–35.
- WILSON, J. D., MORRIS, A. J., ARROYO, B. E., CLARK, S. C. & BRADBURY, R. B. (1999) A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agriculture, Ecosystems & Environment* **75**: 13–30.

Revised version received October 9, 2010, accepted May 9, 2011, published October 28, 2011