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Birds breeding in a changing farmland*

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Abstract. As a result of intensified agriculture, farmland in Europe is the habitat where the most pronounced changes have occurred in recent decades. In parallel, breeding populations of birds have been declining over much of Europe. Today, farmland has the largest proportion of Red-List species. This paper reviews studies on the impact of agriculture on birds breeding in the farmland ecosystems of Europe: breeding bird density in relation to farming practice, effects of agriculture on foraging and feeding ecology while rearing young, and consequences for breeding success.

Specialised bird species are most affected by farming practice. They are rare or even absent in intensively managed farmland with a much reduced habitat and structural diversity. As crops grow fast and as their vegetation is very dense, large fields become inaccessible to or unprofitable for ground feeding birds. To exploit alternative food resources, parents feeding nestlings have to cover larger distances to isolated and distant food patches. Reduced food availability in modern farmland and increased time and energy costs of foraging may result in lower body conditions of parent birds and their broods, in a reduced breeding success and lower survival. Some species breeding in intensively farmed areas are at least locally unable to produce sufficient recruits to maintain their numbers in the long term.

Our knowledge of the breeding ecology and population dynamics of farmland birds is growing, but it is still based mainly on short-term and small-scale case studies on a few species. Little is known about whether measures to improve habitat quality (e.g. set-asides) are adequate to halt negative trends in bird populations. Hence, there is a need for internationally coordinated scientific work with important implications for conservation.

Key words: farming practice, vegetation structure, crop diversity, set-asides, habitat use, foraging range, breeding success, conservation

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INTRODUCTION

Farmland, today covering nearly half of Europe, has always been a habitat of gradual change. For centuries, the open and semi-open landscape was a diverse and small-scaled patchwork of fields, interspersed with fallow land, hedges and small woods, marshland and ditches. This mosaic provided a wide variety of habitats for a fauna and flora of a remarkable species richness. However, in the XX century the speed of changes in European farmland has increased dramatically and within less than a hundred years agriculture drastically reduced the small-scaled diversity in rural landscape. Small plots were amalgamated, marginal habitats improved and incorporated in agricultural production. Modern farmland is dominated by large and uniform fields with a few favoured crop varieties. Reviews on changes in European farmland habitats, in agricultural practice and in farmland birds were given by: Bezzel (1982), O'Connor & Shrubb (1986), Tucker & Heath (1994), Hagemeijer & Blair (1997), Pain & Pienkowski (1997).

Economic reasons are among the main thriving forces behind this development. Today, farmers are under strong selective pressure to perform as efficient food producers. For their economic survival, they attempt to achieve maximum yields, by using modern technology to increase their efficiency (Table 1). On the losing side of this development are many plant and animal species originally typical for rural landscapes. They have either lost their habitats, or they cannot cope with

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Table 1. How to maximize food production in modern agriculture?

Aims	Method	Changes relevant for birds
Soil improvement	drainage/irrigation	habitat loss, habitat change
	fertilizers	dense vegetation, fast growth, short crop turn-over rate
Crop protection	pesticides, herbicides	low abundance/diversity of food
Improved efficiency	machines	homogeneous landscape
	specialisation	habitat loss, low crop diversity
	standardised agriculture	large fields, loss of boundaries

the present environmental conditions in modern farmland. E.g., chemicals used in agriculture reduce the species diversity and the abundance of invertebrates, plants and their seeds, and hence the food supply of farmland birds (Pulliainen 1984, Rands & Southerton 1992, Potts 1997, Chiverton 1999). Mainly in the second half of the XX century, bird populations breeding in European farmland have been declining (Hildén & Sharrock 1985, Hildén et al. 1988, Tucker & Heath 1994). This pattern is most evident in the intensively farmed western and central European countries (Berthold et al. 1986, Hanski & Tiainen 1988, Zbinden 1989, Robertson & Berg 1992, Schifferli 1993, Petersen 1994, Saris et al. 1994, Fuller et al. 1995, Baillie et al. 1997, Bauer & Berthold 1997, Schmid et al. 1998). Today, farmland has a higher proportion of vulnerable or threatened bird species than any other habitat (Tucker & Heath 1994). Within Europe, the proportion of endangered farmland birds increases from southern to northern, and from eastern to western countries. It peaks in the NW of the European Union, where farming is most intensive (Tucker 1997, Schifferli 2000).

The impact of modern agriculture on the farmland eco-system is among the prime reasons for the large-scale and long-term declines of bird populations in European farmland (Baillie et al. 1997, Tucker 1997, Siriwardena et al. 1998). Most relevant for bird diversity and abundance in farmland are the low small-scale habitat diversity in intensively farmed areas (Panek 1997, Wilson et al. 1997, Schläpfer 1988, Petersen 1998), and the loss of boundaries, marginal and „unproductive" habitats. Recent changes in farming practice affect the ecology, breeding success and survival of farmland birds. Starlings *Sturnus vulgaris*, as an example, breed less successfully in Finnish farmland dominated by monocultures of cereals and sugar beet than in mixed agricultural landscape where parent birds can forage in pastures (Tiainen et al. 1989). However, there are marked differences between species. Specialists suffer more than generalists. The former breed at much lower densities, or even disappear from intensively farmed areas with a low habitat diversity (Baillie et al. 1997, Schifferli et al. 1999). On the other hand, several species started breeding, with variable success, in arable and pasture land — e.g. several waders (Beintema 1986), Yellow Wagtail *Motacilla flava* (Dittberner & Dittberner 1984). Others tolerate a moderate farming intensity and some may even profit from modern land management (e.g. some corvids, Richner 1989, Mäck 1998). Siriwardena et al. (1998) calculated farmland Common Bird Census indices for 42 species in Britain; between 1968 and 1995, 13 farmland specialists declined on average by 30%, whilst 29 more generalist species increased by an average of 23%.

In this paper I present examples on how agriculture may affect the ecology of birds breeding in European farmland. I review studies on foraging, the use of different habitat types for feeding when rearing offspring and focus on effects on breeding success. Farmland landscape consists of different types of agricultural crops and grasslands. For simplicity, these are summed up by the term „farmed habitats" throughout this paper. „Unfarmed habitat" refers here to hedges, ditches, fallow land remaining unfarmed for prolonged periods and other agriculturally unproductive land.

EFFECTS OF CHANGES IN FARMLAND HABITATS ON BIRD ABUNDANCE

The most striking effects of modern agriculture are the changes in habitats and their structure. Most affected are wet, dry and nutrient poor

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soils as well as field margins and boundaries between neighbouring fields. Because of their rich structural diversity, such habitats are valuable for farmland birds and other wildlife. Agriculturally poor land was originally covered by wet grassland, scrub or fallow land and hedges, ditches or other linear elements; they were left unfarmed or grazed at a very low intensity. Such areas were improved by agriculture for more intensive farming. How do the losses and structural changes of habitats affect the farmland avifauna? Are the modern fields and cultures replacing the less intensively farmed crops and pastures adequate alternatives for foraging and successful breeding?

Bird abundance on farmland is related to the area covered by specific habitat types and to the level of farming intensity. The density of Skylarks *Alauda arvensis*, for example, is correlated positively with cereals and negatively with hedgerow density (Wilson et al. 1997). Meadows, spring-sown crops, small forests and borderlines were recorded more frequently in the territories of Great Grey Shrikes *Lanius excubitor* and winter crops less often than in random sites (Tryjanowski et al. 1999). Fuller et al. (1997), Pain & Pienkowski (1997) and Schifferli et al. (1999) reviewed the results of such comparisons of bird densities and the availability of farmland habitats.

Skylarks, Whinchats *Saxicola rubetra*, Tree Pipits *Anthus trivialis*, Red-backed Shrikes *Lanius collurio*, Yellowhammers *Emberiza citrinella* and other characteristic farmland species are more abundant on farms with an „organic" agriculture (Petersen 1994, Christiansen et al. 1996, Fuller 1997) and on areas farmed at a low intensity (Schifferli et al. 1999 and references on species therein). Trees, hedges and scrub land area correlate positively with the abundance of Yellowhammer (Tryjanowski 1997), Tree Pipit, Red-backed Shrike and other „hedgerow" species. By contrast, semi-open landscapes are avoided by Lapwing *Vanellus vanellus* (Berg et al. 1992), Skylark (Wilson et al. 1997) and other birds of open farmlands. Amongst the best predictors of bird abundance are also various types of farmed habitats (review in Fuller et al. 1997, Chamberlain & Gregory 1999, Schifferli et al. 1999). Although the results differ widely between studies, they have important patterns in vegetation structure in common. Habitat types which are correlated positively with bird abundance have either a sparse and/or low vegetation at the beginning of the breeding season (e.g. spring-sown crops, stubble fields, meadows after mowing). Or the sward structure is typically very diverse in height and cover throughout most of the season, with tall and single plants next to dense growth and bare patches, as for example in pastures grazed at a low intensity, in set-asides and in permanent or rotational fallow land. Such habitat types occur regularly in areas farmed at a low intensity. However, they are removed, fragmented or converted to more productive farmland in more intensive land management. As will be discussed below, areas with a low or patchy vegetation are more easily accessible to birds foraging and moving on the ground than uniformly dense growing crops.

Do correlations of bird density and habitat variables indicate a causal relationship, as it is usually assumed in publications? Several studies in different countries tested effects of farming intensity on plants (Wilson 1992, Lambelet-Haueter 1995, Mayor & Lambelet-Haueter 1996), on insects (Kennedy 1992, Moreby & Aebischer 1992, Potts 1997), and on birds (Beintema & Müskens 1987, Hanski & Tiainen 1988, Berg & Pärt 1994, Fuller et al. 1995, Pain & Pienkowski 1997, Tucker 1997). Do bird species diversity and/or density increase, if farming intensity is locally reduced, as would be expected from the correlations mentioned above? Laussmann & Plachter (1998) compared bird distribution and abundance before and after small plots or boundaries were taken out of production. New species and pairs bred already in the first years of habitat improvements. Birds hold territories in or close to set-aside areas (Lugrin 1999, Schifferli 2000). A gradual increase in wildflower strips over several years allowed a continuous increase of Whitethroat *Sylvia communis* and Corn Bunting *Miliaria calandra* numbers in this farmland area (Jenny et al. 1997) (Fig.1). Positive effects of a reduction in farming intensity and of various

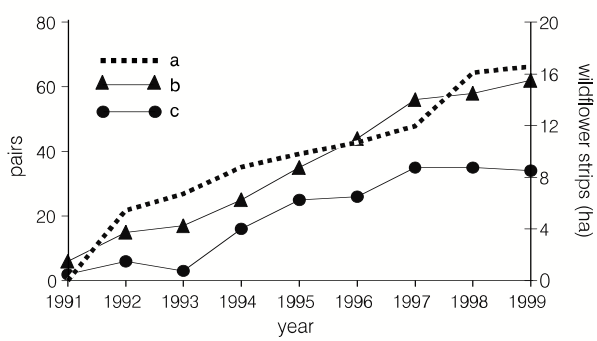

Fig. 1. Wildflower strips (a) and the number of pairs of Whitethroat *Sylvia communis* (b) and Corn Bunting *Miliaria calandra* in the Champagne genevoise (613.5 ha), SW Switzerland. From Jenny et al. (1997), updated.

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types of set-asides have been documented in the following bird species — reviews in Wilson (1995) and Schifferli et al. (1999 including wintering birds), Henderson et al. (2000), wide range of species: Red-backed Shrike (Leugger-Eggimann 1997), Skylark (Wilson et al. 1997, Weibel 1998), Linnet *Carduelis cannabina* and Whitethroat (Berg & Pärt 1994), Whinchat (Labhardt 1988a, Bastian & Bastian 1996), Stonechat *Saxicola torquata* (Lugrin 1999), Corn Bunting (Ward & Aebischer 1994, Eislöffel 1996), Quail *Coturnix coturnix* (Laussmann & Plachter 1998), Grey Partridge *Perdix perdix* (Potts 1997), Yellowhammer (Biber 1993a, Stoate & Moreby 1995, Lille 1996, Kyrkos et al. 1998). To sum up, there is conclusive evidence that farming intensity and the changes in habitats associated with it affect the (local) species richness and density of birds breeding in farmland.

NEST FAILURES IN FARMLAND

A third of farmland species nest on the ground. Their broods suffer from predation (Söderström et al. 1998), destruction by farming machines and trampling by grazing cattle. The proportion of broods destroyed by farming activities varies considerably, between species, years, study areas and their farming regimes. Crick et al. (1994) analysed the British nest record cards from 1924–92 of Buntings. Mayfield estimates of nest survival rates suggest that in the post-1970 period, 31% of Yellowhammer nests were successful, 51% in the Reed Bunting *Emberiza schoeniclus* and 52% in the Corn Bunting. Of the nests that failed for a known reason, the proportion of Yellowhammer and Reed Bunting nests destroyed by farming activities did not differ between nest records from before and after 1970, respectively (Yellowhammer 17% in the first and 19% in the second period, Reed Bunting 18% and 17%) . In contrast, the proportion of Corn Bunting nests destroyed by farming processes increased from 7% of all nests recorded in the first to 21% in second period. However, their overall nest failure rate declined from 69% in the first to 48% in the second period, as both predation and „natural" causes of failures declined, from 31% to 15% and from 32% to 12%, respectively (Crick et al. 1994).

In intensively managed Swiss grassland mowing at intervals of 4–5 weeks destroyed 95 of 98 Skylark nests situated in meadows; overall, 17% of all eggs laid were predated and 37% were lost when the grass was cut (Jenny 1990b). In Britain, 43 % of failing Skylark broods were predated and 26% were victims of farming activities (Wilson et al. 1997). In the Whinchat, 19% of all nest failures were due to agriculture (Bastian & Bastian 1996). Comparing different years, Redshanks *Tringa totanus* lost 47–74% of nests during farming activities, Black-tailed Godwits *Limosa limosa* 52–71% and Oystercatchers *Haematopus ostralegus* 54–76% (Witt 1986). Corncrakes *Crex crex* breeding in dense grassland lost 55% of chicks when meadows were cut from the edge to the centre; mortality was reduced to 32% by reversing the procedure of mowing (Tyler et al. 1998).

Hudson et al. (1994), Peach et al. (1994) and Kooiker & Buckow (1997) reviewed publications on the hatching success of Lapwings in different types of farmland. The mean hatching success of eggs or of clutches in 42 studies in 9 European countries was 53% (Table 2). It varied between areas, years and farming practice. Usually, losses due to farming on arable land exceed those on grassland (Beser & von Helden-Sarnowski 1982, Galbraith 1988, Baines 1990, Shrubb 1990, Berg et al. 1992). Based on daily survival rates of nests in Swedish farmland, Berg et al. (1992) report a hatching success of 67% in grassland. Success rate was lowest in unsown tillage (9%) and highest in sown tillage (78%). The differences on tillage were largely due to farming activities, which, overall, was responsible for 85% of nest losses (Berg et al. 1992). In Germany, clutches started before sowing had a poor hatching success (30%); after field preparation, however, 88% of replacement clutches in maize fields hatched, compared to 81% in grassland (Kooiker 1990, Kooiker & Buckow 1997). The timing and intensity of farming impact on ground nesters also depend on weather conditions at the beginning of the season. Rain and high water tables in spring delay the start of farming processes (Beintema et al. 1985). Up to 89% of Lapwings nesting in Dutch grasslands hatched their chicks before the start of mowing in wet springs (Guldemond et al. 1993).

With an increase in stocking rates, nests in pastures face a growing risk of being trampled by grazing animals (Beintema & Müskens 1987). As a result, hatching success in Lapwings has fallen over past decades to a very poor level in upland grasslands of England and Wales (Shrubb 1990). To predict the impact of grazing on nesting success of Lapwing, Black-tailed Godwit, Redshank, Oystercatcher and Ruff *Philomachus pugnax*, Beintema & Müskens (1987) developed a model. Grazing at high densities and throughout the breeding season have a devastating effect on nest

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survival. According to the model, nesting success rapidly decreases with increasing animal density. Dairy cows have a stronger impact than sheep, and yearling cattle are the worst „tramplers". The model predicts that four yearling cattle per hectare, grazing day and night on a Dutch pasture are sufficient to trample virtually all nests.

Nevertheless, even high losses in individual nests may be compensated, if failing birds relay. This ability plays an important role in the annual productivity (Beintema & Müskens 1987). Lapwings breeding in Swedish farmland prefer tillage for nesting, paradoxically the habitat with the highest losses of clutches laid before sowing (Berg et al. 1992). However, two thirds of failed breeders relay. As 67% of replacement clutches succeed, 55% of all females eventually hatch a brood in tillage, a higher rate than on most other farmland habitats. On permanent pastures with a high density of grazing animals, however, hatching success remains low throughout the grazing period and cannot be compensated by replacement clutches, as these have an equally high failure rate (Beintema & Müskens 1987).

RESOURCES FOR RAISING OFFSPRING — A MATTER OF SCALE AND SPACE

During laying, incubation and while caring for their brood, parent birds and their rapidly growing young need an abundant food supply. To safeguard essential resources from conspecifics, many species hold a territory which includes feeding grounds and/or nest-sites; its quality has strong effects on growth rates and size of nestlings (Richner 1989) and/or on breeding success (Tye 1992, Bollmann et al. 1997, Wilson et al. 1997) and even lifetime reproduction (Hötker 1988). The territory size and particularly the area covered for foraging vary considerably within species. In a local population of Tree Pipits breeding in farmland, as a typical example, the largest territories had 15 times the size of the smallest (0.3–4.3 ha, mean 1.5 ha, Meury 1989, 1991). The size is influenced by the food supply and therefore differs between years and habitat diversity. This concerns Skylark (Schläpfer 1988), Meadow Pipit *Anthus pratensis* (Hötker 1990), Wheatear *Oenanthe oenanthe* (Brooke 1979, 1981), Kestrel *Falco tinnunculus* (Village 1990), Lapland Bunting *Calcarius lapponicus* (Seastedt & MacLean 1979), Yellowhammer (Petersen et al. 1995), Corn Bunting (Fischer & Schneider 1996). Moreover, the home range may also change within season (Schläpfer 1988, Hötker 1990) or in relation to the nesting cycle (Møller 1990). The foraging area may even differ from day to day, e.g. in relation to daily weather. Thus, Swallows *Hirundo rustica* and House Martins *Delichon urbica* hunt on average 170m and 450m from their nests, respectively (Bryant & Turner 1982). During cool or rainy spells they extend their foraging activities to one or more kilometers (Loske 1993).

Between species, the size of the territory or home range generally increases with body mass (Fig. 2) in 61 bird species breeding in open or semi-open farmland. This confirms data presented by Schoener (1968), Newton (1979, for raptors) and Morse (1980). These authors discuss reasons for interspecific variation of territories in relation to food and feeding ecology. Here, the relevant conclusion from Fig. 2 is that in passerines, small areas of just a few hectares are the „working units" of individual pairs for reproduction. A high diversity on a small scale may be crucial, since a single crop type rarely provides a suitable vegetation structure for nesting and foraging throughout the breeding season. As discussed below, Skylarks and other birds nesting and feeding on the ground therefore require structurally diverse crop mosaics (Chamberlain & Crick 1999, Chamberlain et al. 1999). Unless there is some diversity of habitats on the scale of a small territory and within close range from the nest site, parents have to extend their foraging range. To make multiple nesting attempts in uniform and intensively farmed areas, they may have to shift the territory between broods, or abandon an area due

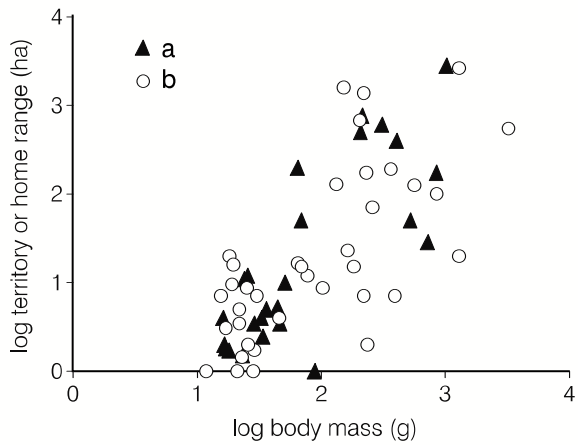

Fig. 2. The size of territory (a) or foraging range (b) in 61 bird species in relation to their body mas. Home range $r^2 = 0.48$, n = 37 species; territory $r^2 = 0.64$, n = 24. Sources are some 50 papers indicated in References.

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to a lack of habitats with a suitable vegetation structure (Schläpfer 1988, Wilson et al. 1997).

OPTIMAL FORAGING AND FARMING PRACTICE

Birds feeding for themselves may freely move over wider areas for foraging. While breeding, however, nidicolous species are tied to a fixed nest site. The brood depends entirely on the nutrients and energy transported to the nest by the parents, which work close to their physical limits (Drent & Daan 1980, Cuthill & Houston 1997). There is strong selective pressure to contribute as many offspring as possible to the future population, by raising a maximum number of viable young. To achieve this goal, parents have to perform as effective food deliverers, by making optimal use of the food resources within their home range (Krebs & Davies 1993, 1997, Maurer 1996). Various models on central place foraging making predictions on possible strategies to maximize foraging efficiency (MacArthur & Wilson 1967) have been tested in farmland birds (overviews in Stephens & Krebs 1986, Maurer 1996, Krebs & Davies 1997).

Important variables in foraging strategy models are the food supply and the distance of food patches from the nest. Food for the brood is transported in flight, a quick and efficient, but energy demanding method. Travelling distance is therefore a significant factor in the energy budget while rearing young and a major component in optimal foraging theory. Thus, parent birds raising nestlings forage close to the nest, as short flight distances minimize energy costs. Distant food patches are hardly worth exploiting, unless large portions can be brought to the young, as confirmed by experimental work (Andersson 1981, Carlson 1985, Carlson & Moreno 1985, Cuthill & Huston 1997, Wright et al. 1998). When feeding for themselves, however, as during laying and incubation, the parent birds may efficiently use food patches throughout their territory. Before hatching, Red-backed Shrikes hunt at a median distance of 57 m from the nest and use their home range according to the availability of perches suitable for hunting (Fig. 3). When rearing young they economise on travelling distances by concentrating their foraging very close to the nest (median distance 26 m, Fig. 3).

Mean or median distances of foraging sites from the nest of birds feeding nestlings of < 100 m have been reported in the Goldfinch *Carduelis carduelis* (Glück 1980), the Corn Bunting

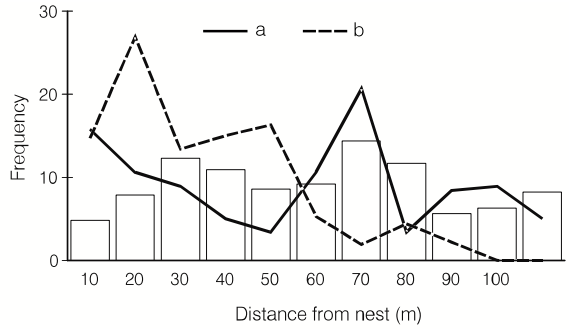

Fig. 3. Frequency distribution (%) of distances of foraging sites from the nest before hatching (a, n = 179), after hatching (b, n = 320) and of perches (columns) of 5 pairs of Red-backed Shrike *Lanius collurio*. Reworked from Spaar & Schifferli (1998).

(Hartley et al. 1995), the Water Pipit *Anthus spinoletta* (Frey-Roos et al. 1995), the Hoopoe *Upupa epops* (Kristin 1993). In the Yellowhammer mean distances varied from 82 m to 184 m, depending on area, season, year and farming regime (Petersen et al. 1995, Lille 1996, Stoate et al. 1998). In the Swallow and the House Martin mean travelling distances were 170m and 450 m, respectively (Bryant & Taylor 1982). Most non-passerine species cover more than 500m between nest and feeding sites: Barn Owl *Tyto alba* (637 m, Brandt & Seebass 1994), White Stork *Ciconia ciconia* (1.3 km, Alonso et al. 1994) and Merlin *Falco columbarius* (1–1.7 km, Sodhi 1992).

In intensively farmed countryside, unfarmed habitats and perches are often removed. Suitable foraging areas may therefore be small and isolated remnants, wide apart and thus distant from the nest. This may increase the time needed for foraging and the travelling distances, and hence the costs of reproduction. Leugger-Eggimann (1997) compared the parental expenditure of Red-backed Shrikes in habitats of varying farming intensity. He found that the parents breeding in areas farmed at a high intensity lost more of their body mass while rearing young. The adults invested more time in flight activity while foraging compared to conspecifics in low-intensity farmland. This is confirmed by differences in travelling distances reported from areas of differing farming intensity (Schifferli et al. 1999). Red-backed Shrikes in areas farmed at a low, medium and high intensity, respectively, collected the food for their broods at mean distances of 27 m, 51 m and 72 m. Assuming a mean of 15 feeding visits by both parents per hour (Glutz von Blotzheim & Bauer 1993), distances covered per day were estimated as 13 km, 24 km and 34 km in the three categories of farming intensity (Schifferli et al. 1999).

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ACCESS TO FOOD IN DENSE AND FAST GROWING CROPS

Food supply for foraging birds is reduced in intensive farmland. This is well documented in Moreby et al. (1994), Brooks et al. (1995), Lille (1996), Campbell et al. (1997) and Potts (1997). Moreover, growth of fertilised monocultures and manured meadows is fast, uniform and dense. Height and density of vegetation affect locomotion of birds nesting and/or feeding on the ground. Cover and height also influence the detectability of prey by foraging birds. Starlings, for example, foraging in grass taller than 6 cm moved more slowly, were stationary for longer periods and had stops of longer duration than in short grass (Brownsmith 1977); Water Pipits take longer to find prey in tall than in short vegetation (Brodmann et al. 1997). In the White Stork, intake rates decrease with vegetation height, although the food supply shows an opposite trend (Sakl 1989).

Agricultural crops nowadays grow rapidly. Within a few weeks after sowing, fields may become impenetrable or unprofitable for foraging (Eiserer 1980). Ground-feeding birds therefore often prefer sparse cover and short vegetation. Wintering Golden Plovers *Pluvialis apricaria* and Lapwings forage in autumn sown cereals up to 8cm and 11cm in height, respectively (Mason & MacDonald 1999). In the breeding season, Lapwings avoid densely growing vegetation, if it exceeds 4–7 cm. At medium and low plant density, vegetation heights of up to 15–18 cm and up to 18–38 cm, respectively, are tolerated (Klomp 1954). Although it is widely recognized that foraging is limited by a combination of vegetation height and density, the second parameter is rarely quantified (methods and references in Schäffer 1999). We therefore have to rely on data of plant height. This is justified, as vegetation height and density are often correlated (Weibel 1998). Many waders, pipits, larks, wagtails, thrushes and corvids feed on sparsely covered or bare ground, and in vegetation less than 10 cm tall (Fig. 4). The attraction of short grass is most striking in meadows, where birds congregate shortly after mowing to profit from easy access to invertebrates that have suddenly lost all their shelter.

Species, which run or hop usually avoid dense vegetation exceeding 10 to 20 cm in height. Exceptions are long-legged species as the Black-tailed Godwit which is able to walk slowly and takes short steps through tall vegetation by lifting the legs (Klomp 1954). Some *Acrocephalus* warblers have skeletal adaptations to hold on stems and move in thick vegetation (Leisler 1975, 1980). Meadow Pipit and Tree Pipit with long claws and a wide foot span can move and forage in tall vegetation, especially if the grass is depressed by rain or snow (Hötker 1990). Small ground-feeding passerine birds hardly visit vegetation taller than 20 cm. Exceptions are fallow land, rough grazing

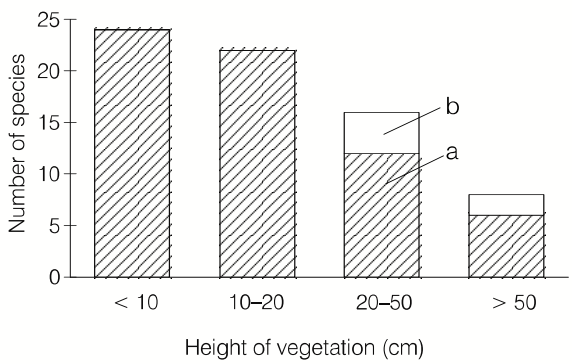

Fig. 4. Number of bird species foraging and vegetation height (n = 38 species). a — number of species feeding on the ground, b - number of species foraging by sallying in the vegetation or above it. Each of the 38 species was counted only once; species foraging in more than one class were split accordingly. Sources are some 50 papers indicated in References.

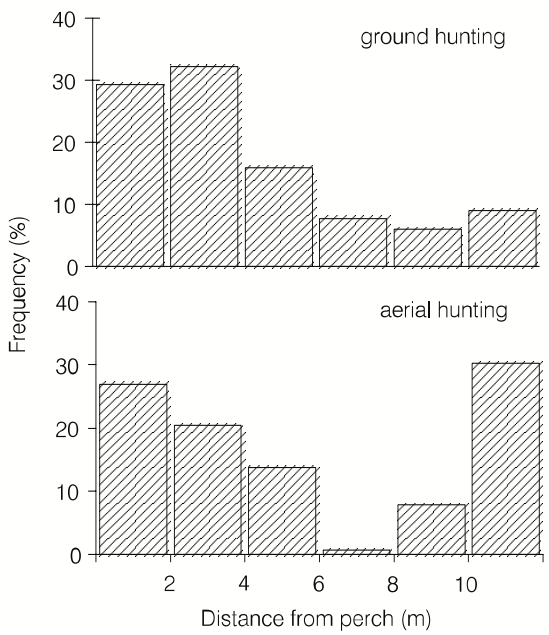

Fig. 5. Foraging sites of the Red-backed Shrike in relation to the distance the from perch (frequency distribution, %); ground hunting (n = 584 flights, mean = 4.7 m, median = 3.3 m) and aerial hunting (n = 152 flights, mean distance from perch = 6.9 m, median = 4.4 m). 10 pairs breeding in S Switzerland in an area farmed at low intensity, cf. Spaar & Schifferli (1998), Schifferli (1989, 2000), Schifferli et al. (1999).

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or set-aside areas up to 50 cm or even more. These habitats often show a high diversity in vegetation density and height and they typically have bare patches allowing easy access. Such habitats are exploited also by species hunting from perches (e.g. Stonechat, Wheatear: Brooke 1981, Greigh-Smith 1983, Moreno 1984). Whinchats hunt in or above mature hay meadows from strong stems or fences as vantage points (Labhardt 1988b, Bastian & Bastian 1996). In Shrikes and Chats hunting from perches is the major foraging technique for hunting in the vegetation, on warm days also in the air (Greigh-Smith 1983, Solari & Schudel 1988).

Red-backed Shrikes catch prey mostly on the ground and within 3–4 m from the perch (Fig. 5), presumably because more distant insects are more difficult to detect in the vegetation. Hence, each small bush in farmland provides access to a hundred square metres of hunting grounds (Spaar & Schifferli 1998). They hunt predominantly on meadows, pastures or fallow grassland up to 10 cm in height (Fig. 6). Prey above tall vegetation is exploited primarily by aerial flights. Yosef & Grubb (1993) studied Loggerhead Shrikes *Lanius ludovicianus* foraging in tall substrates and after mowing, respectively. When hunting in low vegetation, they spent less time in flight and shifted from aerial to ground hunting. In the absence of vantage points, Kestrels have to change from a sit-

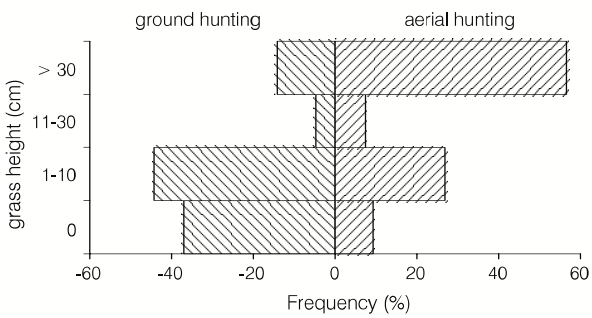

Fig. 6. Vegetation height at feeding sites of the Red-backed Shrike. Aerial hunting (n = 108 flights) and ground hunting (n = 125 flights). 4 pairs breeding in S Switzerland in an area farmed at low intensity, data in Spaar & Schifferli (1998), Schifferli (1989, 1999), Schifferli et al. (1999).

and-wait strategy to hover flight (Buner 1998). However, this hunting technique is more energy consuming than hunting from perches (Rudolph 1982, Masman & Klaassen 1987).

In Shrikes, Whinchats and other sit-and-wait predators, small bushes, fence posts, wires and other vantage points are important requisites for

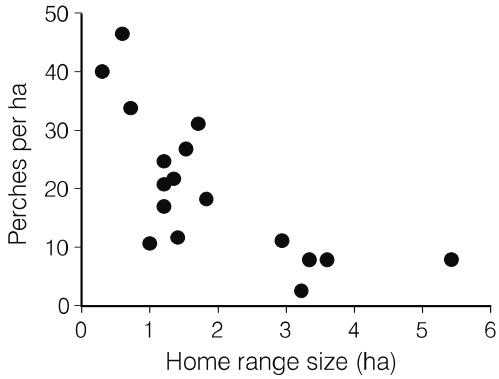

Fig. 7. Home range size of the Red-backed Shrike in relation to the density of perches. Data in Spaar & Schifferli (1998), Schifferli (1989, 2000), Schifferli et al. (1999).

foraging. Home range area and/or territory size are therefore correlated with the density of suitable perches, as shown for the Red-backed Shrike (Fig. 7). An effect of perch density on territory size was documented in Great Grey Shrikes (Yosef 1993, Schön 1994, Rothaupt 1995), Woodchat Shrikes *Lanius senator* (Schaub 1996, Rehsteiner 2000), Red-backed Shrikes (Solari & Schudel 1988), the Mediterranean Grey Shrike *Lanius meridionalis* (Görlich 1997) and the Whinchat (Bastian & Bastian 1996).

In many species, access to dense and tall vegetation for foraging in cereals is limited to bare parts within fields or to the edges. Skylarks use patches of stunted growth or tramlines to get into densely growing cereal crops (Odderskär et al. 1997, Weibel 1998, Schön 1999). In contrast, „compact" gallinaceous birds, like the Pheasant *Phasianus colchicus* (Hill & Robertson 1988), Red-legged Partridge *Alectoris rufa*, Grey Partridge (Rands 1988, Potts 1997), several long-legged waders (Beintema et al. 1985, Beintema 1986), storks (Alonso et al. 1994) and herons are able to move in densely growing crops. Quail (Glutz von Blotzheim 1973) and Corncrake (Schäffer 1999) are among the species that require dense and tall vegetation for foraging in shelter.

Whereas dense cover is impeding free movement for foraging, tussocks and patches of thick vegetation are favoured nest-sites of many open-breeders. However, growth may be very rapid and uniform. Skylarks usually nest in vegetation 10–40 cm in height and a ground cover of 20–40% (Griesser & Hegelbach 1999). In cereals, the parents may soon have difficulties in locating and reaching their nests in large and uniform fields; reaching their young for feeding may become difficult in very dense vegetation (Wilson et al. 1997).

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To sum up, most fields and crops in modern farmland are accessible only in the early stages of growth and from the edges or bare patches. Within a few weeks fields are either impenetrable or have to be exploited by energy demanding aerial hunting. If suitable food resources are lacking close to the nest, the parents have to undertake longer travelling distances. This is likely to increase the energy costs of feeding nestlings. Multi-brooded species with a long breeding season, as the Skylark, may have to shift or leave their territories between broods.

BREEDING SUCCESS AND FARMING

Do increased energy costs of reproduction reduce breeding success in intensively managed farmland with a low habitat diversity? Hoopoes breeding in the Rhone valley in southern Switzerland feed their young on Molecrickets *Gryllotalpa gryllotalpa*. These are collected in the intensively farmed plains. As long as there were no suitable nest-sites nearby, Hoopoes bred in natural cavities on the foothill slopes, up to 1–2 km from the Molecrickets (Arlettaz et al. 2000). Breeding success declined with increasing altitude of the nest-site above the plain, presumably due to higher costs of transporting food from lower lying and distant food patches. As soon as nest-boxes were placed in the plain, these attracted the Hoopoes closer to their food resources and this improved their breeding success (Fournier & Arlettaz 2001).

In the Red-backed Shrike, Brandl et al. (1986) report differences in breeding success between habitats: More fledglings were raised in pastoral farmland than where meadows predominate. In contrast, Leugger-Eggimann (1997) and Schifferli et al. (1999) found no differences in the number of fledglings in areas farmed at different intensities, although travelling distances were longer where agriculture was more intensive. However, adults and nestlings were lighter in high intensity farmland. Lower body conditions in birds from suboptimal habitats might reduce future survival, as has been shown for the Kestrel (Dijkstra et al. 1990, Daan et al. 1996) and several other bird species (Richner 1989, Golet et al. 1998, Wright et al. 1998, Both et al. 1999, review in Magrath 1991). Nevertheless, breeding success depends primarily on nest predation (Farkas et al. 1997, Söderström et al. 1998, Söderström 1999) and on weather conditions (Stauber & Ullrich 1970, Mann & Brandl 1986; reviews in Rudin 1990, Lefranc 1993). In a long-term study on population dynamics, Jakober & Stauber (1987) conclude that 2.9 young per pair should fledge per season for population stability. Whether breeding success is above or below this threshold appears to depend more on predation and weather conditions, two less predictable environmental variables, than on habitat differences. This might be expected if birds are able to assess at the time of settlement whether the quality of a territory allows successful breeding (Goodburn 1991, Bollmann et al. 1997), at least under favourable environmental conditions and avoid unrewarding areas.

Of special interest is a study by Richner (1989) on the Carrion Crow *Corvus c. corone*, one of the generalist species with stable or increasing populations in farmland (Hagemeijer & Blair 1997). Richner (1989) compared broods raised in urban habitat and rural landscape. Pairs in farmland fledged more young; these grew more rapidly and were heavier when leaving the nests and larger in size, which increased their chances of acquiring a territory. Carrion Crows breeding in farmland therefore achieved a substantial fitness gain compared to conspecifics in urban landscape.

Is the breeding success in modern farmland with increased costs of reproduction and heavy nest losses due to grazing animals and other farming activities still sufficient to maintain the population? Is the number of offspring adequate to balance the annual adult mortality? Or are populations in intensively farmed landscape sinks which depend on immigration? To estimate the productivity required for population maintenance, we need information on the survival rate of parent and first year birds from fledging to the next breeding season. Peach et al. (1994) and Catchpole et al. (1999) analysed ringing recoveries of Lapwings to estimate juvenile and adult survival rates. Peach et al. (1994) found mean annual survival rates of 0.705 in adults and 0.595 in juveniles. They conclude that about one young surviving to independence per year and pair is required to maintain the Lapwing population. Table 2 and Fig. 8 show the annual production of young, based on 37 studies from 9 mainly western European countries. On average, the annual breeding success of the Lapwing was 0.7 young/pair and in 27 of the 37 case studies it was below the threshold of one young/pair (Table 2, Fig. 8). It is therefore not surprising that the Lapwing has been decreasing in western Europe (van Strien & Pannekoek 1998), where the bulk of the population breeds (Hagemeijer & Blair 1997).

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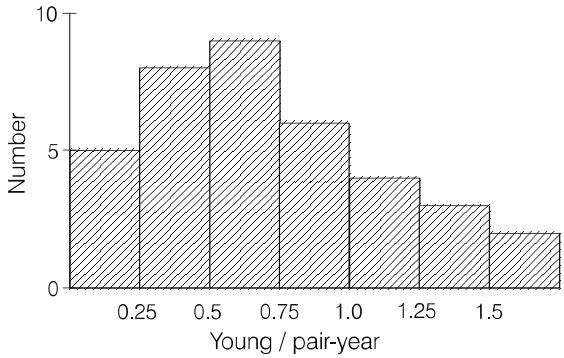

Fig. 8. Frequency distribution of breeding success in the Lapwing *Vanellus vanellus* (number of young/pair-year surviving to at least 2–3 weeks after hatching) in 37 studies in 9 European countries (cf Table 2). Data in Kooiker & Buckow (1997), Peach et al. (1994), Hudson et al. (1994), updated by information in Bollmeier (1992) and Zöllner (1994).

Table 2. Hatching rate of clutches and breeding success at least 10–20 days after hatching in Lapwings *Vanellus vanellus* in various habitats. Means and s.d. of percentage of clutches hatching and number of young surviving for at least 10–20 days after hatching. n — the number of studies. Data from reviews in Imboden (1970, 1974), Hudson et al. (1994), Peach et al. (1994), Kooiker & Buckow (1997) and updated with figures in Bollmeier (1992) and Zöllner (1994).

Habitat	hatching, %			young/pair-season		
	mean	SD	n	mean	SD	n
Arable	56	20	15	0.75	0.51	10
Grassland	52	15	15	0.84	0.54	14
Pasture	46	23	7	0.64	0.26	6
Mixed	32	17	3	0.37	0.33	5
Unfarmed	84		2	0.91		2
Total	53	20	42	0.72	0.48	37

Breeding success exceeds one young (Fig. 8) in clutches hatching in saltmarshes (Ettrup & Bak 1985), *Molinetum* marshland (Heim 1978), grassland farmed at a low intensity (Schoppenhorst 1996), spring-sown cereals or uncultivated land; least productive are winter cereals and pastures with heavy grazing (Bollmeier 1992). In intensively managed farmland, perspectives are best in years with unusually rainy periods with an adequate food supply at hatching and/or farming activities delayed to after hatching. The main reason for the deficit in production is the low survival of chicks. In arable land, invertebrates retreat below the soil surface during dry periods and soon become inaccessible to chicks. Under such conditions, the young grow slower on arable crops than on meadows or saltmarshes (Ettrup & Bak 1985), or they even starve (Matter 1982). The parents lead broods hatching on dry arable crops to moist depressions, grassland or open ditches with more adequate food resources (Matter 1982, Berg et al. 1992). Johansson & Blomqvist (1996) document initial movements exceeding 300 m between nest sites and home ranges used for chick-rearing. Families from arable fields left to feed in the same habitats as broods from pastures. The chances to find good food patches within reach of the hatchlings are best in broods in or close to uncultivated land, saltmarshes or grassland farmed at a low intensity (Heim 1978, Matter 1982, Etrup & Bak 1985, Bollmeier 1992, Bairlein & Bergner 1995, Kooiker & Buckow 1997).

Movements of families in search of food are typical for nidifugous birds. The distances covered are related to food distribution and abundance. The foraging range of Pheasant families, for example, generally increase with age (Hill & Robertson 1988). Larger distances are covered in low quality habitat. Negative correlations of Pheasant and Grey Partridge chick survival with distance moved indicate that increased travelling distances may reduce survival and hence fitness (Green 1984, Hill 1985).

Data on Curlew *Numenius arquata* (Grant et al. 1999), Black-tailed Godwit (Witt 1989, Struwe-Juhl 1995), Yellowhammer (Biber 1993b, Kyrkos 1997, Kyrkos et al. 1998), Whinchat (Bastian & Bastian 1996) and Skylark (Wilson et al. 1997) suggest that breeding success in modern farmland might at least locally be insufficient for long-term population stability. In the Skylark, the British breeding population has been declining in recent decades, although the success rate of individual nests has increased (Chamberlain & Crick 1999). A possible explanation for the population decline is that too few females relay to replace failing nests (Chamberlain et al. 1999). In English farmland with intensive cereal production, 11% of broods survived from laying to leaving the nest (Wilson et al. 1997). Assuming a juvenile survival rate of 20–35% from leaving the nest to the next breeding season, the parents would have to make at least three nesting attempts to fledge sufficient young to maintain the population. In reality, they are unlikely to make more than one in intensively farmed cereals. The results of detailed studies on Skylark breeding ecology (Schläpfer 1988, Jenny 1990a,b, Fuller et al. 1995, Poulsen 1996, Weibel 1998, Chamberlain & Crick 1999, Chamberlain & Gregory 1999, Chamberlain et al. 1999) lead to the

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conclusion that „without structurally diverse crop mosaics which allow breeding pairs to make multiple nesting attempts without recourse to territory shifts or abandonment, Skylark populations in arable landscapes in lowland England are likely to be demographic „sinks", unable to sustain their numbers in the absence of immigration." (Wilson et al. 1997, p. 1475).

SUMMING UP ....

This review on birds breeding in European farmland pinpoints some of the biologically important features in modern land management. Agriculture concentrates on a few highly productive crop types, growing on large and homogenous fields; unproductive habitat elements are eliminated, crops are protected and soils improved for increased production. These changes in the farmland eco-system lead to lower densities or the absence of many specialised birds. Species breeding in farmland with a reduced habitat and structural diversity may suffer from higher costs of reproduction, reduced breeding success and chick survival. For some species it has been shown at least locally and for many it is suspected that birds in modern farmland are „sink" populations, as they are unable to produce sufficient recruits to maintain their numbers in the long-term.

.... AND LOOKING FORWARD

To reduce production, some farmland has been taken out of production and to reduce agricultural impact on wildlife; „organic" and „ecological" farming is subsidised in several countries. To document whether such measures are adequate to halt or even reverse negative trends in farmland birds, a European network of breeding bird population monitoring is essential, as proposed by the European Bird Census Council EBCC (Marchant et al. 1997, Gibbons 1998).

Set-aside areas rarely cover more than 5–10% of farmland. Usually, they are small plots or narrow strips, far apart and isolated. Case studies mentioned in this review have shown that birds readily settle in or close to such areas and use them for foraging. However, little is known on the costs of reproduction and breeding performance in farmland with a few and scattered set-aside areas. Coordinated ecological and population studies are needed to find out, for example, how much of farmland should be set-aside, how these plots should be managed, of what size and how close to each other they should be to allow successful breeding.

Equally important is long-term and international work on population parameters: breeding success, first year and adult survival rates, juvenile recruitment rates and dispersal. Examples are the EURING Swallow Project (Jenni 1998) and various capture-recapture programmes (Peach et al. 1998). Little is known on survival in the first weeks after fledgling, although it is suspected that mortality is high immediately after fledging (Hötker 1982, 1990, Bignal et al. 1987, Thompson et al. 1997, Kenward et al. 1999, Naef-Daenzer et al. 1999).

Thus, birds breeding in a rapidly changing farmland and their ecology and population dynamics provide an unique challenge for scientific work with important implications in conservation biology.

ACKNOWLEDGMENTS

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STRESZCZENIE

[Ptaki lęgowe wobec zmian w rolnictwie]

Od stuleci krajobraz rolniczy był mozaiką pól, nieużytków, zarośli, zadrzewień, mokradeł i cieków melioracyjnych. Zapewniało to bogactwo środowisk i różnorodność gatunkową. W ciągu ostatnich 50 lat intensyfikacja produkcji rolnej, którą umożliwił postęp technologiczny (Tab. 1), drastycznie zmniejszyła tę różnorodność. Spowodowało to wielkie zmiany w awifaunie lęgowej Europy (Tucker & Heath 1994, Hagemijer & Blair 1997). Praca jest przeglądem badań nad różnorodnymi skutkami tych zmian dla awifauny lęgowej krajobrazu rolniczego: nad wpływem działalności rolniczej na zagęszczenie awifauny lęgowej, możliwości wyżywienia, wyniki lęgów i dynamikę populacji lęgowych. Omawia też potrzeby dalszych badań.

Na terenach rolnictwa ekstensywnego stwierdzono wyższą liczebność i różnorodność gatunkową awifauny (Fuller 1997, Schifferli et al. 1999, Fig. 1). Korzystne jest tu szczególnie rozrzedzenie i mała wysokość roślin uprawnych na początku okresu lęgowego, oraz ugorowanie i nieużytki.

Jedną z przyczyn ubożenia awifauny na terenach intensywnego rolnictwa jest zmniejszona różnorodność i mała obfitość bazy pokarmowej (Pain & Pienkowski 1997). Szybki wzrost, gęstość i mała różnorodność intensywnych upraw polnych i łąkowych utrudniają ptakom żerowanie i przemieszczanie się. Wróblowe żerujące na ziemi preferują rzadką roślinność o zróżnicowanej wysokości (Fig. 4, 5, 6, 7). Intensywne uprawy są mało dostępne lub zmuszają do męczącego polowania z powietrza.

Intensywne, szybko rosnące uprawy zmniejszają wydajność pokarmową terytorium lęgowego, od czego zależy pomyślność lęgów — przeżycie i kondycja potomstwa (Richner 1989, Wilson et al. 1997). Wielkość terytorium u większych gatunków na ogół wzrasta proporcjonalnie (Fig. 2). Energochłonność przynoszenia pokarmu pisklętom jest istotnym czynnikiem strategii lęgowej — intensywne uprawy stwarzają pod tym względem gorsze warunki (Fig. 3, Cuthill & Huston 1997, Wright et al. 1998). Szybko rosnące monokultury często nie zapewniają możliwości wyżywienia w ciągu całego okresu trwania lęgu (Chamberlain et al. 1999), często także zmuszają do przenoszenia drugiego lęgu do innego terytorium (Schläpfer 1988).

Istotne jest czy w pogorszonych warunkach lęgowych na terenach intensywnego rolnictwa ptasie populacje mogą reprodukować swój stan czy też mają tam bilans ujemny, uzupełniany imigracją. U czajki w zachodniej i środkowej Europie bilans ten jest ujemny (Peach et al. 1994, Tab. 2, Fig. 8) i jej stan w zmniejsza się (van Strien & Pannekoek 1998). Sukces lęgowy kulika wiekiego (Grant et al. 1999), rycyka (Struwe-Juhl 1995), trznadla (Kyrkos et al. 1998), pokląskwy (Bastian & Bastian 1996) i skowronka (Wilson et al. 1997) wskazuje, że co najmniej w niektórych regionach nie może on zapewnić długookresowej stabilności populacji. Brytyjska populacja skowronka zmniejsza się w ciągu ostatnich dziesięcioleci, mimo wzrostu sukcesu lęgowego (Chamberlain & Crick 1999). Może to być spowodowane zmniejszonymi możliwościami założenia gniazda w warunkach intensywnnego rolnictwa (Chamberlain et al. 1999). Dla wyjaśnienia tych problemów potrzebna jest europejska sieć monitoringu ptasich populacji lęgowych (Gibbons 1998).

Potrzebne są też badania nad rolą dla ptaków ugorowania, stosowanego w rozwiniętych krajach europejskich. Ważne są również długookresowe międzynarodowe badania demograficzne jak np. program EURING dotyczący dymówki (Jenni 1998) i inne programy oparte na znakowaniu ptaków (Peach et al. 1998).

Gwałtowne przemiany w rolnictwie są wyzwaniem i okazją dla różnorodnych badań powiązanych z ochroną przyrody.

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