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Effects of wildflower strips in an intensively used arable area on skylarks (*Alauda arvensis*)

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Dedicated to my mother

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Zusammenfassung

Die Feldlerche *Alauda arvensis* ist ein häufiger und weit verbreiteter Vogel der offenen Kulturlandschaft. Seit den späten 1970er Jahren gehen ihre Bestände in allen Ländern West- und Zentraleuropas dramatisch zurück. Verschiedene Aspekte der Intensivierung der Landwirtschaft wurden als Ursachen der Populationszusammenbrüche genannt wie Flurbereinigungen, Verkürzung der Fruchtfolge, vermehrter Einsatz von Kunstdünger und Pestiziden sowie Vorverlegung des ersten Schnittes und häufigere Mahd im Grünland.

Seit 1993 müssen die Schweizer Landwirte Teile ihrer landwirtschaftlichen Nutzfläche für den ökologischen Ausgleich ausscheiden. Buntbrachen, als ein Typ der ökologischen Ausgleichsflächen, sind vor allem in Ackerbaugebieten von Interesse. Sie sind meist 3-10 m breit, werden mit einer Saatgutmischung aus einjährigen Segetal-, zweijährigen Ruderal- und perennierende, dikotylen Wiesenarten eingesät und dürfen nicht mit Pflanzenhilfsstoffen behandelt werden.

In der vorliegenden Arbeit wurde die Nistplatzwahl, der Bruterfolg, das Nestlingswachstum und die Nestlingsnahrung von Feldlerchen in einem intensiv ackerbaulich genutzten Gebiet, das mit Buntbrachen ökologisch aufgewertet wurde, untersucht. Die Einflussgrössen auf den Nestraub und die Nesträuber wurden zudem mit einem Kunstnest-Experiment studiert. Insbesondere interessierten die Auswirkungen der Buntbrachen auf die obengenannten Fragenkomplexe. Die Feldarbeit wurde zwischen 1996 und 1998 im intensiv ackerbaulich genutzten Gebiet Widen (5.3 km^2) des Schaffhauser Klettgaus (Nordschweiz) durchgeführt, in welchem die Schweizerische Vogelwarte Sempach und das Planungs- und Naturschutzamt des Kantons Schaffhausen viele Landwirte zur Anlage von Buntbrachen motiviert haben.

Die relative Verteilung der Nester in den Kulturen sowie ihre räumliche Lage innerhalb der Felder wurde mittels compositional analyses bestimmt. Der Bruterfolg wurde

anhand der Mayfield-Methode berechnet. Halsringproben wurden zur Erfassung der Nestlingsnahrung verwendet.

Die Verteilung der Nester (n = 396) auf die Kulturen war im Laufe der Brutsaison abhängig von der Vegetationsstruktur. Buntbrachen, Grünbrachen und Kunstwiesen hatten die höchste relative Nutzung. Relativ mehr Nester wurden im Randbereich als in der Mitte der Felder gefunden. Die Grösse der Gelege betrug 3.6 ± 0.04 Eier (n = 396), diejenige der Brut beim Nestverlassen 3.3 ± 0.07 (n = 202). Beide zeigten eine Zunahme von April bis Juni mit einem anschliessenden Rückgang im Juli. Gelege in Revieren mit Buntbrachen waren signifikant grösser (3.7 ± 0.06; n = 175) als in diejenigen ohne (3.5 ± 0.05; n = 221).

Der Bruterfolg, definiert als die Wahrscheinlichkeit, dass pro Brutversuch mindestens ein Jungvogel das Nest verlässt, betrug 22.4 ± 0.5%; zwischen 1995 und 1997 lediglich 17.8 ± 0.5%, 1998 jedoch 37.8 ± 0.9%. Der Bruterfolg war vom Neststandort abhängig und lag zwischen 3.5 ± 2.9% bei Wegrandnestern und 34.1 ± 0.7% bei Nestern in Getreide; in Buntbrachen 18.0 ± 0.2%. Nester, die näher als 10 m vom Feldrand angelegt wurden, hatten einen Bruterfolg von 23.8 ± 2.6%, während diejenigen weiter gegen die Feldmitte einen Bruterfolg von mehr als 20% hatten. Prädation verursachte 72% der Brutverluste und war in der Nestlingszeit häufiger als während der Bebrütung.

Die täglichen Wachstumsraten des Gewichts und der Länge der 3. Handschwinge von Feldlerchennestlingen variierten stark (Gewicht -2.0-6.5 g/d; Federlänge 0-8.5 mm/d). Bei 16% der Messungen (n = 642) wurde eine Gewichtsabnahme oder keine messbare Gewichtszunahme festgestellt. Die Wachstumsraten waren abhängig von der Brutgrösse, dem Schlüpfdatum und der Temperatur, diejenige der Federlänge zusätzlich vom Vorhandensein von Buntbrachen im Revier. Die Auswirkungen der Buntbrachen waren in der ersten Hälfte der Brutsaison und bei nasskaltem Wetter stärker ausgeprägt.

Feldlerchen ernährten ihre Nestlinge zu 75% mit Spinnen (Araneae), Zweiflüglern (Diptera) und Käfern (Coleoptera); Schmetterlinge (Lepidoptera) und Hautflügler (Hymenoptera) machten weitere 15% der Nahrung aus. Mit zunehmendem Alter der Nestlinge stieg der Anteil der Käfer, Zweiflügler und Hautflügler, während derjenige der

Schmetterlinge und Spinnen abnahm. Die Nahrungszusammensetzung von Bruten in Revieren mit Buntbrachen unterschied sich kaum von derjenigen ohne.

Das Kunstnestexperiment zeigte, dass die Erfolgswahrscheinlichkeit stark von der Nestkultur abhängig ist. Sie variierte zwischen $3.3 \pm 13.2\%$ in Mais und $28.8 \pm 3.6\%$ in Winter-Weizen. Die tägliche Überlebensrate in der ersten Woche nach Nestanlage (0.83 ± 0.004) war signifikant kleiner als in der zweiten (0.94 ± 0.004) und der dritten (0.96 ± 0.004). Während die Erfolgswahrscheinlichkeit in einem der beiden Untersuchungsgebiete vom ersten zum zweiten Jahr abnahm, stieg sie im andern Gebiet an. Die Überlebensrate war nicht abhängig von der Distanz des Nestes zum Feldrand. Ausser in Buntbrachen war die Überlebensrate der Kunstnester kleiner als diejenige der Feldlerchennester. Je 14% der prädierten Nester (n = 1493) wurden von grösseren Raubsäugern und Corviden geplündert, 12% von kleineren Nagetieren und bei 60% wurden trotz Fixierung sämtliche Eier entfernt oder vollständig zerstört. Da weder Corviden noch Nagetiere in der Lage waren, die Eier vollständig zu entfernen, kann angenommen werden, dass Raubsäuger wie Fuchs oder Dachs den grössten Teil der Kunstnester zerstörten.

Buntbrachen haben verschiedene positive Auswirkungen auf die Feldlerche und werten die intensiv genutzte Agrarlandschaft ökologisch auf. Wesentlich scheint vor allem ihre hohe Attraktivität zur Nestanlage aber auch zur Nahrungssuche. Damit Feldlerchen von den Buntbrachen profitieren können, müssen diese eine heterogene Vegetation mit schütter bewachsenen Stellen aufweisen und in offenen Agrarlandschaftsräumen in genügender Zahl angelegt werden.

Summary

Until recently, the Skylark *Alauda arvensis* was a common and widespread bird of farmland in Europe. However, in the last few decades their populations have decreased dramatically in all countries of Central and Western Europe. Many factors associated with the intensification of agriculture may have contributed to their decline, including the reparcelling of agricultural land, the loss of natural and semi-natural elements, a reduction in crop rotations, more frequent application of agro-chemicals, and earlier and more frequent mowing of grassland.

Since 1993, Swiss farmers have been encouraged to use some of their arable land for 'ecological compensation', as part of a policy aimed at enhancing biodiversity. Wildflower strips are one of the several officially recognised types of ecological compensation area, and are of particular importance in arable regions. They consist of 3-10 m wide strips which are sown with a mixture of annual, biennial and perennial species from both arable land and grassland; they are not sprayed with herbicides.

The study described here was carried out from 1996 to 1998 in the Klettgau region of northern Switzerland. Most of the work was carried out in a site known as the Widen (5.3 km^2), but an additional site was used for artificial nest experiment (Plomberg, 4.7 km^2). In this intensively used arable area, large numbers of wildflower strips have been established as part of a major scheme sponsored by the Swiss Ornithological Institute and the cantonal authorities.

The selection of nesting sites by skylarks, breeding success, nestling growth and nestling diet were investigated. In addition, predation from nests were studied using artificial nests. A major aim of the work was to determine the effects of wildflower strips on these aspects of skylark ecology.

The relative use as nesting sites of different crop types, and also of different locations within fields, was studied using compositional analyses. The Mayfield method was

applied to estimate survival probabilities of both skylark nests and imitation nests. The diet of nestlings was investigated with the help of neck collars.

The suitability of different crop types as nesting sites changed during the course of the breeding season, according to the state of vegetation development. Overall, wildflower strips, set-aside and grassland had the highest use. In addition, more nests were found in locations close to the field boundary than in the centre of fields. The mean size of clutches was 3.6 ± 0.04 eggs (n = 396), while the mean number of chicks at nest leaving was 3.3 ± 0.07 (n = 202). At both stages, there was in increase in the mean number from April to June followed by a decrease in July. Clutches in territories with wildflower strips (3.7 ± 0.06; n = 175) were significantly larger than in those without (3.5 ± 0.05; n = 221).

Mean breeding success, defined as the probability that at least one nestling left the nest per nesting attempt, was $22.4 \pm 0.5\%$ averaged over the study period, though it varied between years; it was $17.8 \pm 0.5\%$ in the period 1995-1997 and $37.8 \pm 0.9\%$ in 1998. Breeding success ranged from $3.5 \pm 2.9\%$ on tracks to $34.1 \pm 0.7\%$ in cereal fields; at $18.0 \pm 0.2\%$, it was relatively low in wildflower strips. The failure rate of nests near to the field border was higher than in the middle of a field. Predation caused 72% of all nest failures (n = 193) and was more frequent during the nestling stage than during incubation.

Daily growth increments measured in terms of both weight and length of the third primary feather varied widely (weight -2.0-6.5 g/d; feather length 0-8.5 mm/d): The data for weight were especially variable, and 16% of the recorded daily growth increments were either zero or negative (n = 642). Growth in terms of both weight and feather length was significantly influenced by hatching date, brood size and temperature; the results for feather length were also positively affected by the area of wildflower strips in a territory. The growth performance index tended to be higher in territories which included wildflower strips, especially during periods when growth was poor.

Up to 75% of the diet of skylark nestlings consisted of spiders (Araneae), dipterans (Diptera) and beetles (Coleoptera); butterflies (Lepidoptera) and hymenopterans

(Hymenoptera) made up another 15%. The proportions of beetles, dipterans and hymenopterans increased with increasing age of nestlings, while those of butterflies and spiders decreased. There was no convincing evidence that dietary composition is affected by the presence of wildflower strips in a territory.

The success probabilities of artificial nests were affected by crop type, ranging from $3.3 \pm 13.2\%$ to $28.8 \pm 3.6\%$ in winter wheat. The daily survival probability was lower in the first week of exposure (0.83 ± 0.004) than in the second (0.94 ± 0.004) and the third (0.96 ± 0.004). Between the two study years, the failure rates decreased in one study area, but increased in the other. No evidence was found that success probability was affected by the distance of the nest to the field boundary. Except in wildflower strips, the survival probabilities of artificial nests were lower than those of skylark nests. Of the total of 1493 nests which were predated, 14% of the losses could be attributed to corvids and 12% to small rodents. A further 14% were taken by larger mammals, which were probably also responsible for the 60% of eggs which were removed without trace.

Overall, there is convincing evidence that wildflower strips are beneficial for breeding skylarks. In particular, they offer suitable sites for nesting and hunting throughout the breeding season. However, these habitats are only of value to skylarks if the vegetation is sufficiently low and sparse.

General introduction

The skylark *Alauda arvensis*, Linné 1758, was formerly a common and widespread bird of farmland in the Palearctic (Cramp 1988). It is a ground-nesting species which searches for food and nests in open habitats such as grassland and arable crops. The species has therefore been less affected than some other farmland birds by the removal of hedgerows and trees in the course of agricultural intensification. Nevertheless, skylark populations have decreased greatly since the mid 1970s in all countries of Western and Central Europe (Tucker & Heath 1994; Hagemeijer & Blair 1997; Chamberlain & Crick 1999). A number of studies have been carried out which identify some of the factors responsible for the observed population declines. Firstly, breeding success tends to be lower in intensively used areas than in natural or semi-natural habitats (e.g. the dune-landscape studied by Delius (1963, 1965). In particular, many broods are lost in intensively managed grassland as a result of regular mowing (Jenny 1990). Secondly, it has been shown that the density of breeding pairs tends to be lower in areas where the diversity of crops is low and the fields are large (Schläpfer 1988). In such areas, the availability of suitable nesting sites with low and sparse vegetation is restricted. In the intensive agricultural areas there are often fewer breeding attempts per pair and season, even though breeding success may be low (Jenny 1990, Daunicht 1998). There is evidence that the structure of territories is less stable throughout the breeding season and many territories are given up as early as May (Schläpfer 1998; Jenny 1990; Daunicht 1998).

Nowadays, the skylark is the focus of considerable attention by conservationists (Donald & Vickery in press). Because skylarks are still relatively common, they are a valuable indicator species in programmes to promote more wildlife-friendly farming practices.

Since 1993, Swiss farmers have been encouraged by financial incentives to establish ecological compensation areas as part of a policy to enhance biodiversity in the agricultural landscape. Several types of compensation area are supported, including less

intensively managed meadows and pastures, hedgerows, wildflower strips, and others. In arable areas, wildflower strips are particularly important. These are narrow strips of land, mostly 3-10 m wide, which have been sown with a mixture of annual, biennial, and perennial wildflowers of arable and grassland habitats. The application of herbicides and other pesticides is prohibited at all time, while other farming operations are prohibited between August and March.

It is commonly assumed that wildflower strips are beneficial for skylarks because they have a heterogeneous vegetation of high floristic diversity (Ullrich 1999), they are not disturbed by farming operations during the breeding season of farmland birds, and they are rich in both diversity and numbers of arthropods (Bürki & Hausammann 1993; Lys 1994; Lys & Nentwig 1994; Frank & Nentwig 1995; Kramer 1996; Nentwig 1996). Indeed, previous work has shown that wildflower strips are attractive to skylarks searching for food (Weibel 1998).

This study was carried out between 1996 and 1998, in the Klettgau region of northern Switzerland. This is an area of intensive arable agriculture. Since 1991, the Swiss Ornithological Institute at Sempach and the cantonal authorities have promoted a scheme to introduce large numbers of wildflower strips into this area to enhance the habitat for birds, and especially the rapidly declining population of grey partridges *Perdix perdix* (Jenny *et al.* 1997; Jenny & Weibel 1999; Jenny, Weibel & Buner 1999).

One of the aims of this thesis was to investigate whether the presence of wildflower strips has any measurable effect on the growth of skylark nestlings. In addition, the possible effects of wildflower strips on the diet of nestlings were investigated. It has been hypothesised that wildflower may function as nesting 'traps' for skylarks because the dangers of predation are particularly high in these areas. The reason for this suggestion is that many predators are known to use linear structures such as wildflower strips as travel lines; furthermore, wildflower strips support a high mouse and vole density (Buner 1998), which may make them especially profitable for predators such as the fox *Vulpes vulpes*. For these reasons, nest site selection and breeding success were investigated and predation was studies in an artificial nest experiment.

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Chapter 1

Nest site selection and breeding success of skylarks *Alauda arvensis* in an intensively used arable landscape with special reference to wildflower strips

Summary

Changes in agricultural practice in Central Europe have led to severe decreases in skylark populations in the last few decades. Previous work has shown that the decreases may be attributed, in part, to a reduction in the number of breeding attempts per season and also to brood losses associated with particular farming operations.

This study investigated the selection of nest sites and breeding success of skylarks in an intensively used arable landscape in northern Switzerland between 1995 and 1998. Of special interest was the possible influence of wildflower strips sown as ecological compensation areas on the breeding biology of skylarks. Nest site selection was investigated using compositional analysis, and breeding success was estimated by the Mayfield method.

The suitability of the different crop types as nesting habitat changed in the course of the breeding season according to the state of vegetation development. Wildflower strips, set-aside, and grassland had the highest use relative to their area. In addition more nests were found near to the field boundary. Mean clutch size was 3.6 ± 0.04 (n = 396) but varied both within and between seasons. Clutches in territories with wildflower strips were significantly larger than in those without.

Mean breeding success, defined as the probability that at least one nestling left the nest per nesting attempt, was low ($22.4 \pm 0.5\%$). The most important cause for total brood

losses was predation. Breeding success was 17.8 ± 0.5% in 1995 - 1997 but increased to 37.8 ± 0.9% in 1998. Breeding success ranged from 3.5 ± 2.9% on tracks to 34.1 ± 0.7% in cereals; in wildflower strips it was 18.0 ± 0.2%. The failure rate of nests near to the field border is higher than in the middle of a field. The daily survival probabilities were significantly higher during the egg period (0.94 ± 0.006) than during the nestling period (0.92 ± 0.006).

Wildflower strips may functions as 'nesting traps', as they are attractive for nesting skylarks, though the breeding success is low. However, number of breeding attempts and mortality of both juveniles and adults might be more important than breeding success. Therefore wildflower strips may have an overall beneficial effect for skylark populations as they provide suitable nesting habitats throughout the entire breeding season.

Introduction

The introduction of modern intensive farming systems has been associated with a dramatic decline in skylark populations in Central and Western Europe in the last few decades (Tucker & Heath 1994; Hagemeijer & Blair 1997, and references therein). Reproduction is no longer sufficient to sustain populations. Two main factors have been identified as responsible for the decrease in reproduction rate of skylarks.

Firstly, the restructuring of the arable landscape, with large field sizes and a restricted crop rotation, has led to a loss of potential nesting habitats and a reduction in the time when they are suitable for nesting. In Central Europe and Great Britain, skylarks usually make two breeding attempts (Cramp 1988), but are able to replace lost nests within a few days up to six times (Jenny 1990a). As nesting habitat, skylarks prefer relatively sparse vegetation with a cover of 20-50% and a height of 15-25 cm (Jenny 1990a). It has been suggested that the shift from spring towards winter cereals and maize during the

last few decades has led to the loss of suitable nesting habitats. In addition, fields are available for a shorter period, because most crops are more densely sown and grow faster. In an intensively used arable area with large fields in northern Germany skylarks made on average less than two nesting attempts (Daunicht 1998), and in the lower Reuss valley in Switzerland on average 2.3 breeding attempts, even though many broods were lost (Jenny 1990a). Furthermore, territories may be abandoned as early as May on intensively used arable areas (Schläpfer 1988; Wilson *et al.* 1997; Daunicht 1998).

The consequences of the low number of breeding attempts become apparent from estimates of the breeding success needed to sustain a population. Delius (1965) found in a semi-natural dune landscape in southern England an annual productivity per pair of 4.6 young leaving the nest and a first year return rate of 25%, which was sufficient to sustain the population. In contrast, Wilson *et al.* (1997) estimated that if there were only two breeding attempts per pair and season in intensively managed cereals, there must be no mortality between nest leaving and first breeding if the population was to be sustained.

The second factor responsible for low reproduction rates in agricultural landscapes might be an increase of egg and nestling mortalities. In grassland, the increased frequency of mowing is the greatest problem (Schläpfer 1988; Jenny 1990a, b). For example, less than 25% of broods survived in intensively managed meadows which were cut every four weeks; such a success rate is probably insufficient to sustain the population (Jenny 1990a, b). In semi-natural and arable landscapes predation is the most frequent cause of nest failures of skylarks (Delius 1965; Schläpfer 1988; Suárez *et al.* 1993; Daunicht 1998; Donald *et al.* 1998). The risk of predation from skylark nests depends on many factors including the density and activity of predator species, the type of vegetation surrounding the nest, its structure, and the distance between a nest site and the field border (Jenny 1990a; Donald *et al.* 1998). In very dense crops such as winter wheat, skylarks are often forced to build their nests in the tramlines or even on the verges of tracks, where the predation rate is particularly high (Daunicht 1998; Donald & Vickery in press). However, not all studies come to the same conclusions; Chamberlain & Crick

(1999) found no evidence for an increase in either clutch or brood mortality since the 1960s; in fact, they even found a slight decrease.

Food availability is also affected by modern farming practices. Poulsen *et al.* (1998) found smaller clutches in territories including silage grass or winter barley, presumably because less invertebrate food is available in these crops compared to territories in set-asides. Furthermore, Schläpfer (1988), Wilson *et al.* (1997) and Poulsen *et al.* (1998) found a higher nestling mortality due to starvation in territories with intensively used cereal fields. However, these are relatively minor effects of modern farming practices compared to the loss of nesting habitats and brood losses.

The new direction in Swiss agricultural policy aims to promote biological diversity in farmland by introducing various types of "ecological compensation areas". In our study area in northern Switzerland, the Swiss Ornithological Institute at Sempach and the cantonal authorities have promoted the establishment of ecological compensation areas, and in particular wildflower strips, as an attempt to support the rapidly declining population of grey partridge *Perdix perdix* (Jenny *et al.* 1997; Jenny & Weibel 1999; Jenny, Weibel & Buner 1999). In strips of arable land 3-10 m wide annual weeds, biennials, and also perennial forbs are sown. These wildflower strips are not sprayed with herbicides or other pesticides, and other farming operations are only allowed outside the breeding season.

Strip-management has been reported as less beneficial for nesting skylarks than whole field management (Chaney, Evans & Wilcox 1997). It has been suggested that these strips serve as traps for nesting skylarks, as the nesting habitat is good but the predation risk is high. We were particularly interested in the possible influence of wildflower strips on nest site selection, clutch size, mortality and breeding success, and aimed to answer the following questions: (i) What is the relative importance of different crop types as nesting habitats? (ii) Do skylarks select particular areas within a field for their nests? (iii) How do clutch size and the number of young leaving the nest vary seasonally and between years? (iv) What are the temporal patterns of mortality at the egg and nestling stages? (v) Is breeding success sufficient to sustain the population?

Study site and methods

Study site

The study was carried out in an area of the Swiss Klettgau (15 km west of Schaffhausen; 47°42' N, 8°30' E; 400-470 m a.s.l.). The study site, known as Widen, has an area of 530 ha and its boundaries are defined by the connecting roads between the villages of Neunkirch, Gächlingen, Siblingen, and Löhningen. In the central parts of this area, the soils are stony and calcareous shallow brown earth of rather low fertility. The soils in the eastern and southern parts have developed on alluvial loam and are deeper and of higher fertility.

Most of the area is used for agriculture. The remaining semi-natural elements are a few trees, hedges and groups of bushes growing alongside three straightened streams and a small nature conservation area of 1.8 ha. The land was reparcelled about 1920, and most of the fields are small (mean 0.81 ha). The arable area covers 453 ha; in 1998, the crops consisted of cereals (47% of the arable area), root- and oil crops (29%), maize (9%), ley grassland (7%) and vines (1%). Sites for ecological compensation (i.e. areas managed for biological diversity under a subsidy scheme) occupied 19 ha (4% in 1998), of which 6.3 ha were wildflower strips. In addition, 3% of the arable area was set-aside (Grünbrachen), a value which is relatively high for the Swiss plateau, and reflects the limited fertility of the soils.

The climate is relatively warm and dry (mean annual temperature 8.5 °C; mean annual precipitation 915 mm). However, the weather conditions during the four breeding periods 1995-1998 varied considerably. In 1995 and 1997 there was 40% and 12% more rain respectively than the long-term average during the breeding seasons of skylarks (Fig. 1). The mean monthly temperatures were also generally higher. All meteorological data are from the climate station Hallau, 3 km west of the study area (Schweizerische Meteorologische Anstalt 1996).
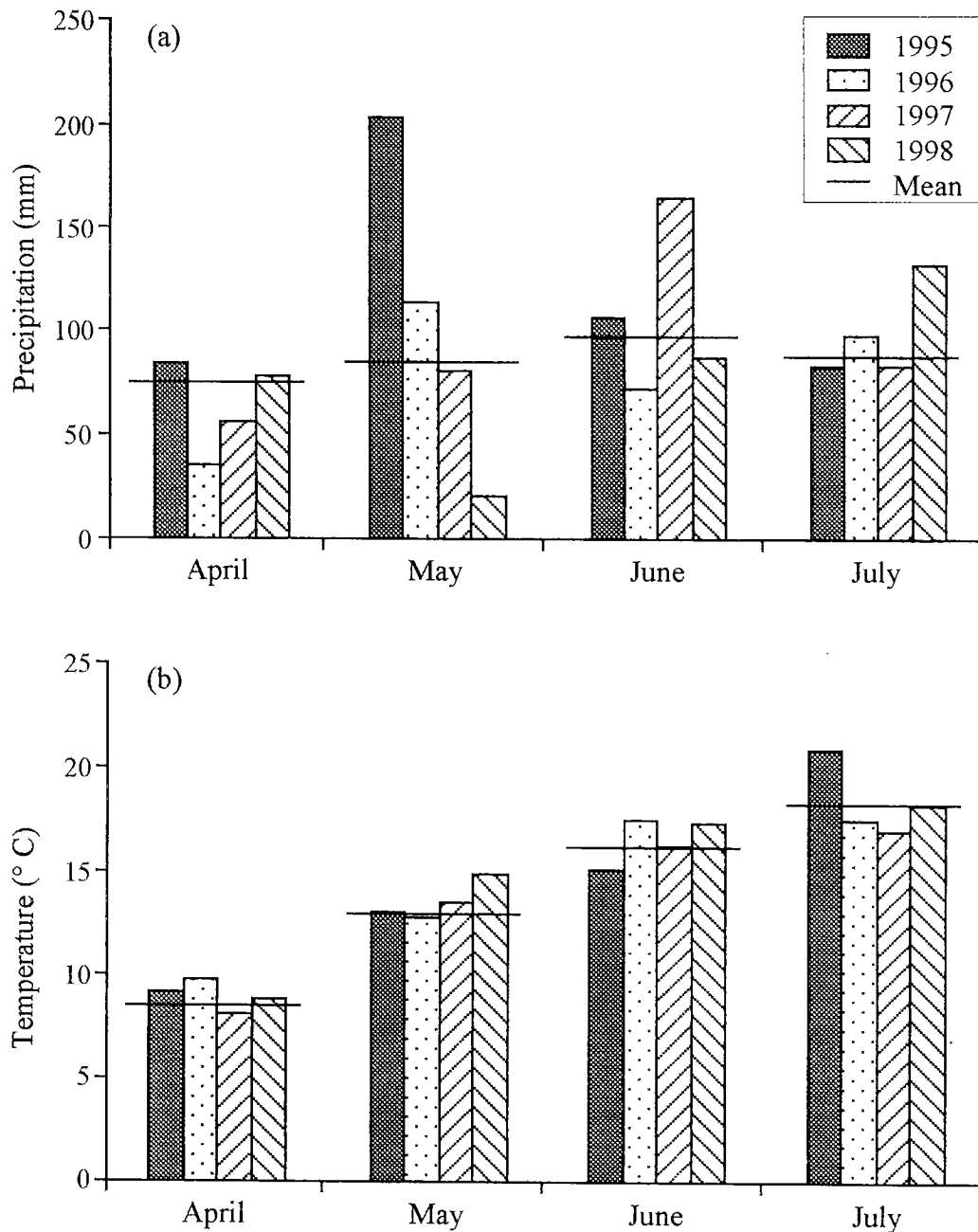
Fig. 1: Sum of monthly precipitation (a) and monthly mean temperature (b) during the breeding seasons of skylarks in 1995-1998; long-term average is indicated with a line.

The mean densities of potential predators in the study region in 1995-1998 were estimated to be: red foxes *Vulpes vulpes* 2.5 km^{-2}, house cats *Felis silvestris f. catus* 1.3 km^{-2}, badgers *Meles meles* and marten *Martes foina* each 0.1 km^{-2}. Until 1998 no special game keeping was carried out. In 1999, the density of foxes was reduced to ca. 1.1 foxes/km^{-2} by hunting in winter until the beginning of the close period (1 March).

Breeding biology

Breeding biology of skylarks was studied in the seasons 1995-1998. During the period when skylarks are territorial, songflights and intraspecific interactions were mapped on a daily basis. These observations were recorded on a map (1:7500) showing the current land use including crop types, and were afterwards integrated onto a map of territories and digitised using a geographical information system (ArcInfo/GIS). The size of each territory, and the area and number of different crop types within the territory were determined using the GIS.

Nest sites were located approximately from observations of females carrying nest material or returning several times to the same spot within a field, and from the feeding and alarm behaviour of birds. To make these observations, a tent was used as a hide. Most nests could then be found by flushing the incubating females or the feeding birds from the nest. The position of each nest was marked on the map, and notes were made of the crop type, its mean height and cover within 1 m of the nest. The distance from the nest to the field border was measured both with the furrow (referred to here as the 'distance to track' as this type of boundary is defined in all cases by tracks), and perpendicular to it ('distance to field edge' as in most cases the boundary is defined by another crop type).

In each breeding season, all territories in which nests were found were pooled to get the total area of the different crop types. The number of nests per crop type was then compared with the total areas, using compositional analysis (Aitchison 1986; Aebischer, Robertson & Kenward 1993). Kendall's coefficient of concordance (Sokal & Rohlf 1995) was used to test the rankings of the log-ratios for consistency between the years. To test whether nests were randomly distributed with respect to features such as distance to the field edge and the track, the fields were subdivided into 10 m distance classes; the relative use was calculated applying compositional analysis (Aitchison 1986; Aebischer, Robertson & Kenward 1993).

In those nests which were only found after hatching the clutch size was assumed to be the same as the number of young. Nests containing only one egg or nestling were excluded from the analyses. Clutch size and brood size when leaving the nest were tested using nonparametric methods (e.g. Kruskal-Wallis test; Sokal & Rohlf 1995), both for effects of year and season and for differences in habitat quality, expressed as the availability of wildflower strips within the territory.

Breeding success

Estimates of breeding success were based on the Mayfield method (Mayfield 1961, 1975; Johnson 1979; Hensler & Nichols 1981; Hensler 1985; Aebischer in press). This method provides information on the mean daily survival probabilities (DSP) of the eggs and nestlings. In our study, a nest was defined as successful when at least one nestling left the nest. Therefore breeding success represents the probability that at least one nestling survives from egg laying to nest leaving per nesting attempt and can be calculated by the following formula:

Breeding success $= DSP_{egg}^{IT} * DSP_{nestling}^{NT}$.

Where DSP_{egg} is the daily survival probability during the egg period (laying and incubation together);

$DSP_{nestling}$ is the daily survival probability during the nestling period;

IT is the period between laying of the first egg and hatching (estimated as clutch size + incubation time - 1) on the assumptions that one egg is laid each day, and incubation lasts 11 days (Cramp 1988);

NT is the period between hatching and nest leaving (taken as 8 days).

All nests were revisited at least every third day, so that important data such as date of hatching, nest loss and nest leaving could be determined reliably.

Survival probabilities were compared by applying two-tailed standard tests to make pairwise comparisons (Hensler 1985), and otherwise χ^2-tests (Sauer & Williams 1989).

Multi-way comparisons were applied to investigate differences in the DSP's using the procedure of Aebischer (in press).

The annual productivity per pair and season was calculated as: number of breeding attempts per pair and season * brood size at nest leaving * breeding success.

Results

Nest distribution

The suitability of the different crop types as nesting habitat changed during the breeding season according to the state of development of the vegetation. Grassland and set-asides were used as nesting habitat during the entire breeding period. However, there was some variation in the use of other crop types depending on the structure of the vegetation. The earliest nests were mainly in winter cereals. Nests in wildflower strips were most common in May and June and root crops, maize and sunflowers were used mainly in June and July (Fig. 2).

The compositional analysis of the data for the nests per crop type indicated that their use was not random (Wilk's $\Lambda = 0.02$; $d.f. = 4$; $P < 0.005$). Overall, wildflower strips, set-asides, and ley grassland had the highest relative use while winter rape and winter rye were used least (Fig. 3). There was a significant consistency in the rankings of relative use of the various crop types throughout the years (Kendall's $W = 0.48$; $d.f. = 13$; $P < 0.05$). But, there were no significant differences between the crop types in the first nine rankings (until maize/sunflowers).

Compositional analysis of nest sites in relation to distance from the field edge revealed significant non-random location of nests within fields (Wilk's $\Lambda = 0.03$; $d.f. = 4$; $P < 0.01$). The two distance classes nearest to the field edge were used more frequently than those 20-40 m from the field edge (Fig. 4a). The relationship of nest position with respect to distance to the track was less distinct (Wilk's $\Lambda = 0.09$; $d.f. = 4$; $P < 0.05$). The four distance classes nearest to the track were used more commonly (Fig. 4b).
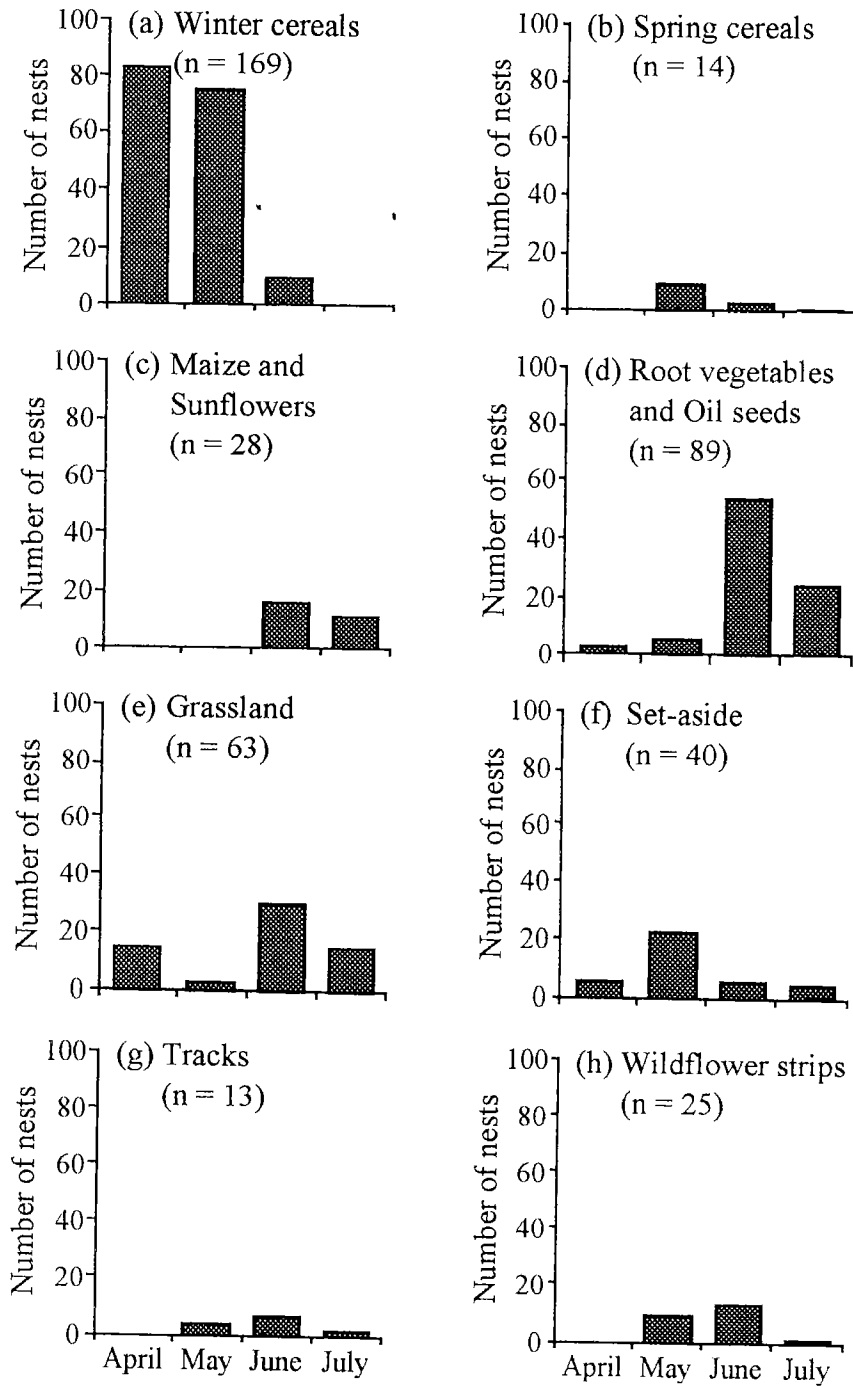
Fig. 2: Seasonal distribution of skylark nests in the various crop types.
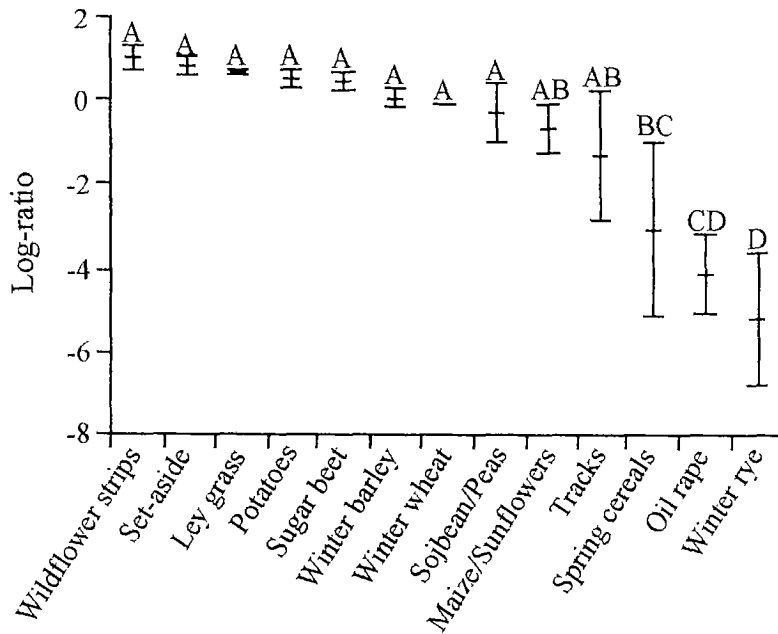
Fig. 3: Log-ratios (mean ± SE) of the crop types arranged according to the ranking of the relative habitat use for nesting. From high relative use (wildflower strips) to low relative use (winter rye); same letters indicate statistically not separable values (t-test; $P < 0.05$).

Clutch size

Clutch size averaged over the entire study period was 3.6 ± 0.04 eggs (n = 396). A log-linear model showed that the variation in clutch size could be partly explained in terms of time of year ($\chi^2 = 19.5$; $d.f. = 3$; $P < 0.0005$), availability of wildflower strips within a territory ($\chi^2 = 9.0$; $d.f. = 1$; $P < 0.005$), and between season differences ($\chi^2 = 9.4$; $d.f. = 3$; $P < 0.05$).There was no significant not interaction.

Clutch sizes increased from April to June, and decreased in July (Table 1); between years, it ranged from 3.4 ± 0.09 in 1995 to 3.7 ± 0.08 in both 1996 and 1998. Mean clutch sizes in territories including wildflower strips were significantly larger than in

those without. This tendency was evident for all years and for all months, and the difference in the combined data is highly significant (with strips : 3.7 ± 0.06; $n = 175$; without strips: 3.5 ± 0.05; $n = 221$; $H = 6.8$; $d.f. = 1$; $P < 0.01$; Kruskall-Wallis test).
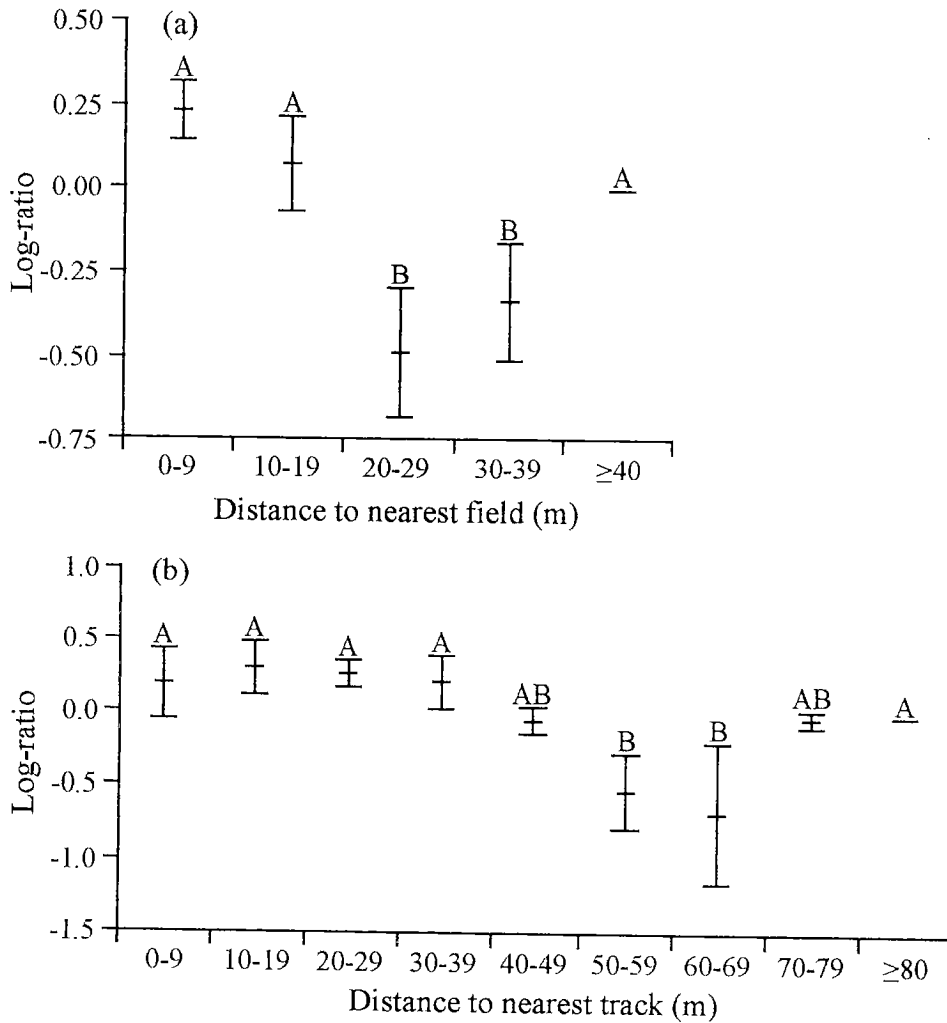
Fig. 4: Relative use of different distance classes from the field edge (a) and the track (b) as nesting habitat. Log-ratio (mean $\pm$ SE); same letters indicate statistically not separable values (t-test; $P < 0.05$).

In total, nestlings hatched in 309 of 396 nests; in 82% of these all eggs hatched, in 16% one egg was either infertile or the embryo died during incubation, and in 2% more than one egg failed. Thus from a total of 1425 eggs 4.7% failed. There was no significant variation in the proportion of nests with unhatched eggs, either between years or

according to laying date; there was, however, a slight decrease in the proportion of failures from early to late broods. The proportion of nests with unhatched eggs increased significantly with increasing clutch size ($\chi^2 = 11.4$; $d.f. = 3$; $P < 0.01$); the proportion increased with increasing clutch size. Interestingly, a higher proportion of nests in territories with wildflower strips had unhatched eggs compared to those without wildflower strips ($H = 4.9$; $d.f. = 3$; $P < 0.05$; Kruskall-Wallis test), a trend which was consistent throughout all years. There was no relation between nest location within a field and the proportion of unhatched eggs, either in terms of distance to the track or to the field edge.

Overall, brood size at nest leaving was 3.3 ± 0.07. There was significant monthly variation in the brood size at nest leaving ($\chi^2 = 15.1$; $d.f. = 3$; $P < 0.005$), the trend being the same for clutch size (Table 1). In all years, brood size at nest leaving was slightly higher in territories with wildflower strips compared to those without, but none of the differences reached significance. Overall, mean brood size in territories with wildflower strips was 3.4 ± 0.15 ($n = 76$) compared to 3.2 ± 0.13 ($n = 126$) in those without wildflower strips. This difference is similar to that found in clutch size.

Table 1: Seasonal variation in clutch and brood sizes of skylarks in the breeding seasons 1995-1998 (mean $\pm$ SE). The number of nests is given in parentheses.

	April	May	June	July	Mean
Clutch size	3.4 ± 0.08	3.6 ± 0.07	3.9 ± 0.07	3.4 ± 0.11	3.6 ± 0.04
	(100)	(126)	(119)	(51)	(396)
Brood size	3.0 ± 0.11	3.2 ± 0.11	3.8 ± 0.12	3.4 ± 0.19	3.3 ± 0.07
	(59)	(63)	(58)	(22)	(202)

Breeding success

The skylark nests in the study area suffered from high predation, which caused 71% of all nest losses, while nest abandonment accounted for 10%, and farming operations

(mainly mowing) 13%. There were two cases of death from other causes (trampling, death of the adult female; Table 2). The proportion of failed nests which were predated did not differ significantly between years or according to laying date, though there were differences between crop types ($\chi^2 = 18.6$; $d.f. = 5$; $P < 0.002$). Starvation of broods occurred only in 1995 and 1996; in both years May was wet and cold, causing 5% of mortality (combined data).

Table 2: Synopsis of the proportions of nests at which nestlings hatched and left the nest, and the causes of nest failures in 1995 - 1998. The numbers are percentages of the number of nests found.

Year	Number of nests			Nest losses during egg period				Nest losses during nestling period			
	found	hatched	success-ful	pre-dation	farming opera-tions	abandon-ment	others	pre-dation	farming opera-tions	starva-tion	others
1995	70	67.1	44.3	21.4	1.4	10.0	0.0	12.9	2.9	7.1	0.0
1996	102	79.5	39.2	13.7	2.0	3.9	1.0	32.4	2.0	4.9	1.0
1997	113	76.1	48.7	11.5	7.1	5.3	0.0	23.9	3.5	0.0	0.0
1998	111	85.6	69.4	10.8	2.7	0.9	0.0	14.4	1.9	0.0	0.0
Total	396	78.0	51.3	13.6	3.5	4.5	0.3	21.5	2.5	2.5	0.3

Partial brood mortality, mainly due to starvation, occurred in 10% of all broods. The proportion of broods with partial mortality was independent of seasonal effects and the presence of wildflower strips within the territory, but not independent of annual effects ($G = 8.94$; $d.f. = 3$; $P < 0.05$). The percentage of broods with partial mortality was 9% and varied between 7% in 1998 and 16% in 1995.

Overall, losses were higher during the nestling phase than during laying and incubation (Fig. 5). The daily survival probabilities (DSP's) during the egg period were generally higher than during the nestling period, and these differences were significant in 1996 ($z = 2.68$; $P < 0.01$), and in all years taken together ($z = 2.50$; $P < 0.02$).
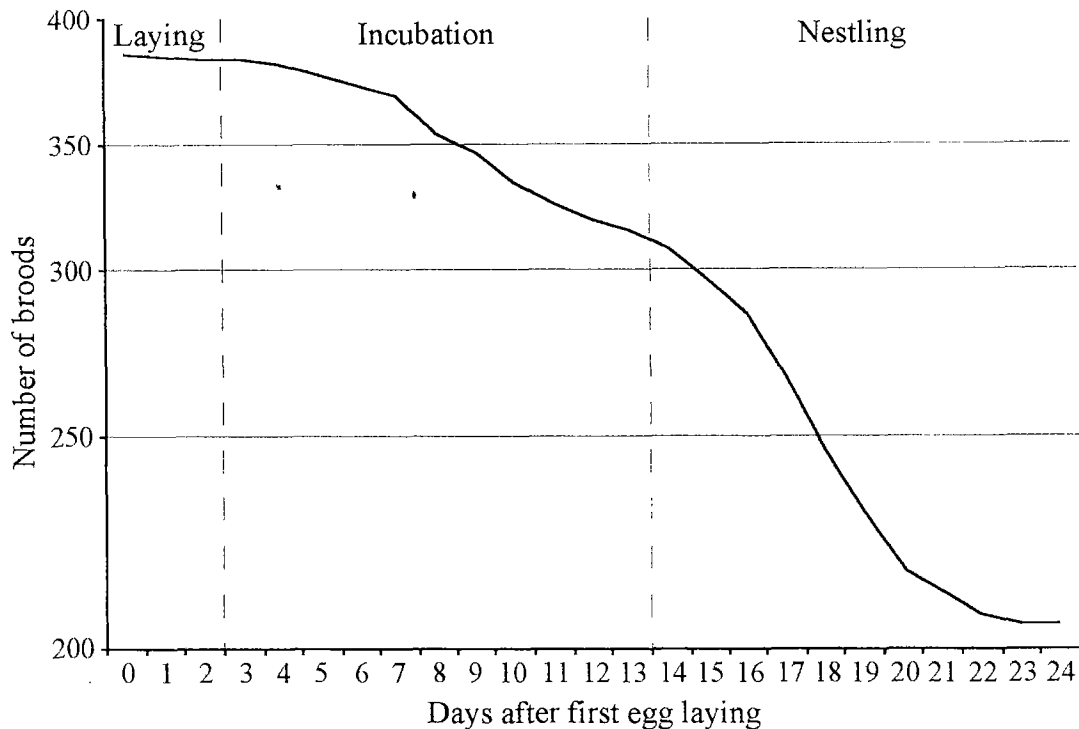
Fig. 5: Number of surviving broods with brood age. Day '0' is the laying day of the first egg; young left the nest between day 21-24.

A two-way analysis of the DSP's during the egg period revealed significant variation between years ($D = 18.5$; $d.f. = 6$; $P < 0.005$), but not between crop types ($D = 3.0$; $d.f. = 3$; $P > 0.1$); there was no significant interaction between crop types and years ($D = 13.6$; $d.f. = 17$; $P > 0.05$), indicating that the annual trends did not vary between crop types.

The DSP's during the nestling phase showed significant variation between the crop types ($D = 13.4$; $d.f. = 3$; $P < 0.05$), but not between breeding seasons ($D = 4.5$; $d.f. = 6$; $P > 0.05$). As for the egg phase, the interaction between crop types and years was not significant ($D = 23.0$; $d.f. = 16$; $P > 0.01$).

The mean annual breeding success for the three seasons 1995-1997 was $17.8 \pm 0.5\%$, but in 1998 it was much higher at $37.8 \pm 0.9\%$ (Fig. 6a); the null hypothesis of homogeneity is clearly rejected ($\chi^2 = 37.2$; $d.f. = 3$; $P < 0.0001$). Breeding success was not equal between crop types ($\chi^2 = 49.3$; $d.f. = 5$; $P < 0.0001$), being highest in cereals and root crops and lowest in maize and on the verges of tracks (Fig 6b).
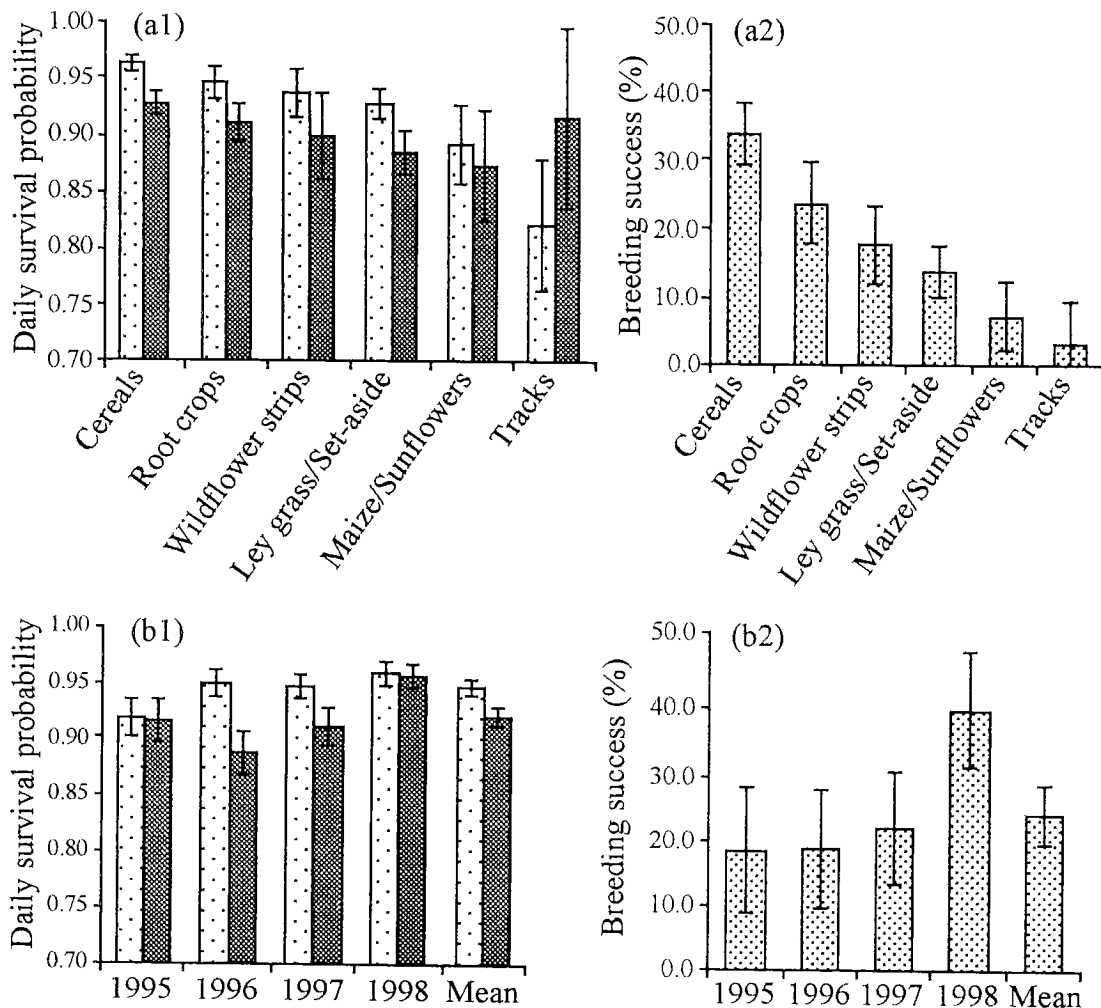
Fig. 6: Daily survival probabilities (a1, b1) for egg period (light shaded) and nestling period (dark shaded) and breeding success (a2, b2; mean ± SD) for the different crop types (a1, a2) and for the four study periods 1995-1998 (b1, b2).

In addition, we found interesting differences between the crop types and in the temporal patterns of breeding success within the crop categories. In cereals, the breeding success was similar in winter wheat and winter barley (35.4 ± 1.0% and 34.5 ± 1.3%), and significantly higher than in spring cereals (25.8 ± 3.2%; $z > 2.5$; $P < 0.01$). The breeding success decreased from 50.0 ± 1.1% in April to 27.7 ± 1.0% in May and to 9.7 ± 3.6% in June. The breeding success in sugar beet (29.5 ±1.5%) was significantly higher than in both potatoes (24.0 ± 2.2%; $z = 2.07$; $P = 0.02$) and other root crops (19.4 ± 2.2%; $z = 3.79$; $P < 0.0001$). Nests in root crops had a similar breeding success in June and July (27.2 ± 1.5% and 26.7 ± 1.2%). In wildflower strips it varied seasonally, being highest in May (16.8-18.8%). Breeding success was not significantly higher in intensively used grassland (15.8 ± 1.6%) than in set-asides (13.1 ± 1.1%). In July, the breeding success for nests in grassland was 20.0 ± 2.0%, which was higher than that in April (14.7 ± 2.8%) and significantly higher than that in June (14.3 ± 1.4%) and in May (9.4 ± 1.7%). Breeding success in maize decreased slightly from 8.7 ± 2.3% in June to 6.9 ± 2.2% in July.

Breeding success was significantly lower in nests wihin 10 m of a field edge compared to nests elsewhere in a field ($z > 4.11$; $P < 0.001$); it was highest 20-29 m from the field boundary, and decreased for nests ≥30 m from it to the same level as nest 10-19 m (Fig. 7). However, no evidence was found for a distance effect for the DSP's either for the egg period ($D = 3.8$; $d.f. = 3$; $P > 0.1$) or for the nestling period ($D = 3.8$; $d.f. = 3$; $P > 0.1$).

The mean number of breeding attempts per pair and season could not be precisely ascertained. However, we found pairs, which initiated one to four nesting attempts and up to three successful broods and season. If we assume a mean of two breeding attempts, the mean annual productivity per pair was 1.5 ± 0.4 birds leaving the nest. On this basis, annual productivity ranged from 0.2 ± 0.5 in nests on tracks to 2.1 ± 0.6 in cereals. The equivalent figures assuming three breeding attempts would be an average of 2.2 ± 0.4 and a range from 3.2 ± 0.6 in cereals to 0.3 ± 0.5 on tracks.
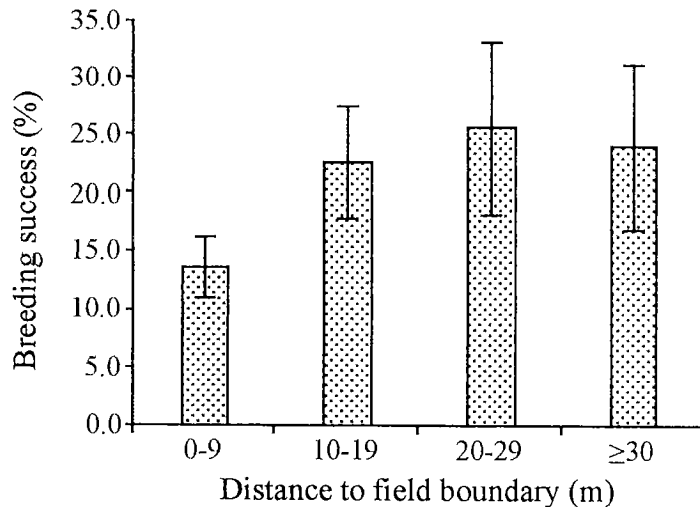
Fig. 7: Breeding success (mean ± SD) in different distances to the field boundary.

Discussion

Nest distribution

Crop types such as wildflower strips, set-aside and grassland, which offer suitable nesting conditions throughout the breeding season, had the highest values of relative use. Winter cereals were the crops most commonly used for first breeding attempts, whereas root crops were the commonest nest habitats for breeding attempts in June and July. Skylarks are able to use nearly all crop types for nesting, but most of them only for a limited period. For this reason, they need a small-scale mosaic of different crops to have suitable nesting habitats throughout the breeding season. In our study area this was usually the case, the territories containing an average of four different crop types (Weibel *et al.* in press a). In areas with larger fields and a more restricted crop rotation, wildflower strips may be of greater significance because they increase the crop diversity and offer nesting sites throughout the breeding season.

Schläpfer (1988) and Chamberlain *et al.* (1999) suggested that the decrease in spring cereal cultivation has led to a loss of valuable nesting crop for second broods and therefore to fewer breeding attempts. We could not confirm this suggestion. We suggest that in our study area, spring sown cereals were less attractive to nesting skylarks because winter cereals remained usable for nesting until mid-May, as the soils area were of only moderate fertility. In addition, spring sown cereals consisted mainly of oat, which has a dense sward.

The apparently higher numbers of nests within a distance of 40 m from a track could be the result of observer bias, since most observations were made from such tracks. However, there is no reason to suspect any such bias in the results which show a distinctly higher relative nesting density within 20 m of other field borders. Both Schläpfer (1988) and Pätzold (1983) also observed more nests near field borders than in the middle of fields, and suggested that it is easier for a skylark to locate visually a nest which is close to a field border.

Chaney, Evans & Wilcox (1997) concluded that narrow strips of non-rotational set-asides around the field boundaries were less beneficial for nesting skylarks than whole field set-aside, but in their study the strips were often close to hedgerows from which skylarks usually keep a certain distance. Our study shows that wildflower strips can be valuable nesting habitats. However, it is essential that the vegetation is heterogeneous and contains gaps in which the birds can move. In this respect, our findings are consistent with those of Edwards *et al.* (in prep.), who found that field margins had a high density of skylark nests especially when the vegetation is sparse.

Clutch size

The mean clutch size, the mean brood size at nest leaving and also the percentage of unhatched eggs in this study were within the range reported in other work (Delius 1965; Frank 1984; Schläpfer 1988; Jenny 1990a; Wilson *et al.* 1997; Daunicht 1998; Poulsen *et al.* 1998; Chamberlain & Crick 1999). Most of these authors also found a seasonal

pattern of clutch and brood size. The variation in clutch size is probably influenced by food availability (Schläpfer 1988). Support for this hypothesis comes from Poulsen *et al.* (1998) who found significantly greater clutch sizes in set-aside than in grass or spring barley. Similarly, in our study, clutches were larger in territories with wildflower strips, and these are known to support more invertebrates than adjacent fields (Bürki & Hausammann 1993; Lys 1994; Lys & Nentwig 1994; Frank & Nentwig 1995; Kramer 1996; Nentwig 1996). However, other factors may also influence clutch size. For example, Chamberlain & Crick (1999) found an increase in both clutch and brood size since the 1950s which could be a result of either reduced use of pesticides toxic to birds or density-dependent effects associated with the decline in skylark populations.

The cause of the higher partial clutch mortality in territories including wildflower strips compared to those without is unknown. Partial reduction of some broods during the nestling stage is probably caused by starvation during bad weather conditions. Schläpfer (1988) concluded that the higher partial brood losses in an agricultural landscape in comparison to a semi-natural dune landscape was a result of starvation of nestlings during periods of food shortage. Similarly, more starved nestlings were found in intensive cereals than in set-asides and organically managed fields (Wilson *et al.* 1997; Poulsen *et al.* 1998). In 1996, evidence was found for a higher proportion of partial brood mortality in territories without wildflower strips (Chapter 2), but this could not be confirmed for the entire study period.

Breeding success

The survival probability of skylark nests was higher during the egg period than during the nestling period. Breeding success varied in a wide range between crop types and year. In addition, it was lower for nests near to the field boundary.

In many of the published skylark studies breeding success has been calculated as the ratio of the number of nest-leaving birds to the number of laid eggs. However, unless all nests are found at the time of laying, breeding success is overestimated by this method

because it does not take account of nest failures and mortality before the nests are found (Hensler & Nichols 1981). This fact facilitates a comparison between the different studies. In our study, many of the nests were not found until the nestling stage, and so the Mayfield method was the only appropriate approach. As the daily survival during the egg period was generally higher than during the nestling period, to disregard these differences would cause an underestimate of breeding success.

Nest success probabilities of skylarks, calculated with the Mayfield method, but with no distinction between egg and nestling periods, have been estimated as 25% (Yanes & Suárez 1997), 23% in intensively managed fields, and 34% in organically managed fields (Wilson et al. 1997). Chamberlain & Crick (1999) calculated a breeding success of 36% for the period 1962-1975, and 40% for 1976-1994. Except in 1998, the breeding success in the Klettgau skylark population was generally lower than in these studies, mainly caused by the predation risk. In Switzerland, the density of predator species, especially foxes, has increased since 1985 (Breitenmoser et al. 1995). However, the proportion of predated nests is only slightly higher in our study than in that of Schläpfer (1988) in 1984-86. Our results confirm those of Donald et al. (1998) that breeding success increases with distance of a nest from a field edge and is also affected by the structure of vegetation. Consistent with our study, Chamberlain & Crick (1999) found a higher mortality during the nestling period, probably because more frequent nest visits by feeding adults and begging by the young attracted predators. The predators were probably mainly mammals, since these tend to move along the field boundaries and have well-developed auditory and olfactory senses. It was also found that larger mammalian predators such as foxes and badgers were the most common predators of artificial nests in the study area (Chapter 4).

The results suggest that, wildflower strips are traps for nesting skylarks, as they attract them to nest there, although the probability of success is low. Predation pressure is high close to the field boundaries and broods in wildflower strips are therefore especially at risk. In other crop types preferred for nesting, e.g. set-asides and cultivated grassland, breeding success may also be low because many small rodents occur in these crop types,

and they are therefore also attractive for predators (Buner 1998). However, there is no evidence that predation of skylark nests by mice is common (but see Bures 1997).

The exceptionally high breeding success in 1998 was surprising. Two circumstances coincided in this breeding season, namely a dry period between end-April and end-May, and the reduced red fox density. Moreover, winter cereal grow very badly during the dry period in May and therefore they were suitable for nesting skylarks for a longer period. As the proportion of predated nests was only slightly lower in 1998 than in the previous years, we suggest that predator-removal had only a small influence on breeding success, though we can not quantify the impact of the lower fox density. Although in several studies a positive effect of predator-removal on breeding success was found, the effects on breeding and post-breeding numbers are not clearly proved (Newton 1998).

Though the values of breeding success reported here are lower than in most other studies, the number of breeding pairs slightly increased from 1996 to 1999 (Weibel *et al.* in press a; pers. observation). Assuming a 30% adult mortality (Delius 1965) and 65-80% mortality between nest leaving and first breeding (Wilson *et al.* 1997), we can conclude that, at least 4.6 breeding attempts per season and pair are necessary to sustain the population. Such a value which hardly be achieved by the local skylark population, even though there is small scale mosaic of crops which allows for multiple breeding (Weibel *et al.* in press a, b). As the predator density is similar in the wider region, we suggest that the slightly increasing number of breeding skylarks in the study area is not caused by immigration. Furthermore, we conclude that breeding success is not the crucial point causing the populations declines. The number of breeding attempts, first year and adult mortality may be more important, a conclusion similar to that of Chamberlain & Crick (1999). Our lack of reliable data on the exact number of breeding attempts in the study area, the skylark mortality between nest leaving and first breeding, and the immigration rate mean that we can not calculate the breeding success which is necessary to sustain the population.

Practical implications

Part of the motivation for this study was to understand the significance of wildflower strips for the breeding success of skylarks. The results have shown that wildflower strips offer suitable nesting habitats throughout most of the breeding season, providing that they are not sown too densely. However, with a breeding success less than 20% wildflower strips are nesting traps. On the one hand because they are narrow strips with a high predator activity along the boundary; and on the other, the high density of small rodents make them attractive for predators. The data show that predation risk is also high in whole field set-asides. Nevertheless, wildflower strips and whole field set-asides do allow multiple breeding, which may be more important.

Furthermore, wildflower strips are a good habitat for skylarks searching for food, thanks to the high invertebrate supply during the breeding season and a high seed abundance during the autumn and winter, from which nestlings and adults profit (Weibel 1998; Chapter 2). In addition, there is presumably a higher mortality amongst juveniles with poor body condition, and more generally due to a loss of stubble fields as suitable feeding grounds in winter (Chamberlain & Crick 1999). Under these circumstances, wildflower strips are likely to be particularly valuable for skylark populations in arable landscape.

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Chapter 2

Effects of habitat quality and weather conditions on growth rates of skylark *Alauda arvensis* nestlings

Summary

Modern intensive farming regimes in Central Europe have led to a severe decrease in skylark populations. In Switzerland, there have been attempts to enhance the biodiversity of intensively used agricultural land by introducing various kinds of 'ecological compensation sites', including wildflower strips.

The study investigates whether the presence of wildflower strips affects habitat quality for skylarks, and in particular whether it enhances the growth rates of nestlings. Nestling weight and the length of the third primary feather were recorded for nestlings from a total of 64 broods during the 1996 breeding season.

The daily growth increments as a function of body size were fitted to the data using various forms of the logistic growth curve. The mean value per nest of the residuals from the fitted growth curve was used as an index of the growth performance of a brood. Growth rates based on both weight and feather length varied widely and were significantly influenced by hatching date, brood size and temperature; growth rates based on feather length were also affected positively by the area of wildflower strips in a territory. Especially during periods when growth was poor, the value of the growth performance index tended to be higher in territories including wildflower strips. Furthermore, in territories which contained wildflower strips there was less nestling mortality due to starvation, and weight was more strongly related to feather length.

We conclude that wildflower strips do have a beneficial effect on nestling growth even though the average amount of wildflower strips per territory is only 6%.

Introduction

This study concerns the growth of skylark nestlings in the Klettgau, an intensively farmed arable area of northern Switzerland. Many farmland birds, including the skylark, grey partridge *Perdix perdix*, quail *Coturnix coturnix* and corn bunting *Miliaria calandra*, have shown alarming population declines in Central Europe during the last two decades (Tucker & Heath 1994; Hagemeijer & Blair 1997, and references therein). These declines are almost certainly linked to the introduction of modern intensive farming systems. The associated changes in farming practice - the application of pesticides and fertilisers, increasing field sizes, the reduced use of crop rotations, and the use of larger and more efficient agricultural machines – have led to a loss in biological diversity in farmland regions. Recently, policies have been introduced in many European countries, including Switzerland, aimed at enhancing the diversity of wildlife in areas of intensive agriculture. However, for such policies to be successful it is essential to have a good understanding of the ecological requirements of the species to be promoted.

Many factors contribute to the successful production of a brood of birds. The body condition of nestlings is known to be affected by their genetic constitution, the number of siblings, parental effort, food availability, parasites and weather factors (Gebhardt-Henrich & van Noordwijk 1991; Rodenhouse & Holmes 1992; Siikamäki 1996; Tripet & Richner 1997). Moreover, studies of the great tit *Parus major* (Perrins 1965; Schifferli 1973; Tinbergen & Boerlijst 1990; Gebhardt-Henrich & van Noordwijk 1991) and of several other species (see Magrath 1991) have shown that post-fledgling survival correlates with fledgling weight. The predictability of nestling food at the time of egg laying, and the stability of the food supply during the nestling period, have therefore influenced the evolution of clutch size and growth strategy (O'Connor 1978). For those bird species with a predictable and stable food supply, clutch size can be optimised (e.g. blue tits *Parus caeruleus*). Some species cope with a rather unpredictable and irregular food supply by storing surplus energy, sometimes in form of fat (e.g. house martins *Delichon urbica*); in contrast, when the food supply at the time of egg laying is

unpredictable, but stable during the nestling period, an adjustment of brood size occurs through the loss of the smallest nestlings which die during periods of food shortage (e.g. house sparrows *Passer domesticus*). Amongst ground-nesting birds the risk of predation is particularly high at the nestling stage (Ricklefs 1969a) and there has probably been strong selection to reduce the nestling period through accelerated nestling growth (Lack 1968; Ricklefs 1969b).

Skylarks feed their nestlings almost exclusively on invertebrates. In intensively used grasslands in the Swiss plateau, various Diptera species composed more than half of their diet, while Orthoptera, Lepidoptera, Araneae, and Coleoptera were of relatively minor importance (Jenny 1990). In contrast, in a study on arable land in the Klettgau area of northern Switzerland, the diet was more balanced amongst these invertebrate groups (Weibel 1995, Chapter 3). A similar dietary spectrum was reported from a mixed agricultural landscape in southern England (Poulsen 1993; Poulsen, Sotherton & Aebischer 1998).

Increased use of pesticides has reduced the availability of invertebrate food for skylarks, while the denser and faster growing crops have made it more difficult for them to search for food. The reduced diversity and abundance of weeds caused by herbicide applications has also affected the abundance of some herbivorous insects such as butterflies and sawflies, which are important as nestling food (Sotherton 1991). Furthermore, it has been shown that the tall, dense structure of many crops, e.g. spring barley, may prevent birds from searching for food except in the tramlines and in unsown plots (Odderskær *et al.* 1997). Low and sparse vegetation and vegetation gaps are also used as food searching places by other ground-feeding birds (Bowden 1990; Stiebel 1997; Vogel 1998). Potts (1986) showed that the lower availability of food is an important mortality factor for grey partridge chicks.

Skylarks and other ground-nesting birds face a high risk of predation during the nestling stage; it is therefore important for them to achieve an adequate body size quickly and to leave the nest as soon as possible. Good growth performance of skylark nestlings is almost certainly linked to high invertebrate food abundance (Evans, Wilson & Browne 1995). Previous work has shown that the adults prefer to search for food in areas sown with wildflower strips, especially when these have a heterogeneous vegetation structure

and have not been sown too densely (Weibel 1998). It is known that these areas support much greater numbers of invertebrates than the adjacent crops (Bürki & Hausammann 1993; Lys 1994; Lys & Nentwig 1994; Frank & Nentwig 1995; Kramer 1996; Nentwig 1996).

The main objective of the work reported here is to investigate how the presence of wildflower strips affects the growth of skylark nestlings. The specific questions addressed by this study are: (i) Do skylark nestlings grow faster in a territory which contains wildflower strips? (ii) What other factors affect growth? (iii) Is there less nestling mortality caused by starvation in territories which contain wildflower strips?

Material and methods

Study area

The study was carried out in the Klettgau region of the northern Swiss plateau at 450 m a.s.l. (15 km west of Schaffhausen, 47.42' N, 8.31' E). The study area covers 5,30 km^2, including 0.47 km^2 of settlements. It is an intensively used arable landscape with a crop rotation dominated by winter cereals (wheat 1.63 km^2, barley 0.42 km^2), maize (0.55 km^2) and oil-seed rape (0.30 km^2). Intensively managed grasslands occur on 0.37 km^2, set-asides (Grünbrachen) and less intensively managed meadows occupy 0.18 km^2. Other crops including potatoes, sunflowers, spring cereals and soybean are of minor importance. The average field size is 0.8 ha.

The soils are mainly shallow brown earths which have developed on a rather stony, calcareous substrate. The climate is relatively warm and dry (annual average temperature 8.5°C; annual average precipitation 915 mm; 1931-1990). May 1996 was exceptionally rainy and cold, while precipitation and temperature in June and July were close to the long-term average (Fig. 1). The meteorological data were collected at the weather station at Hallau, 3 km west of the study area.

Recent agricultural policy in Switzerland aims to promote biodiversity in farmland by creating or maintaining various types of "ecological compensation area". These include wildflower strips - areas of arable land 3-10 m wide sown with mixtures of annual arable weeds (e.g. *Centaurea cyanus, Agrostemma githago*), biennials (e.g. *Echium vulgare,*

Verbascum spp.), and perennial grassland species (e.g. *Salvia pratensis,*
Chrysanthemum leucanthemum). No farming operations are permitted on these areas
between March and September, and the use of herbicides and fertilisers is prohibited
altogether. Since 1990, schemes to sow wildflower strips in the Klettgau area have been
promoted, mainly by the Swiss Ornithological Institute at Sempach, and the cantonal
authorities; the principal aim of these schemes has been to maintain the vanishing
population of grey partridge (Jenny *et al.* 1997; Jenny & Weibel 1999; Jenny, Weibel &
Buner 1999). A large number of such strips with a total area of 0.06 km^2 have been
established in the study area.
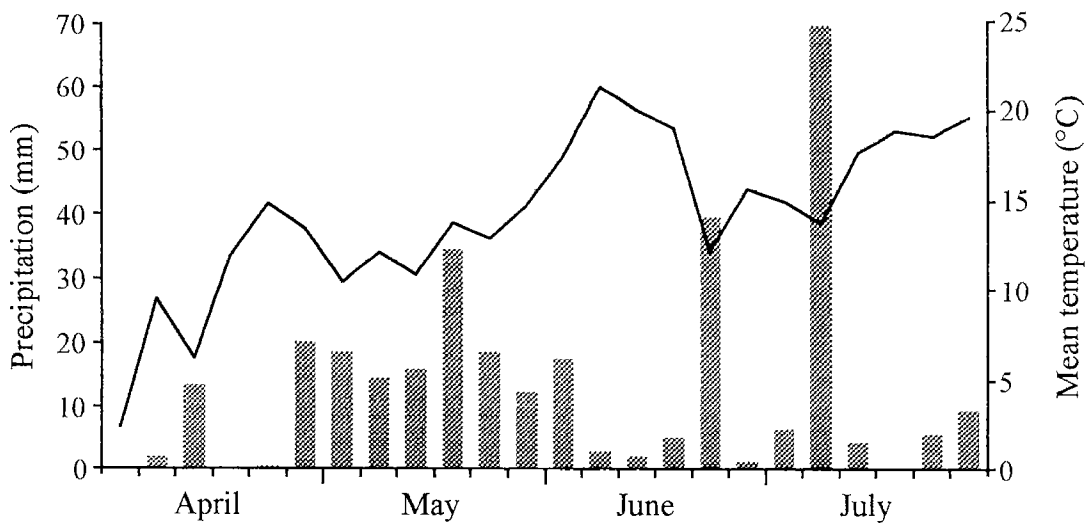
Fig. 1: Mean temperature and amount of precipitation for five consecutive days during
the 1996 breeding season of the skylarks in the Klettgau study area. Meteorological data
were collected at the weather station Hallau, 3 km west of the study area.

Materials and methods

Throughout the 1996 breeding season (from the laying of the first egg of the earliest
clutch on 11 April to the start of the last brood on 25 July) all territories of skylarks

were mapped by observing on a daily basis songflights and sites of antagonistic behaviour. These observations were recorded on a map (1:7500) showing the current land use including crop types. The raw data were subsequently used to produce a map of territories. This was digitised using a geographical information system (GIS, ArcInfo) in order to determine for each territory the areas of different crop types and the numbers of adjacent territories.

Information about the breeding state and the exact nest locations were mainly obtained by observing females carrying nest material or returning several times to the same spot within a field, and from mating, copulating, feeding and alarm behaviour, using a tent as a hide. In total, 110 nests were found: 38 during nest construction and laying, 14 during incubation, and 58 during the nestling phase. In 42 nests at least one nestling left the nest, and 68 nests failed, mainly due to predation (Chapter 1). Of the nests studied, 23 were in territories without wildflower strips, 23 were in territories with <3.5% of wildflower strips, and 18 had ≥3.5% wildflower strips. The average proportion of wildflower strips in territories with this habitat was 6%.

The nests were revisited every third day during the incubation phase and daily between 17.00 and 19.00 p.m. during the nestling phase. Nestlings were weighed with a spring balance (Pesola) to the nearest 0.5 g and the length of the third primary feather was measured to the nearest 0.5 mm. A total of 642 nestling measurements from 64 nests could be taken on at least two consecutive days.

Growth model

As for other bird species (O'Connor 1984), increases in both body weight and the length of the third primary feather of skylark nestlings have been shown to follow a sigmoid growth curve (Pätzold 1983). Both growth parameters were fitted to various formulations of the sigmoid growth equation (the logistic growth equation, Gompertz' growth equation, and Richards' growth equation; Richards 1959, O'Connor 1984). In each case the complete data were used in order to produce an average growth equation for the population. As the exact hatching date was rarely known, the use of a time independent growth model was necessary. For example, the logistic equation ($W = A/(1 + e^{-k(t-t_0)})$) cannot be used, while the differentiated form

(dW/dt = KW(1 - W/A)) is useable because it it is based on growth rate and not on body size as a function of age.

The best fitting equation (the logistic equation) was chosen and used for further analyses. Because the data for individual birds within a nest are not independent, mean values of nestling weight and feather length per nest were used. For each nest and measurement the residual of the growth equation R_t was calculated. Growth increments for consecutive measurements at the same nest were significantly intercorrelated (weight: $r_s = 0.28$, $P < 0.0005$; feather length: $r_s = 0.43$, $P < 0.0001$). However, residuals between the measured and the calculated daily growth rates (R_t) were not correlated, either with age (weight: $r_s = -0.12$, $P = 0.11$; feather length: $r_s = -0.12$, $P = 0.10$) or body size (weight: $r_s = -0.10$, $P = 0.15$; feather length: $r_s = -0.01$, $P = 0.92$). An average residual value R_{tn} was therefore calculated for each nest.

The average residual values R_{tn} were tested for possible correlation with the following factors: precipitation, mean temperature, date of hatching, brood size, territory size, number of adjacent territories, number of different crop types within a territory, and the arcsin-transformed amount of the different crop types per territory. The only variables which were significantly correlated with R_{tn} were the mean temperature during the nestling period, the date of hatching, the brood size, and the area of wildflower strips per territory. Multiple linear regression analyses were carried out to establish the proportion of variance of the R_{tn} explained by these correlated variables.

To show the effects of the individual variables, the residual values R_{tn} of territories were compared for early v. late broods, dry v. wet periods, and warm v. cold weather conditions, and for brood sizes of <4 v. ≥4 nestlings (two-way ANOVAs with interactions). For this purpose the territories were divided into those containing (i) no wildflower strips, (ii) < 3.5% wildflower strips, and (iii) ≥ 3.5% wildflower strips. There were no statistically significant differences between territories with different proportions of wildflower strips for the variables temperature, date of hatching, and number of siblings. In addition, weight was expressed as a function of feather length (quadratic linear regression) and the residual values were tested for correlation with the

same factors. The coefficient of variation between broods was compared for territories with and without wildflower strips.

For the statistical analyses the JMP (version 3.2.1; SAS Institute) software package was used. Throughout this paper the level of significance is $P < 0.05$, and mean values $\pm$ 1 *SE* are presented if not otherwise indicated.

Results

Growth pattern

The data for nestling weight exhibit an approximately sigmoid time-course; after an initial period of slow growth the curve has a nearly linear segment between the third and eighth day after hatching and thereafter the growth rate declines slightly (Fig. 2a). A striking feature of the data is the enormous range in weight of chicks of the same age. The coefficient of variation was 28.9% for 3-day chicks and decreased with the increasing age of the nestlings to a value of 14.9% at 8 days. It is also of interest that the coefficient of variation tended to be smaller in territories containing an area of wildflower strip (Table 1).

Table 1: Comparison of the coefficients of variation (%) of the broods between territories with and without wildflower strips for weight and feather length data.

Age (d)	Weight			Length of the third primary feather		
	Amount of wildflower strips per territory					
	0%	>0%	all	0%	>0%	all
3	34.3	24.9	28.9	23.9	18.4	21.2
4	25.8	20.9	22.7	27.3	20.2	21.9
5	24.6	21.7	22.7	23.8	21.9	22.6
6	21.5	20.3	20.9	21.6	23.2	22.0
7	20.3	15.8	17.8	22.6	18.9	20.2
8	19.9	11.1	14.9	22.0	14.6	18.2
9	17.7	14.1	16.1	15.8	17.7	19.5
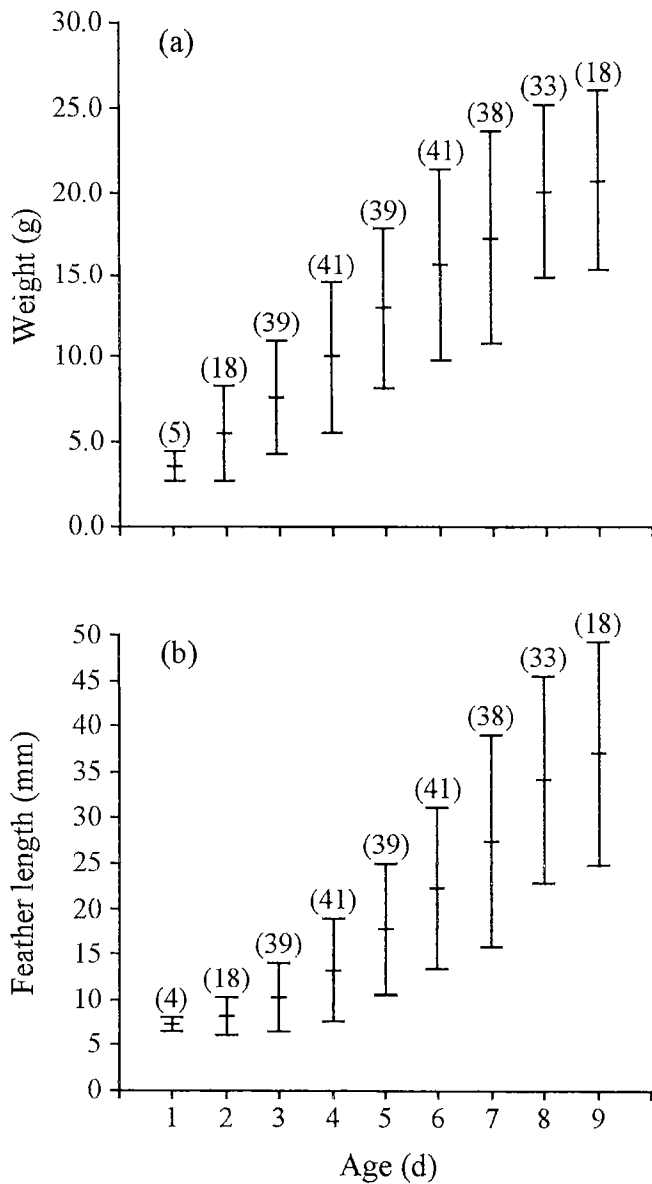
Fig. 2: Weight increase (a) and increase in length of the third primary feather (b) as mean per broods with age of skylark nestlings in the Klettgau study area in 1996 (Mean ± 95% range). Day 1 is the day of hatching. In cases when the exact date was not known, it was estimated from body size and plumage development. All measurements were taken between 5 and 7 p.m. Number in parentheses indicate the sample sizes.

To illustrate the variability of nestlings, Fig. 3 shows the individual growth curves for four selected broods during the first breeding period in May. In nest (a), one nestling

starved at the age of 3 days and the nest was predated on the seventh day. All nestlings in the other nests left the nest successfully. Especially for weight, the range within the broods are relatively small for nests (b) and (d), while in nest (c) it is very large. The figure shows that small hatchlings usually do not catch up with their larger siblings. However, a period of reduced growth while in the nest, e.g. nest (b) between the fifth and eighth days, does not necessarily lead to a lower final weight. In fact, periods of slow growth are relatively common, and weight losses can occur at any stage in the nestling phase. Of the 642 individual records of daily weight increment, 105 are ≤ 0 mm; these records occurred mainly during first breeding attempt in May (17%), when it was unusually cold and wet.

The data for the growth of the third primary feather also showed an approximately sigmoid curve, with the fastest growth occurring between the fourth and eighth days. As for weight, there is a large range in feather growth amongst chicks of the same age, and the coefficient of variation tends to be smaller in territories with wildflower strips (Figs 2 below, 3 and 4). Five percent of all measurements showed a daily growth ≤ 1 mm, and in six cases there was no measurable increase in length during a 24 h period.

Growth models

None of the growth equations explained more than a small proportion of the variance of the weight data. Although the fitted parameters were significant, the R^2 values ranged from 0.07-0.08. In contrast, each of the growth models based on feather length data explained 45% of the variance (Fig. 5). However, the estimates of asymptotic feather length calculated with the Gompertz' and Richards' growth equations differed from the logistic growth, and were much larger than values in the literature (Pätzold 1983). Furthermore, the asymptotic feather length in both the Gompertz' and Richards' growth models had large standard errors. For these reasons, further analyses are based on the logistic model.
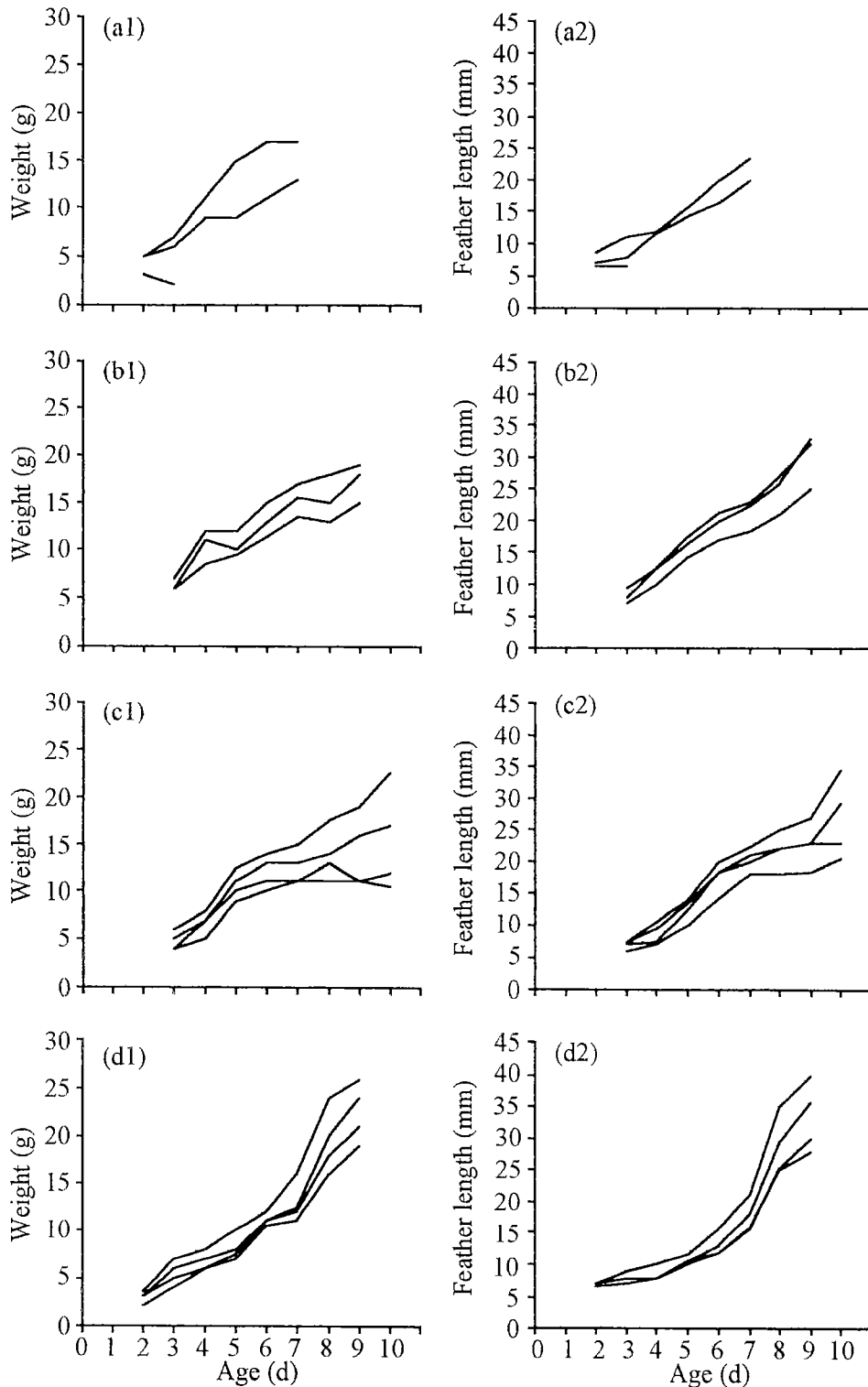
Fig. 3: Individual growth curves of nestlings in four selected broods during the first breeding attempt in May 1996 in the Klettgau study area; left hand side for weight (a1-d1), and right hand side for feather length (a2-d2). The letters indicate different nests. In nest (a), one nestling starved at the age of three days, the others were predated four days later. In the nest (b), (c), and (d), all nestlings successfully left the nest.
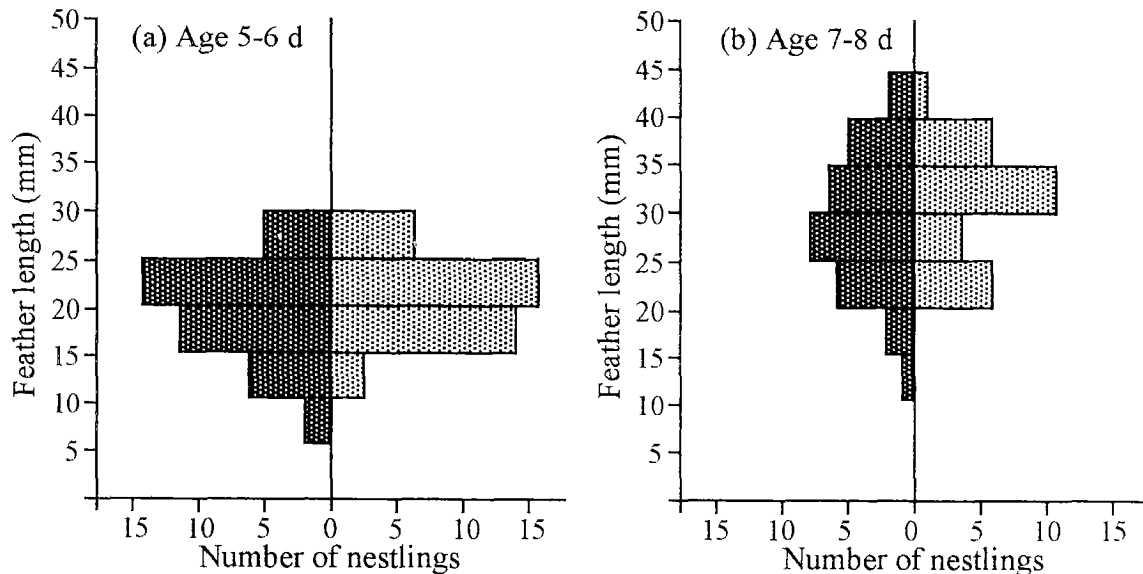
Fig. 4: Frequency distribution of feather length classes for skylark nestlings of an age of 5-6 days (a) and 7-8 days (b) for territories with wildflower strips (light shaded) and those without (dark shaded).

Factors affecting growth

The multiple regression model for the weight data explained 41% of the variance of R_{tn} with temperature, brood size, and hatching date being significant factors (Table 2). The area of wildflower strips (%) within the territory showed a positive but not significant regression coefficient. In the equivalent model using the feather length data, the same factors as for the weight data were significant, and the area of wildflower strips per territory also significantly influenced R_{tn} (Table 2).

The residual values (R_{tn}) of feather length tended to be highest for broods with territories containing $\geq 3.5\%$ wildflower strips, followed by those for broods with $<3.5\%$ wildflower strips; residual values for broods from territories without wildflower strips were the lowest and mostly negative. These differences were larger during periods when conditions for nestlings were poor (rainy, cold, early breeding attempts) than during good conditions (Fig. 6), though in no case was the effect of wildflower strips statistically significant. There was also no evidence for a significant interaction between

the amount of wildflower strips and other factors. The models were significant for both hatching date and temperature (Table 3). None of the two-way analyses of variance for the residual value R_{tn} for the weight curve reached significance.

The equation expressing weight as a quadratic linear function of feather length was: weight = -1.56 + 1.01 * feather length - 0.01 * (feather length)^2; R^2 = 0.92. The residual values were independent of age (r_s = 0.03; P = 0.6), but significantly correlated with brood size (r_s = -0.20; P < 0.005), mean temperature at the day of measurement (r_s = -0.17; P < 0.05), and number of different crop types per territory (r_s = -0.17; P < 0.05). The coefficient of variation for the residual values in territories with wildflower strips was significantly smaller than in those without wildflower strips (V_{with} = -0.49 ± 1.169; $V_{without}$ = 3.58 ± 1.504; t = 2.14; $d.f.$ = 176; P < 0.05).

Table 2: Determination of factors affecting skylark nestling growth, expressed as mean residual values per nest (R_{tn}) of weight and length of the third primary feather, based on a multiple linear regression.

	Estimate	d.f.	SS	F	P
Weight (R^2 = 0.41; $d.f.$ = 59)					
Intercept	-326.62	1			
Brood size	1.17	1	14.25	8.02	0.006
(Brood size)^2	-0.16	1	9.70	5.46	0.02
Hatching date	0.00	1	7.45	4.19	0.05
Temperature	0.07	1	10.99	6.19	0.02
Length of the third primary feather (R^2 = 0.68; $d.f.$ = 58)					
Intercept	-439.47	1			
Brood size	1.70	1	29.02	20.71	<0.0001
(Brood size)^2	-0.22	1	18.74	13.38	0.0006
Hatching date	0.00	1	13.39	9.56	0.003
Temperature	0.11	1	24.32	17.36	0.0001
Wild flower strips	0.07	1	10.60	7.57	0.008
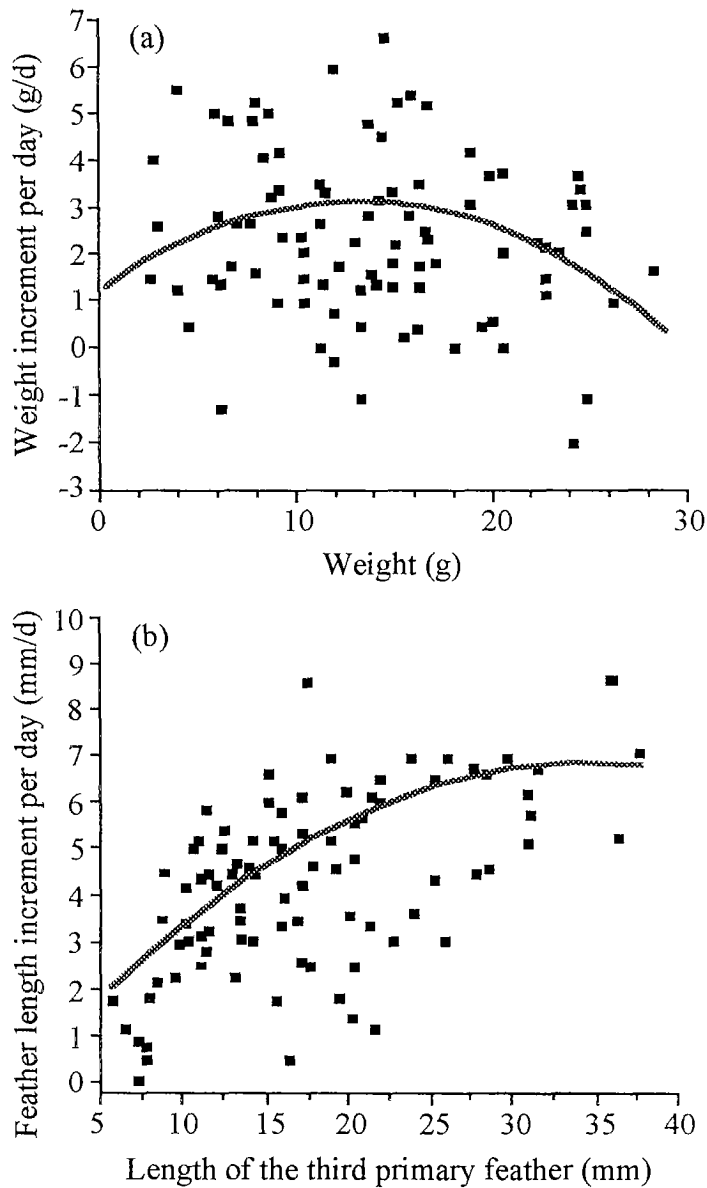
Fig. 5: Mean weight increment per day as function of the actual weight (a) and length of the third primary feather (b). The line is the fitted logistic growth curve. Calculations based on mean per broods.

Taken together, these results suggest that the poorest conditions for growth occur in territories without wildflower strips. Further confirmation comes from the cases of chick starvation. Ten nests were observed in which some of the nestlings starved. These nests were compared using Wilcoxon's signed rank test with other nests with a similar

hatching date, the area of wildflower strips per territory being used as the basis for the ranking. The result indicated that the territories in which starvation occurred tended to have a lower proportion of wildflower strips (n = 10, P < 0.025); indeed, 6 of these territories contained no wildflower strips at all.

Table 3: Two-way analyses of variance for the mean residual value R_{tn} of the growth model based on feather length. The variables tested are the amount of wildflower strips per territory (0, < 3.5%, ≥3.5%), hatching date (< 1 June, ≥ 1 June), mean temperature during the nestling stage (< 15° C, ≥ 15° C), and brood size (≤ 3, ≥ 4). As the same data were used for three-fold statistical analyses, the P-value was corrected as P < 0.015.

	d.f.	SS	F	P
Hatching date				
Model	5	29.70	5.63	0.0003
Wild flower strips	2	9.10	4.31	n.s.
Hatching date	1	14.32	13.57	0.0005
Interaction	2	4.53	2.14	n.s.
Error	58	61.22		
Temperature				
Model	5	26.98	4.89	0.0008
Wild flower strips	2	2.58	1.17	n.s.
Temperature	1	8.91	8.08	0.006
Interaction	2	0.16	0.07	n.s.
Error	58	63.95		
Brood size				
Model	5	16.00	3.20	n.s.
Wild flower strips	2	10.14	3.93	n.s.
Brood size	1	5.96	4.61	n.s.
Interaction	2	0.59	0.23	n.s.
Error	58	74.92		
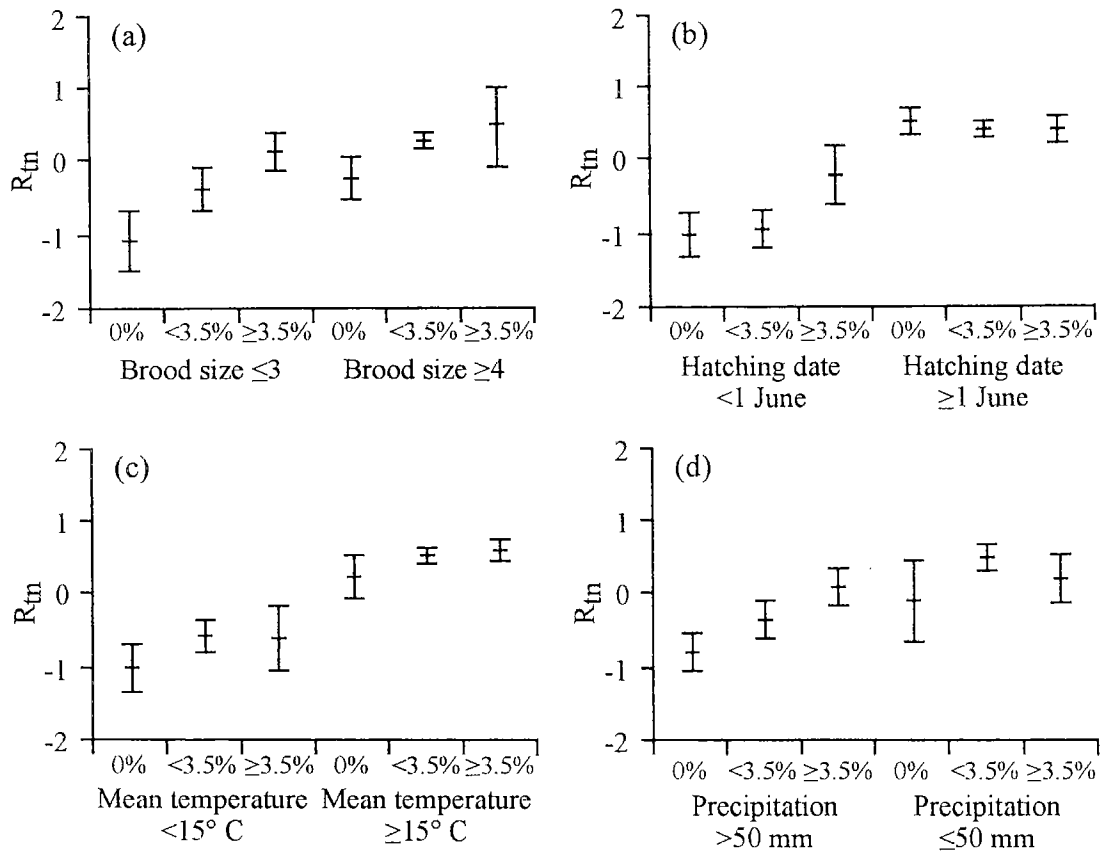
Fig. 6: Mean residual values R_{tn} of the growth model based on feather length curve for broods in territories with 0%, >0 - <3.5%, and ≥3.5% wildflower strips per territory. These values are shown for (a) brood sizes ≤3 v. ≥4, (b) hatching date <1 June v. ≥1 June, (c) mean temperature during the nestling stage <15° C v. ≥15° C, and (d) mean precipitation during the nestling period >50 mm v. ≤50 mm.

Discussion

The pattern of growth

Skylark growth, measured either as increase in body weight or length of the third primary feather, can be described with a logistic growth curve. Whereas weight growth is nearly completed during the nestling stage, feathers continue to grow until an age of at least 16 days (Pätzold 1983). This study has revealed a remarkably wide range in the

growth rates of skylark nestlings. The growth curve of individual birds is often characterised by retarded growth during bad conditions whereas high growth rates are achieved during good conditions. Although hatching is approximately synchronous (Delius 1963), a large range of body condition can occur within one brood, making an accurate determination of hatching date based only on weight data impossible.

Skylarks search for food mainly on invertebrates which live on the soil surface or in the lowest stratum of vegetation (Jenny 1990). The abundance and activity of these invertebrates fluctuate widely according to weather conditions, population cycles, and agricultural practices. Moreover, the skylark requires a habitat with sparse vegetation in which searching for food is possible (Odderskær et al. 1997; Weibel 1998). For these reasons, the predictability of nestling food at the time of egg laying and the stability of the food supply for nestlings are low, and we would expect a resource storage strategy, which is typified by retarded growth during bad conditions (O'Connor 1978). Indeed, weight losses and reduced growth on the one hand and large daily weight and feather length increase on the other were common. The slight increase in clutch size from the first breeding attempt in April to the second clutches in June, followed by a decrease in July (Delius 1963; Chapter 1) may reflect general changes in food availability for both the nestlings and the females (Delius 1963, Schläpfer 1988, Jenny 1990). Nothing is known of fat reserves and metabolic rates of skylark nestlings, especially during bad growth conditions.

There is little published information about growth performance of skylarks. However, Evans, Wilson & Browne (1995) working in southern England, also found a large variance in growth performance and marked differences in weight growth curves in territories of different quality. Unfortunately, nothing is known of the post-nestling survival of birds in relation to nutrition while in the nest. Chamberlain and Crick (1999) found no evidence that the population declines of skylarks are related to a reduction in the breeding success; however they suggested that an increase in first-year mortality due to poor body conditions caused by food shortages during the nestling period may be a contributory factor. Further research should focus on the relation between nestling body condition and first-year survival.

Growth models

A model based on changes in body weight is potentially the most informative, since, as shown for great tits, metabolic rates are more strongly related to body weight than to age (Drent & Daan 1980). However, because of the large variation in the weight data, the proportion of the variance explained by the growth model is very low. Body weight is more sensitive to short-term environmental fluctuations than linear measurements of body size e.g. tarsus and feather length (Gebhardt-Henrich & van Noordwijk 1991), and factors like defaecation during handling mean that weight data tend to be rather noisy. For this reason, linear growth parameters are probably more useful when examining growth differences due to environmental factors such as habitat quality.

For the purposes of comparison with the data presented here, the logistic growth model was fitted to data from three other studies. Pätzold (1983) presents data for only five nests at a site near Dresden during the first breeding attempt in the years 1960 and 1961 (R. Pätzold, pers. comm.). Evans, Wilson & Browne (1995) present growth data for skylark nestlings based on a sample of 82 nesting attempts in 1993 and 1994. The data are in a graphical form, and for the purposes of comparison with the data presented here, numerical values have been estimated from their figures. Data are also available from a preliminary study in the Klettgau area in which 127 nestling measurements in 56 nests were taken on at least two consecutive days in 1994 (M. Jenny & G. Keller, unpubl. data). The growth parameters obtained from these studies for the first 10 days after hatching are shown in Table 4. There were no statistically significant differences amongst the two Klettgau studies and the British study. However, in the German study the slope parameter k for the weight data was at least twice as high as in the other three. The other variables of the growth equation (asymptotic weight, shape for feather length curve, and asymptotic feather length) did not differ significantly in any study. The much higher growth rates (weight curve) in the study from Dresden (Pätzold 1983) may be simply a result of the small sample size.

Table 4: Comparison of growth parameters for the nestlings in the first 10 days after hatching between the data of (1) Pätzold (1983), (2) Evans, Wilson & Browne (1995), (3) Jenny & Keller (unpubl.) and (4) this study (Mean ± 1 SE), with slope parameter k and asymptotic body size A. The growth parameters were compared using the Tukey-Kramer method. Significant differences are indicated with a *.

	Weight		Length of the third primary feather		
	k	A	k	A	n
(1)	1.04 ± 0.16	24.02 ± 1.01	0.37 ± 0.00	56.42 ± 10.48	18
(2)	0.36 ± 0.15	26.49 ± 5.46			129
(3)	0.41 ± 0.06	25.75 ± 2.00	0.34 ± 0.04	75.49 ± 14.19	56
(4)	0.52 ± 0.03	23.11 ± 0.78	0.38 ± 0.02	70.28 ± 6.07	193
$MSD_{1,2}$	0.42*	10.9			
$MSD_{1,3}$	0.33*	4.49	0.07	35.29	
$MSD_{1,4}$	0.31*	2.50	0.04	23.73	
$MSD_{2,3}$	0.32	16.1			
$MSD_{2,4}$	0.30	10.8			
$MSD_{3,4}$	0.13	4.21	0.08	30.25	

Factors affecting growth

Skylarks produced larger broods and the nestlings showed better growth during the later part of the breeding period when the weather was warmer. Broods in territories with wildflower strips also grew better than those in territories without them, though this result was only significant for feather data. The differences in the residual values for the feather data were larger during poor growth conditions. In addition, weight and feather length data were more closely correlated in broods from territories with wildflower strips than in those without. Finally, fewer nestlings starved in broods in territories with wildflower strips than in those without. Lower growth rates of passerine nestlings during rainy and cold weather conditions have been reported by other authors (e.g. Rodenhouse & Holmes 1992; Siikamäki 1996), though in study presented here growth appears to be less affected by rainfall than by low temperatures. However, this may

simply be because the use of an average R_{tn} makes it difficult to detect the short-term consequences of a single rainfall event.

Shkedy & Safriel (1992) found no correlation between brood-size and growth rate for the two lark species, crested lark *Galerida cristata* and desert lark *Ammomanes deserti*. The effect of sibling number in our study is mainly caused by a few cases of small broods which have a low value of R_{tn}. These small broods were mainly caused by starvation of some nestlings within a brood and by unhatched eggs. A partial reduction of brood size due to predation is very rare; nestlings either all survived or were all taken (Chapter 1). Hatching success is also affected by environmental conditions, being reduced during periods of high rainfall (Rodenhouse & Holmes 1992).

The beneficial effects of higher food availability for nestling growth have been investigated for several bird species, mainly in food limitation or supplementary feeding experiments (Rodenhouse & Holmes 1992; Simons & Martin 1990; Wiehn & Korpimäki 1997). The findings of Evans, Wilson & Browne (1995) that skylark nestlings on organic farms have better body condition than those on conventional farms, and of Wilson *et al.* (1997) that brood starvation occurred almost exclusively in intensively managed winter cereals and not in organically managed fields, can be attributed to better food supply for nestlings. This conclusion is supported by the data from Moreby *et al.* (1994) who found a higher abundance of many chick-food insects on organic farms. Evans, Wilson & Browne (1995) reported that the mean index of body condition was higher for nestlings in a grassland territory than for those in cereal fields, which fits with the finding of Jenny (1990) that there is more insect food in grasslands than in cereal fields. In England, a higher invertebrate abundance has also been found in set-asides than in crops; though some nestlings starved in broods in conventionally managed spring barley fields, there was no nestling mortality due to starvation in broods in set-asides (Poulsen, Sotherton & Aebischer 1998).

Wildflower strips are known to be much richer in invertebrates than adjacent fields (Lys 1994; Frank & Nentwig 1995; Nentwig 1995; Kramer 1996), and wildflower strips are attractive to skylarks searching for food throughout the breeding season (Weibel 1998). Especially during poor growth conditions the beneficial effects of wildflower strips were measurable.

Practical implication

The evidence presented here suggests that wildflower strips provide a more secure food supply, thanks to the higher invertebrate abundance and a vegetation structure which facilitates foraging. However, although nestling mortality due to starvation may be reduced in territories with wildflower strips, predation is known to be a much more significant cause of mortality during the nestling stage (Chapter 1). It may be that wildflower strips have an indirect effect upon nestling survival by influencing the amount of predation. Firstly, well fed nestlings may be less at risk of predation because they can leave the nest sooner. Secondly, a higher begging frequency of poorly fed nestlings may attract predators. There may even be effects of wildflower strips upon post-nestling survival, since birds which were better fed as nestlings may have a better chance of subsequent survival. In fact, little is known about post-nestling survival, especially in the period between the birds leaving the nest and achieving full independence, and for this reason the full significance cannot be assessed of wildflower strips for skylark populations. Even so, it seems clear that they are of significant benefit and their creation in intensive farmland is to be encouraged.

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Chapter 3

The diet of nestling skylarks *Alauda arvensis* in an intensively used arable landscape with wildflower strips

Summary

The diet of nestling skylarks in an area of intensive arable agriculture in northern Switzerland was investigated. Neck collars were used to collect the food items for nestlings brought by the parent birds. Dietary composition was analysed in relation to time of year, nestling age, and presence or absence of wildflower strips within the territory.

Araneae, Diptera, and Coleoptera were the most abundant food items, and amounted to nearly 75% of the total; Lepidoptera and Hymenoptera for another 15%. For broods in April and May, items of 5 orders made up for 95% of the diet, namely Araneae, Diptera, Coleoptera, Lepidoptera, and Hymenoptera. For later broods, these arthropod orders were still dominant, but another 3 orders made up for 95% of the diet. With increasing age of the nestlings the amount of Coleoptera, Diptera and Hymenoptera increased, whereas that of Araneae and Lepidoptera decreased. Small differences in diet was found between territories with and those without. However, diet composition was affected by season, nestling age, territory composition, and brood size. Nearly 50% of all food items were 6 to 10 mm long, with little variation throughout the season.

The results confirmed that skylarks are not particularly specialised in regard to their diet and that they tend to take the most frequent prey. The study in an arable used area contrasted the findings in grassland dominated landscapes.

Keywords: arthropod food, ecological compensation areas, Klettgau, neck collar

Introduction

Skylarks are ground-feeding birds, which raise their nestlings almost exclusively on arthropods (Cramp 1988; Jenny 1990; Poulsen, Sotherton & Aebischer 1998). In intensively managed grassland in the Swiss Plateau, skylarks collected their food mainly in short grassy habitats (Jenny 1990). Most prey items were dipterans (Diptera), especially craneflies (Tipulidae), grasshoppers (Orthoptera), and butterflies (Lepidoptera). Jenny (1990) showed that the relative importance of the different arthropod taxa in the nestling diet varied according to their abundance, although adults tended to search for larger and more profitable prey items. He concluded that skylarks are not particularly specialised with regard to the diet, and that abundance and accessibility of prey are the most important factor determining searching behaviour. Skylarks searching for food are mainly restricted to low and sparse vegetation (Jenny 1990; Odderskær *et al.* 1997; Weibel 1998); even when arthropod abundance was lower than in denser vegetation, which has been showed by Odderskær *et al.* (1997).

Many factors including nestling age, crop type within the territory and crop management influence the species composition of the nestlings' diet. In mixed arable used land in southern England the diet of very young skylark nestlings consisted mainly of soft-bodied sawfly (Hymenoptera) and lepidopteran caterpillar; however, at an age of about five days there was a shift towards more hard-bodied arthropods such as adult beetles (Poulsen *et al.* 1998). The diet was affected by the crop type in which the parents searched for food; for example, more soft-bodied items like larvae and spiders were taken in set-aside areas whereas in silage-grass and barley hard-bodied insects predominated.

Other studies have shown that the caterpillar of sawflies and butterflies are less abundant in cereal fields sprayed with insecticides or herbicides than in natural grassland, set-aside and less intensively managed cereals (Potts & Vickerman 1974; Moreby & Aebischer 1992; Sotherton, Moreby & Langley 1987; Sotherton & Moreby 1992; Moreby *et al.* 1994; Brooks *et al.* 1995). Various authors suggested that in intensively used arable regions food for skylark nestlings is sometimes in short supply, which may account for recent declines

in skylark populations (Schläpfer 1988; Jenny 1990; Tucker & Heath 1994; Evans, Wilson & Browne 1995; Chamberlain & Crick 1999). The available data suggest that the risks of nestling starvation are greatest during the first breeding attempt in April and May (Chapter 1), when the weather conditions are harsher. Elmegaard *et al.* (1998) found evidence that in spring barley fields subjected to full pesticide treatment food abundance was reduced, nestling food was less diverse, and the number of fledglings produced per field was reduced by more than a third. The decrease in reproductive output was caused by lower nestling survival and poorer condition of adult birds.

Since 1993, Swiss agriculture policy has aimed to promote farmland biodiversity by introducing 'ecological compensation areas'. These areas, include less intensively managed meadows, hedges, and wildflower strips, and are supported under a subsidy scheme. The wildflower strips are 3-10 m wide and sown with a mixture of annual arable weeds, biennials, and perennial grassland forbs. The use of herbicides and other pesticides is prohibited completely and no farming operations are allowed during the breeding season of farmland birds. The Swiss Ornithological Institute at Sempach and the canton authorities have promoted the establishment of wildflower strips in the study area since 1991 (Jenny *et al.* 1997; Jenny & Weibel 1999).

It is known that wildflower strips are richer in both numbers and diversity of arthropods than adjacent intensively used fields (Bürki & Hausammann 1993; Lys 1994; Lys & Nentwig 1994; Frank & Nentwig 1995; Kramer 1996; Nentwig 1996). The higher food abundance and a heterogeneous vegetation structure with gaps make the wildflower strips attractive for skylarks searching for food (Weibel 1998). Furthermore, there is some evidence that nestlings grow faster in territories including wildflower strips (Chapter 2).

The main aim of this study is to describe the diet of skylark nestlings in an intensively used arable region, and to evaluate the importance of different factors affecting dietary composition. As part of the study, nestling diet of broods in territories including wildflower strips are compared with those without wildflower strips.

Study site and methods

Study site

The study was carried out in an area of the Klettgau region in northern Switzerland (15 km west of Schaffhausen; 47°42' N, 8°30' E; 400-470 m a.s.l.). The study site has an area of 530 ha and its boundaries are defined by the connecting roads between the villages of Neunkirch, Gächlingen, Siblingen, and Löhningen. In the central parts of this area, the soils are shallow calcareous brown earths of rather low fertility. Towards the south and east, the soils have developed on an alluvial loam and are generally deeper and more fertile. The climate is relatively warm and dry (mean annual temperature 8.5 °C; mean annual precipitation 915 mm; weather station Hallau, 3 km west of the study area).

Arable land covers 453 ha (85% of the total area). The average field size is small (mean 0.81 ha). In 1997, 15 different crops were cultivated: cereals (47% of the arable land), root vegetables and oil seeds (29%), maize (9%), permanent and ley grassland (7%) and vines (1%). The amount of set-aside (Grünbrachen) was relatively high for the Swiss Plateau (3%), reflecting the limited fertility of the soils. Ecological compensation areas covered 19 ha (4% of the arable land), of which 6.3 ha were wildflower strips.

Data on arthropod abundance are partly available as their were investigated in the study area in 1992 by the Swiss Ornithological Institute. Arthropods were collected using pitfall traps and sweep netting in maize, root vegetables, winter wheat, verges of tracks, ley grassland, and wildflower strips. Samples were taken weekly from 23 April to 28 May and from 25 June to 30 July. Three pitfall traps were placed in two fields of each crop type. The pitfall traps data are presented to show the differences in the number of sampled items between both crops and May and July for the most frequent arthropod groups (Schweizerische Vogelwarte Sempach, unpublished data; Fig. 1). In the first sampling period in May 1992, beetles were most frequent, mainly due to Carabidae and Staphylinidae in winter wheat and in maize. In July, spiders ranked first followed by beetles and dipterans. Hymenoptera and Lepidoptera were more frequent in wildflower strips, on the verges of tracks, and in grassland than in arable crops.
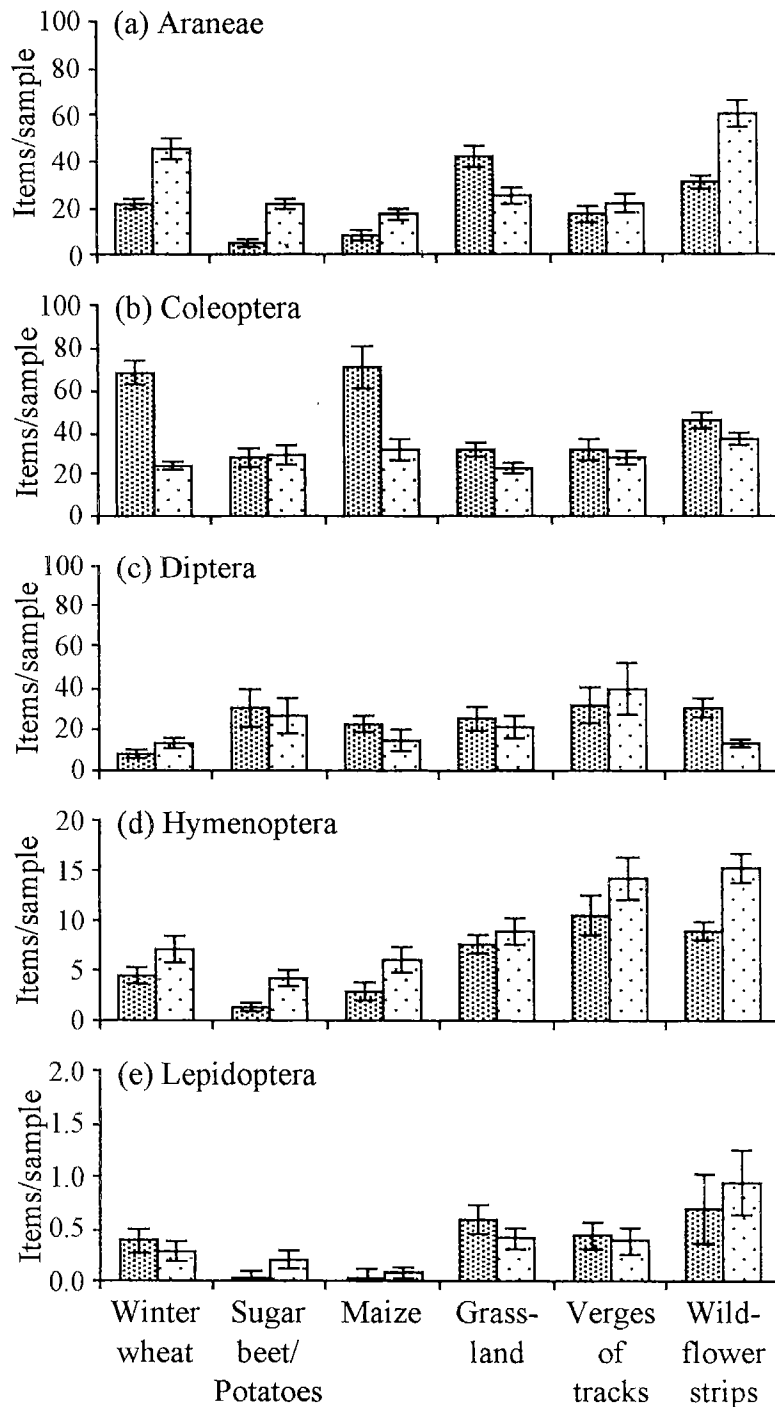
Fig. 1: Abundance of arthropod orders which are most frequently found. Arthropods were collected using pitfall traps in 1992 between 23 April and 28 May (dark shaded bars) and from 25 June to 30 July (light shaded bars). The data have been collected by the Swiss Ornithological Institute at Sempach (unpublished data).

Methods

Three methods have been used in previous studies to investigate the diet of skylark nestlings: direct observation, faecal analysis, and neck collars (Jenny 1990; Poulsen 1993; Poulsen & Aebischer 1995; Poulsen, Sotherton & Aebischer 1998). Direct observations with photographic documentation are only possible if the nest is clearly visible (Jenny 1990), and small prey items are easily overlooked. Faecal analysis has been applied in skylarks by Poulsen (1993), Poulsen & Aebischer (1995), and Poulsen *et al.* (1998), and in several other species including gamebirds and small passerines (Green 1984; Davies 1977). Normally, skylark nestlings defecate spontaneously during handling. Faecal analysis is scarcely invasive and it is possible to sample throughout the entire nestling period; however, differences in the digestibility of the prey can make the interpretation of the results very difficult (Poulsen & Aebischer 1995). Neck collars prevent nestlings from swallowing the food that they have received from their parents, thereby allowing identification of the food items (Jenny 1990; Poulsen & Aebischer 1995). The neck collar method is more invasive, and cannot be used on nestlings younger than 4 days; furthermore it may reduce the feeding frequency, because the nestlings are prevented from begging (Johnson, Best & Heagy 1980). In a comparative study using both neck collars and faecal analysis, Poulsen & Aebischer (1995) detected no differences in the diet of skylarks; they therefore recommended the non-invasive faecal analysis. However, we decided to use the neck collar method because prey items are easier to identify, and previous skylark studies indicated no reduction in the feeding rate of birds with collars (Jenny 1990; Poulsen & Aebischer 1995).

Nestling diet was studied in the breeding seasons 1997 and 1998. The neck collars were made from 0.8 mm copper wire with a grey plastic insulation, as described by Jenny (1990). Collars were placed on the nestlings for a period of one hour, and after their removal, nestlings were fed by hand with maggots of honey bee drones. Neck collars were applied between the fourth and the seventh day after hatching; before that nestlings are too small and afterwards there is the risk of premature leaving the nest (Jenny 1990). Most samples (88%) were taken between 8.00 and 12.00 a.m., though a few were earlier (5%) or

in the afternoon and evening (7%). Sampling was only carried out during dry weather. The collected food items were stored in 70% alcohol, and subsequently measured to the nearest 1 mm and identified, at least as far as taxonomic order. Additionally, the stage of development was determined for the holometabolous insects. For the identification of diet items, publications by Stresemann *et al.* (1992, 1994a, 1994b) were used. For each of the nests used in the study, brood size, age of the nestlings, and presence or absence of wildflower strips in the parent territory were recorded.

In total, 117 samples of neck collars were collected; in 13 no food items were obtained, apparently because the neck collars were too loose. The successful samples were from 73 broods, including two which were used on four occasions, five used three times, 15 used twice, and 51 broods were used only once. In April and May, 64 samples were taken from first broods, and 40 from later broods in June and July. The age distribution of the nestlings sampled was as follows: 9 of 4 days, 21 of 5 days, 37 of 6 days, and 37 of 7 days. Of the 73 broods, 22 territories included wildflower strips.

A log-linear model and Spearman rank correlation coefficients were calculated to find the factors affecting dietary composition. The variables included in the analyses were: season (April/May v. June/July), brood size (2/3 v. 4/5), nestling age (4/5 v. 6 v. 7 days), and territory composition (i.e. presence or absence of wildflower strips). The correlation coefficients of intercorrelated parameters were corrected by applying a path analysis (Sokal & Rohlf 1995). Statistical analyses were carried out using the JMP software package (version 3.2.1; SAS). Mean values ± 1 *SE* are presented unless indicated otherwise.

Results

Number of items per nestling

The median number of items per food sample was 2.6 per nestling per hour (n = 104); with a 95%-range from 0.3 to 9.5. It was significantly correlated with both brood size (r_s = -0.29; $P < 0.01$) and nestling age (r_s = 0.27; $P < 0.05$). It was not affected by week of

sampling ($r_s = 0.09$; $P > 0.3$), and did not differ between territories with wildflower strips and those without (Kruskall-Wallis test $H = 1231.5$; $P > 0.5$).

Taxonomic composition of the diet

Of a total of 890 food items, 868 could be identified at least to the level of order. Two thirds of all prey items were insects, almost one third were Arachnida, and 5% were of other classes including some non arthropods (Tab. 1). Araneae, Diptera and Coleoptera were the most frequent prey classes accounting for almost three-quarter of the diet; Lepidoptera and Hymenoptera for another 15%. Shells of *Helicella obviva* (Stylommatophora) were found in three samples, pieces of Lumbricidae (Oligochaeta) four times, and Myriapoda 17 times. Plant material, mainly cereal grains, were found in 7 samples in May 1997. More than half of neck collar samples (i.e. all food items brought to a brood in one hour) contained Araneae and Diptera, and over 40% contained Lepidoptera and Coleoptera. In samples containing Araneae, Diptera or Coleoptera, on average 3.6 items per sample of these arthropods were fed; the mean number of the other classes ranged from 1 (Stylommatophora, Opiliones) to 2.6 (Homoptera); except Chilopoda, where 14 individual were brought in one sample.

Eighty-two per cent of the 159 Coleoptera in the diet could be classified to family level. Most of them were Carabidae (74%) and Chrysomelidae (12%); Elateridae (5%), Staphylinidae (4%), Coccinelidae (2%), and Scarabidae (2%) were of minor importance.

The Hymenoptera (n = 38) were represented chiefly by Symphyta (94%), both Formicidae and Tenthredinidae being found only once. The 8 Dermaptera food items were all of one species, the earwig *Forficula auricularia*. Amongst Saltatoria (n = 10), both Caelifera (e.g. Acrididae) and Ensifera (e.g. Tettigoniidae) were found. The 18 Homoptera were composed of Cicadidae (56%), Aphididae (38%), and Tettigometridae (6%). The Neuroptera were represented by lacewings (Chrysopidae). Of the Diptera (n = 224), 67% could be classified to the family level of which 84% were Tipulidae and 16% Syrphidae.

Table 1: Composition of the skylark nestling diet. Relative abundance of taxonomic classes and orders in total sample of identified prey items (n = 868) and their frequency of occurrence in 104 neck collar samples; 22 unidentified prey items were excluded.

Class Order	Abundance of food items (%)		Frequency of the food items (%)	
Gastropoda	0.3		2.9	
Stylommatophora		0.3		2.9
Clitellata	0.7		3.8	
Oligochaeta		0.7		3.8
Arachnida	30.6		70.2	
Araneae		30.4		69.2
Opiliones		0.2		1.9
Myriapoda	2.5		4.8	
Chilopoda		1.6		1.0
Diplopoda		0.9		3.8
Hexapoda	65.9		97.1	
Dermaptera		0.9		3.8
Saltatoria		1.2		6.7
Heteroptera		1.0		4.8
Homoptera		2.1		6.7
Neuroptera		1.3		4.8
Coleoptera		18.3		44.2
Hymenoptera		4.4		24.0
Lepidoptera		10.9		50.0
Diptera		25.8		59.6

Among the holometabolous insects (mainly Coleoptera, Diptera and Lepidoptera), 47% of the food items were imagines, 46% larvae, and 7% pupae. In Hymenoptera only 16% of the items were imagines. While the proportion of pupae was higher for Diptera (16%) than

for the other orders. The proportion of imagines of the total of holometabolous arthropods decreased from 95% by 4-5 day old nestlings, to 52% for nestlings of 6 days and to 36% for those of 7 days. This trend was mainly caused by high number of beetle larvae fed to nestlings older than 5 days. The amount of pupae accounted only 4% in broods early in the breeding season, but for 11% later in the season; the number of larvae decreased correspondingly, whereas that of imagines remained constant (47%). The frequency of the different stages of insect development showed therefore significant effects of nestling age ($\chi^2 = 26.9$; $d.f. = 4$; $P < 0.0001$), of the order of the food items ($\chi^2 = 33.3$; $d.f. = 6$; $P < 0.0001$), and also of the interaction term *age x season x order* ($\chi^2 = 30.5$; $d.f. = 12$; $P < 0.005$).

Adult beetles were mostly fed without head and wing cases; and also adult butterflies were fed without head and wings. Spiders were sometimes fed together with cocoons (9%).

Factors affecting the diet composition

The general linear model reveals significant effects of season, nestling age, territory composition, and brood size on the food composition by taxonomy ($\chi^2 = 208.5$; $d.f. = 42$; $P < 0.0001$; Table 2). In the diet of either early and late broods, Araneae, Diptera, Coleoptera, and Lepidoptera were dominant. There was a shift in the most frequent prey from spiders towards dipterans in the course of the breeding season. In late broods, other arthropod orders, especially Saltatoria, Dermaptera and Chilopoda, contributed to higher proportion of the diet and therefore it consisted up to 95% of 8 orders while in early broods, only 5 orders made up for this proportion (Fig. 2).

Broods of 2-3 young tended to have a higher proportion of Arachnida (33%) and Diptera (29%) than larger broods (27% and 23% respectively). However, Coleoptera increased from 15% of food items in small broods to 22% in large broods. Differences in diet associated with age of nestlings could be detected, even though the study covered only a narrow range of 4 to 7 days of age. The proportions of Coleoptera, Hymenoptera and Diptera increased with nestling age, those of Lepidoptera and Arachnida decreased (Fig. 3).
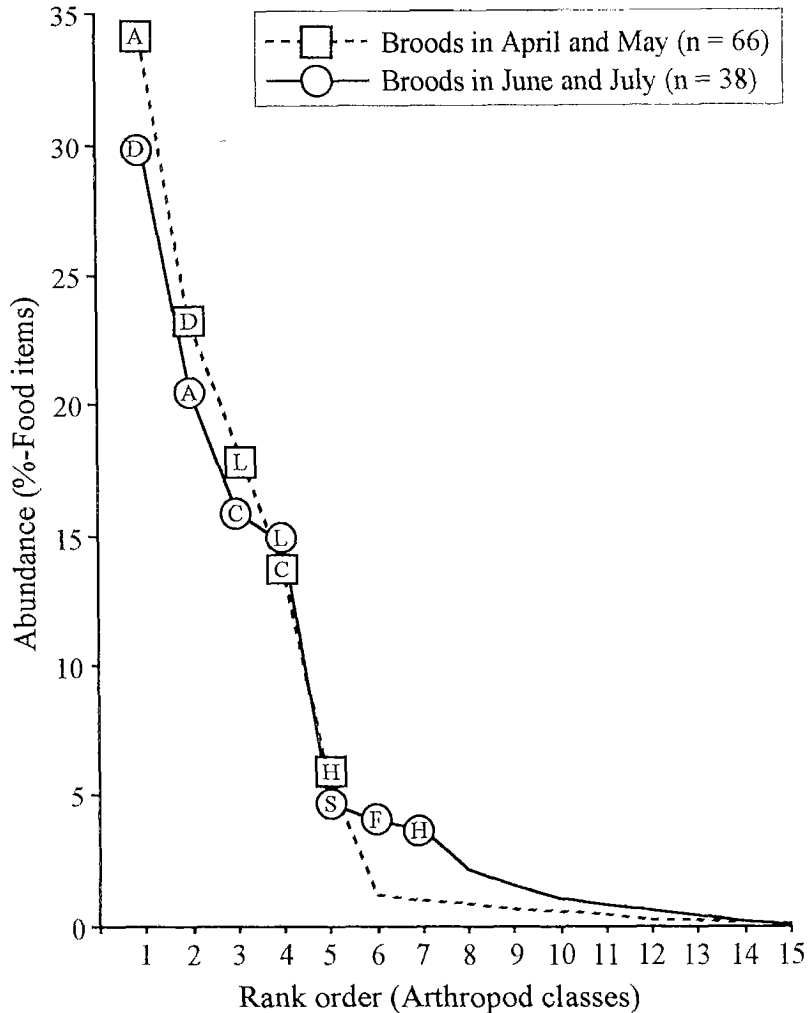
Fig. 2: Frequency-rank diagram for the diet composition of skylark nestling in early and late broods. The arthropod orders are ranked according to their frequency in the nestling diet; for items more frequent than 4% the class is indicated; A, Araneae; D, Diptera; L, Lepidoptera; C, Coleoptera; H, Hymenoptera; S, Saltatoria; F, Dermaptera.

In both territory types, with and without wildflower strips, Araneae, Diptera, Coleoptera and Lepidoptera, were dominant, accounting for 86% of the diet. Among these arthropods beetles and spiders were more frequent in the diet in territories with wildflower strips, and Diptera were correspondingly less frequent in territories without wildflower strips. In territories with wildflower strips, grasshoppers made 5% of the diet (1% in those without), and there were no Chilopoda, Diplopoda, and Heteroptera in the diet in territories with wildflower strips whereas these orders were represented in a small proportion in other

territories. Merely 5 orders made up for 95% of the food items in territories with wildflower strips, 8 in those without. In territories without wildflower strips food items belonging to 9 orders were fed with a frequency of more than 5%; 3 orders more than in those with wildflower strips.

Table 2: General linear model to determine factors affecting the diet composition of skylark nestlings.

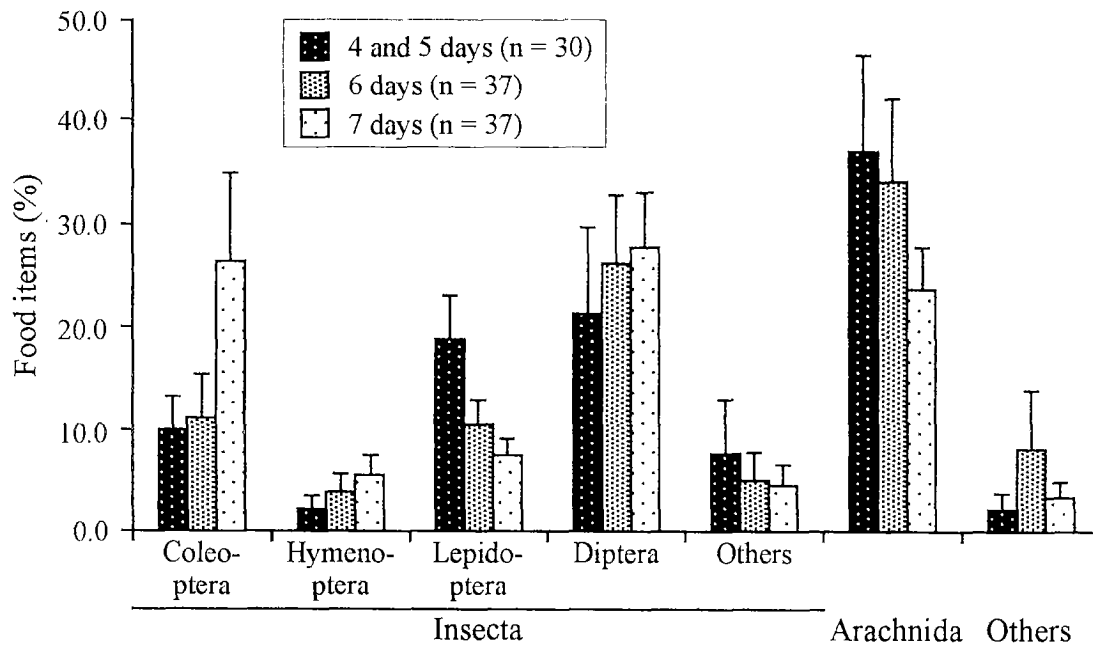| Parameter	$d.f.$	$Wald\ \chi^2$	P
Nestling age	12	76.97	<0.0001
Season	6	27.71	0.0001
Territory composition	6	18.29	0.006
Brood size	6	16.97	0.009
Brood size x Season	6	5.36	n.s.
Brood size x territory composition	6	8.03	n.s.

Fig. 3: Diet composition of skylark nestlings of different ages; n indicates the number of neck collar samples.

Size distribution of the diet

Forty-six per cent of food items were in the 6-10 mm size class, and 24% were 11-15 mm long. The smallest food items were about 3 mm long; they were mostly spiders and also a few aphids and ladybirds. The largest food item recorded was part of an earthworm 41 mm long; most other items >20 mm were caterpillars. The size composition of the items in diet did not vary greatly with nestling age (G = 8.94; $d.f.$ = 8; P > 0.1). However there was a trend for fewer items in the 11-15 mm class and a corresponding increase of items in the >15 mm classes with increasing age. Interestingly, there were no differences with age in the number of smaller items (Fig. 4).
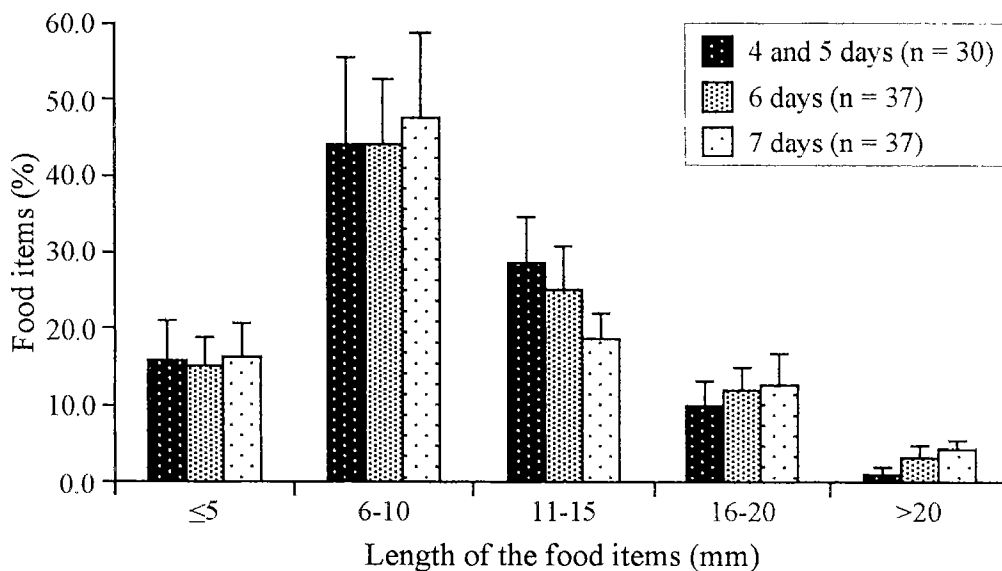

Fig. 4: Size distribution of skylark prey items for different nestling ages; *n* indicates the number of neck collar samples.

Discussion

Our study has shown that spiders, dipterans and beetles are the most abundant food items fed to skylark nestlings, accounting for nearly 75% of their diet. These arthropod classes

are also most numerous collected in pitfall traps in the same area in 1992, which confirm that skylarks take the most frequent prey, and are therefore not particularly specialised in regard to the diet. Spiders are the most important group in early broods, whereas Diptera rank first in later broods. The proportion of spiders and butterflies decreases with the nestling age and that of beetles and hymenopterans increases correspondingly. Almost 50% of food items were 6 to 10 mm long. The number of prey items per nestling and hour is inversely correlated with the brood size; and it is positively correlated with nestling age.

Spiders, dipterans and beetles were also found to be most abundant arthropod groups in arable areas (Duelli, Obrist & Schmatz 1999; Fig. 1). Our results are similar to those of Poulsen (1993) and Poulsen, Sotherton & Aebischer (1998), who found spiders, beetles and soft-bodied larvae of Lepidoptera, Hymenoptera and Diptera to be the most numerous food items. However, they contrast in some respects with the findings of Jenny (1990) who presented results from a grassland-dominated landscape in the Swiss Plateau. He found more dipterans and grasshoppers, but fewer spiders and beetles. Indeed, more than half of the food items collected by Jenny (1990) were dipterans, mainly craneflies (*Nephrotoma* ssp.) and Stratiomyidae (*Geosargus iridatus*) which are mainly abundant in grassland but not in arable habitats.

Jenny (1990) and this study found evidence for a decrease in the abundance of spiders and an increase of dipterans from early to late broods, which partly contrasts the abundance data presented in Fig. 1. In dense vegetation the prey accessibility is lower than in open vegetation, though the abundance may be higher (Odderskær *et al.* 1997); i.e. spiders living on soil (i.e. Lycosidae) are very conspicuous in the early season when vegetation is sparse, but less when vegetation grow up. Additionally, we are not fully concern that the seasonal variation in arthropod abundance sampled in 1992 also occurred in the two study years 5 and 6 years later.

Coleopterans are important prey items in arable used land (Poulsen, Sotherton & Aebischer 1998; this study), whereas in areas with a higher proportion of grassland they become insignificant (Jenny 1990). He concluded that beetle imagines are less profitable as the handling time is high (head and wings are cut off) and the digestibility is lower than by soft-

bodied prey; therefore skylarks should only hunt beetles when they are soft-bodied and frequent. Beetles may become profitable in arable used areas, because of a lack of more valuable prey with a high digestibility, such as soft-bodied larvae (Poulsen 1993). Digestibility, energy content and concentrations of essential nutrients determine the quality of a food item (O'Connor 1984). The widespread use of insecticides can lead to a shortage of the preferred food items (Potts & Vickermann 1974; Moreby & Aebischer 1992; Sotherton & Moreby 1992) and adult birds must compensate for this by taking less desirable food, which may heavily influence reproduction (Elmegaard *et al.* 1998).

Although pitfall traps are not completely appropriate in assessing lepidopteran abundance, our data are similar to those of Jenny (1990); relatively more Lepidoptera were found in the diet compared to arthropod samples either with pitfall traps and D-vac. This indicates, that skylarks search actively for these mainly large, soft-bodied and therefore profitable prey.

Although the territory composition, e.g. presence or absence of wildflower strips, explain a significant part of the variation in the diet composition, the differences between these two territory types are less noticeable. Possibly because the proportion of wildflower strips is too small, only 6% in these territories with this habitat; and only in a few broods neck collars could be used in those territories with wildflower strips. Striking is, that skylark nestling diet is less divers in territories with wildflower strips though various authors found evidence that wildflower strips are richer in both number and diversity of arthropods (Bürki & Hausammann 1993; Lys 1994; Lys & Nentwig 1994; Frank & Nentwig 1995; Kramer & Nentwig 1995; Kramer 1996; Nentwig 1996). But it must be taken into account that not all studied arthropod groups are available for skylarks. Neck collars were used on average three weeks earlier in territories with wildflower strips than in those without, which possibly explain a part of the differences. Otherwise, food was as abundant that skylarks could search for more profitable items (i.e. spiders, grasshoppers). Skylarks may primarily profit from a higher arthropod abundance, but only if they are accessible e.g. in a heterogeneous vegetation with gaps. The arthropod diversity is possibly less important as skylark diet consist mainly of spiders, beetles and dipterans. During harsh weather

conditions, mainly rainy and cold periods in April and May, there is the risk to die of starvation apparently higher and in such conditions nestling growth is faster when the parent territory include wildflower strips (Chapter 2). Therefore, the higher arthropod diversity in wildflower strips may be important as there more arthropods are accessible in unfavourable weather.

This study confirms that skylarks are not specialised predators, which can adapt their food selection to the abundance of potential prey (Jenny 1990; Poulsen, Sotherton & Aebischer 1998). Parent birds also appear to be flexible in their food selection according to the age of the nestlings; for example, we found a decline in the relative importance of spiders and lepidopterans and a corresponding increase in the proportion of beetles between a nestling age of 4 and 7 days. Poulsen, Sotherton & Aebischer (1998) found evidence, that soft-bodied prey were more often fed to young nestlings than to older ones. These finding could not be confirmed; in here presented study, there was an increasing proportion of larvae, mainly Coleoptera, in the diet for older nestlings, reflecting possibly the general tendency towards larger prey items.

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Chapter 4

Predation from artificial nests in an intensively used arable landscape

Summary

Artificial nests have been used to investigate the predation of bird eggs in many types of habitats. However, there have been few studies of farmland birds in open agricultural landscapes, even though rates of nest predation are often very high amongst species such as skylark and grey partridge.

An artificial nest experiment was carried out with real and artificial eggs in two areas of intensive arable use in northern Switzerland. Nests were placed in five different crops at three different distances to the field border over a period of two years. In a parallel study in one area, the breeding success of skylarks was investigated, so that direct comparisons can be made between data for skylark nests and artificial nests. One aim was to identify predators responsible for egg losses and another to investigate how the predation rate differ between crops, nest locations within a field, areas and years

The daily survival probabilities of artificial nests increased significantly from the first week of exposure (0.829 ± 0.004) to the second (0.943 ± 0.004) and third (0.962 ± 0.004). Survival ranged from 3.3 ± 13.2% in maize to 28.8 ± 3.6% in winter wheat and differed also between areas and years, but not in relation to nest locations within a field. In general there was a higher probability of predation where the vegetation was both sparse and low.

The importance of different predator groups varied according to crop type, region, year and vegetation structure. Eggs were completely destroyed or removed in 60% of the predated nests; we strongly suspect that these nests were predated by larger mammals. The predation rate by the various predators differed between the crop types, year, and area.

Predation by small rodents was i.e. highest in wildflower strips and winter wheat in both areas in 1996, whereas in the other cases all eggs were completely removed. Corvids were mainly restricted to vegetation below 60 cm.

Success probabilities of skylarks nests were generally higher than that of artificial nests; especially in grassland, sugar beet, and maize where artificial nests were placed in too low and sparse vegetation for nesting skylarks. The experiment showed the difficulties in assessing success probabilities from artificial to bird nests. Data were only reliable when artificial nests were placed in each similar vegetation, same area and year.

Keywords: edge effect, Klettgau, Mayfield method, skylark, vegetation structure, wildflower strips

Introduction

Experiments using artificial nests have often been used to investigate how predation rates of bird eggs vary in relation to factors such as egg characteristics, clutch size and the density and location of nests within the landscape (reviews see Andrén 1995; Major & Kendal 1996). An advantage of using artificial nests is that it facilitates the identification of the predators because the eggs can be fixed to the nest and any marks left by the predators can be studied (Andrén 1995; Martin 1993). However, it remains controversial whether the data from such experiments have any relevance for predation from real nests (Martin 1987; Stooras 1988; Willebrand & Marcström 1988; Major 1990; Roper 1992; Haskell 1995a, b; Major & Kendal 1995; Yahner & Mahan 1996; Butler & Rotella 1998; Marini & Melo 1998; Ortega *et al.* 1998; Wilson & Brittingham 1998).

Experiments with artificial nests in open landscapes have mostly concerned either duck or wader species in grassland habitats (Baines 1990; Berg, Nilsson & Boström 1992; Berg 1996; Pasitschniak-Arts & Messier 1995). Only Schultz (1991) has investigated predation in an open agriculturally used landscape, simulating nests of skylark *Alauda arvensis*, pheasant *Phasianus colchicus*, and grey partridge *Perdix perdix*. Although predation is known to be an important cause of nest failures for ground-nesting farmland birds including

skylark (Schläpfer 1988; Daunicht 1998; Donald *et al.* 1998; Chamberlain & Crick 1999; Weibel *et al.* in prep.), and grey partridge (Potts 1980; Pegel 1987; Aebischer 1997), it is not thought to be the main cause of recent dramatic declines in populations of these species (Tucker & Heath 1994; Hagemeijer & Blair 1997; Chamberlain & Crick 1999; but see Tapper, Potts & Brockless 1996).

Arable land commonly consists of a mosaic of fields containing different crops, often separated by linear structures such as tracks, field boundaries, and hedges. It has been shown that the predation of skylark nests is influenced by crop type, as a result of differences in vegetation structure or the abundance of prey (Jenny 1990; Donald *et al.* 1998; Chapter 1). Since many predators tend to move along linear structures such as tracks and the borders between fields, we might expect a higher rate of predation from nests close to field borders. Indeed, this tendency has been demonstrated for skylarks by Daunicht (1998), Donald *et al.* (1998) and in Chapter 1.

In Switzerland, current agricultural policy subsidises the maintenance of various kinds of "ecological compensation areas" which are intended to enhance wildlife. In arable land, wildflower strips are particularly important. These are strips of land 3-10 m wide sown with mixtures of selected annual arable weeds, biennials and perennial grassland forbs. In the study area in northern Switzerland, a major scheme was commenced in 1991 to introduce large numbers of wildflower strips into a region where agriculture is intensive. The main aim of this scheme, which was promoted by the Swiss Ornithological Institute Sempach and the canton authorities, was to sustain the vanishing population of grey partridges (Jenny *et al.* 1997; Jenny, Weibel & Buner 1999). Research has shown that these strips were also attractive nesting sites for skylarks, though breeding success was lower than in cereals and root crops (Chapter 1).

The work described here had three main aims. Firstly, we wished to identify the predators responsible for artificial nest losses in arable fields. Secondly, we wanted to investigate whether predation rates differ in the various crop types and in wildflower strips as well as in two area which were differently enhanced. Finally, we was interested in how predation rate was affected by the location of a nest with respect to linear structures such as field

boundaries and wildflower strips. The study was carried out over a two-year period in two separate areas in the same region. Throughout the period, the breeding success of the skylark population in one study area was investigated (Chapter 1), which allowed us to compare directly the results from artificial and real nests.

Study sites and methods

Study sites

The study was carried out during 1996 and 1997 in two sites in the Klettgau region of northern Switzerland (Canton Schaffhausen; 47°42' N, 8°30' E; 400-470 m a.s.l.). This is a low-lying, flat area which represents a former floodplain of the Rhine. It is intensively used for agriculture. The fields are mainly small (<1 ha) and the crop diversity is high (15 crop types), though winter cereals are particularly important. The few semi-natural elements in the landscape include trees and hedges which grow mainly beside the straightened stream channels and the railway line. The climate is relatively warm and dry (8.5 °C annual average; 915 mm annual average precipitation; 1931-1990; climate station Hallau, situated between the two study areas).

Widen

The connecting roads between the villages of Neunkirch, Gächlingen, Siblingen and Löhningen form the boundary of the Widen study area (5.3 km²). The arable land occupied 453 ha and consisted of cereals 47%, root vegetables and oil seed 29%, maize 9%, intensively used grassland leys 7% and vines 1%. The area of set-aside (Grünbrachen) is relatively high for the Swiss plateau (3%), reflecting the low fertility of the soils in this area which encourages farmers to take set-aside payments rather than planting crops. The area of ecological compensation sites was 19 ha (4%), of which 6.3 ha (1.4%) were wildflower strips.

Plomberg

The study site Plomberg (4.7 km^2) is located 6 km west of the Widen area, and lies between the villages Wilchingen and Trasadingen and the national border to Germany. The area used for arable agriculture covers 419 ha, including 42% cereals, 28% root vegetables and oil seeds, and 12 % maize. The proportion of intensively used ley-grass was higher than in the Widen area (14%), but that of set-asides was lower (<1%). There were 13 ha of ecological compensation sites (3%), of which only 0.8 ha (0.2%) were wildflower strips, which is particularly lower than in the Widen area.

The length of boundary lines, i.e. between crops or between tracks and crops, was shorter in the Plomberg area (26 km/100 ha) than in the Widen area (30 km/100 ha); also the length of linear structures, e.g. structures less than 10 m wide, such as wildflower strips, hedgerows, and banks (Jenny *et al.* 1997).

Predators

The densities of predators were estimated by counting them in nights in March with spotlights. The density of red foxes *Vulpes vulpes* was higher in the Plomberg area (3.5 km^{-2}) than in the Widen area (2.1 km^{-2}), though the density of occupied dens was similar (0.7 km^{-2}). Badger *Meles meles* could inadequately be counted (0.1 km^{-2} in both area); the density of occupied sets was higher (Plomberg 0.5 km^{-2}; Widen 0.2 km^{-2}). The density of martens *Martes foina* was similar in each area (0.2 km^{-2}). Other predator species such as ermine *Mustela erminea*, polecat *M. putorius*, and weasel *M. nivalis* were present in both areas.

The mouse-hole density in winter 1996-1997 was slightly higher in the Plomberg area than in the Widen area (Buner 1998).

Two corvid species with similar density of breeding pairs (1.1 km^{-2}) were present in the study area, crows *Corvus corone corone* and Magpies *Pica pica*. Large flocks of 50-100 individuals of premature and unmated crows were often seen in both years in the Widen area, whereas in the Plomberg areas smaller flocks were only observed in 1997.

Methods

Each study area was subdivided into six sections of approximately equal size. In each section three fields each of winter wheat, grassland, maize, and sugar beet were selected. One nest was located in each field, but the distance of the nests from the nearest field boundary (i.e. the distance to another crop type) was varied for the three replicates of one crop. One nest in each crop type was located within a 5 m square 0-5 m from the boundary, one at 15-20 m, and one was at 30-35 m. In addition one nest was placed in a wildflower strip; because the strips are less than 10 m wide, the distance from the boundary could not be varied. All nests were located at the same distance (25-30 m) from a track. In total there were 156 nests (2 study area x 6 sections x (4 crops x 3 distances + 1 wildflower strip) = 156). The locations of nests were marked with two sticks which were slightly higher than vegetation and were placed 5 m from the nest, one of them aligned with the furrow and the other perpendicular to it.

Three different types of 'egg' were used in the experiment. One was a fresh quail egg. This has been used in similar studies, although it's use has been criticised because small rodents may be unable to break the shell (Haskell 1995a, b). The second egg type was a quail egg filled with paraffin wax. This had the advantage that the predators could be identified from the marks they left on the egg as the egg could be fixed to the substrate by a small wire. The third type was a brown plaster egg which was coated with paraffin and of the same size as a skylark egg. In the first year one egg of each type was placed in each nest. In the second year the use of plaster eggs was abandoned because they were very time consuming to make and good results were obtained using the other two egg types. Although rodents were unable to use the quail eggs, they could break the paraffin-filled quail eggs because the shell had been weakened by the small hole through which the wire was fixed. Therefore in the second year one fresh quail egg and two eggs filled with paraffin were used in each nest. The nests themselves were small depressions of 10-15 cm diameter dug with a trowel and padded with dry grass.

In 1996, the experiment started on 14 May and lasted until 16 July. In 1997, the first nests were constructed on 1 May in wildflower strips, grassland, and winter wheat, and on 11 June in maize and sugar beet; all nests were removed on 23 July. Nests were checked after seven days, and those which had been destroyed were replaced within the square of 5 x 5 m², but not in the same nest bowl. A nest was recorded as "successful" when it was not destroyed during a period of three weeks. The successful nests were removed and a new one was built within the same 5 x 5 m² square. Three weeks were chosen to simulate nests of grey partridges. This species vanished a few years ago in the study area and for which a reintroduction project has been started in 1998. The weekly nest control allowed also to give estimates for skylark nests; as a two-week period is similar to the laying and incubation phase of skylarks, for which the breeding success was studied in detail in the same region and year (Chapter 1).

In an area of 1 m² around each nest, the vegetation height was measured to the nearest 5 cm and the vegetation cover was estimated to the nearest 5%. Rubber gloves and boots were worn when the nests were constructed and revisited, and care was taken to minimise damage to the vegetation.

All damaged eggs were collected and any marks on the egg shell or in the paraffin were studied in an attempt to determine the predator. It was found that different predators left characteristic marks which could often be identified with the help of a reference collection of skulls. In practice, not all predators could be identified to the species level, and so the following predator groups were distinguished: rodents (*Microtus arvalis, Apodemus sylvaticus, A. flavicollis*), corvids (*Pica pica, Corvus corone corone*), larger mammals (*Vulpes vulpes, Meles meles, Martes foina, Mustela erminea, M. putorius, Erinaceus europaeus*). A final group contained those nests for which the predators could not be identified, either because there were no determinable marks or because the eggs had been completely removed.

The data of nest losses have been analysed in two ways. Firstly, daily survival probabilities (DSP's) were calculated for each nest in a given area, crop types and distance to the field boundary using the method of Mayfield (Mayfield 1961, 1965; Hensler 1985;

Sauer & Williams 1989; Aebischer in press). Nests which were destroyed by farming operations or which could not been re-found were excluded from these analyses. The weekly survival probabilities were calculated as DSP[7], and the survival probabilities for the three-week period were calculated as the product of the three weekly survival probabilities. To compare rankings of survival probabilities Kendall's coefficient of concordance and Wilcoxon signed rank test was used (Sokal & Rohlf 1995).

Secondly, the proportion of nests predated was calculated both on a weekly basis and for each season. For testing the possible effect of vegetation structure on the proportion of predated nests, the vegetation height and cover of predated and non-predated nests was pairwise compared on a weekly basis for the various crop types (paired t-test; Sokal & Rohlf 1995). Log-linear models were used to analyse multi-way tables of the proportion of nest predated by the various predator groups. Analyses of variances were used for testing of differences in predation rate of the predator groups according to vegetation structure.

Additionally, the success probabilities of all artificial nests for a two-week period were compared with hatching probabilities of real skylark nests. Breeding success of skylarks was studied in the Widen area in 1995-1998 (Chapter 1). As the breeding success in 1995 was similar to that in 1996 and 1997, the data in 1995 were added to increase the sample size, which then allowed to separate the data for the different crop types, similar to that of the artificial nests. For the calculations of skylarks' hatching success a 14 day egg period was assumed (4 eggs, laying each day, 11 days incubation starting on the day the last egg has been laid). The data therefore correspond to the survival probabilities over the two-week period of the artificial nests.

Results

A total of 1914 artificial nests were constructed in both areas over the two-year study period. Of these 78% were predated, 8% were destroyed by farming practices, 1% could not be re-found, and only 13% were not attacked or destroyed during the three-week

period of exposure. The losses of nests caused by farming operations occurred mainly in grassland (80%) and occasionally in sugar beet (11%) and maize (9%).

In total, 1503 artificial nests were predated; 74% were attacked in the first week of exposure, 39% of the remaining nests in the second, and 13% of the remaining in the third. Thus, the daily survival probabilities (DSP's) of the artificial nests increased greatly during the three weeks of exposure (first week $0.829 \pm 0.004 \ll$ second week $0.943 \pm 0.004 \ll$ third week 0.962 ± 0.004; z-test; $\ll$, $P < 0.001$).

Effects of crop type, area, and year

The factors affecting DSP were investigated by multi-way comparisons (Aebischer in press) with study area, year, and crop type as the main effects for each week of exposure; the weekly separation was necessary because the DSP's differed significantly. In the first week of exposure, all terms except the interaction *area x year x crop type* reached significance. An extremely high deviance D was found for the crop effects. Only the crop effect was significant in the second week, while for the third week none of the factor showed a significant effect (Table 1).

In both years, the success probabilities over the three weeks of exposure did not differ between the two areas (1996, $z = 0.08$; $P > 0.9$; 1997, $z = 1.25$; $P > 0.2$; Table 2). Striking is the increase of the success probability in the Widen area in 1996 to 1997, whereas it decreased especially in wildflower strips and winter wheat in the Plomberg area. Taken the data for both areas and years together, the success probability was not equal between the crop types ($\chi^2 = 13.0$; $d.f. = 4$; $P < 0.02$). Nests in winter wheat had the highest success probabilities followed by those in wildflower strips, grassland, sugar beet and maize; this ranking was consistent between the areas and years ($W = 0.91$; $d.f. = 3$; $P < 0.005$).

Table 1: Factors affecting predation risk of artificial nests; Effect test of the three-way classification of the daily survival probabilities of nests, which were predated in the first, the second, and the third week of exposure respectively. The main effects were: year (1996, 1997), area (Widen, Plomberg), and crop type (Wildflower strip, winter wheat, grassland, sugar beet, maize); The deviance D is χ^2-distributed.

Effect	d.f.	Week 1		Week 2		Week 3	
		D	P	D	P	D	P
Main effects							
Year	1	7.8	< 0.01	0.6	n.s.	0.3	n.s.
Area	1	7.2	< 0.01	0.1	n.s.	2.5	n.s.
Crop type	4	186.2	< 0.0001	15.6	< 0.005	5.0	n.s.
Interactions							
Year x Area	7	7.5	< 0.01	1.4	n.s.	0.3	n.s.
Year x Crop type	4	17.2	< 0.005	0.8	n.s.	0.4	n.s.
Area x Crop type	4	20.6	< 0.001	1.9	n.s.	1.0	n.s.
Area x Year x Crop type	7	7.4	n.s.	1.9	n.s.	3.9	n.s.

Table 2: Success probabilities (%) over three weeks of exposure of artificial nests placed in five crop types in two study areas in 1996 and 1997. Success probability was calculated as $DSP_{week1}^7 * DSP_{week2}^7 * DSP_{week3}^7$; standard deviation according to Hensler (1985).

	Plomberg		Widen		
	1996	1997	1996	1997	Mean
Wildflower strips	34.1 ± 13.5	10.6 ± 17.4	25.4 ± 16.2	40.1 ± 9.2	24.5 ± 6.8
Winter wheat	31.5 ± 8.4	19.0 ± 7.5	35.8 ± 6.9	35.2 ± 6.3	28.8 ± 3.6
Grassland	15.1 ± 10.7	8.4 ± 12.1	10.9 ± 12.5	11.0 ± 10.0	11.0 ± 5.7
Sugar beet	5.6 ± 15.5	8.0 ± 18.2	9.1 ± 12.8	24.8 ± 9.3	9.8 ± 6.3
Maize	3.6 ± 21.9	1.4 ± 34.8	3.2 ± 24.7	5.8 ± 27.4	3.3 ± 13.2
Mean	12.6 ± 5.3	10.1 ± 5.7	13.2 ± 5.0	18.8 ± 4.0	13.5 ± 2.5

Effects of nest location

The influence of nest location within fields on the success probability over the three-week period was tested separately for each crop type, area and year. In none of the crop types was there any evidence that the success probability depended upon distance from the edge of the field. Even in only 19% of all cases, nests at closest distance to the field border had the lowest success.

Effects of vegetation structure

The vegetation associated with predated nests tended to be both shorter and of lower cover than that associated with nests which escaped predation. The differences in height and cover of vegetation were significant for all crop types except winter wheat, for which neither height nor cover differences were significant, and wildflower strips where only the difference in cover was significant (Fig. 1). In fact, cover and height were closely correlated with correlation ranging from $r_s = 0.39$ in wildflower strips to $r_s = 0.95$ in sugar beet. Overall the proportion of nests predated was more explained by cover than by height (cover $\chi^2 = 198.1$, $d.f. = 1$; $P < 0.001$; height $\chi^2 = 5.6$; $d.f. = 1$; $P = 0.02$).

Comparison of the 'success' of artificial nests and skylark nests

The success probabilities of skylark nests in grassland and sugar beet were in most cases significantly higher than that of the artificial nests; also in maize and winter wheat but these differences did not reached significance except in one case. Only in wildflower strips, artificial nests reflected the hatching probability of skylark nests (Fig. 2).

Predators

In 60% of the artificial nests all eggs were either removed or totally destroyed, making it impossible to identify the predators. Since the plaster eggs, and those filled with paraffin, were fixed to the substrate with a thin wire, they could not have been removed by corvids

or small rodents; this possibility was tested with crows in a cage. We assume that these nests were predated by larger mammals such as foxes or badgers. In a further 14% of the cases (220 nests) we found clear evidence that nests had been predated by larger mammals (foxes 142 nests; foxes or badgers 37 nests; badgers 28 nests; mustelids 10 nests; hedgehogs 3 nests). Another 14% of the nests were predated by corvids and 12% by small rodents.
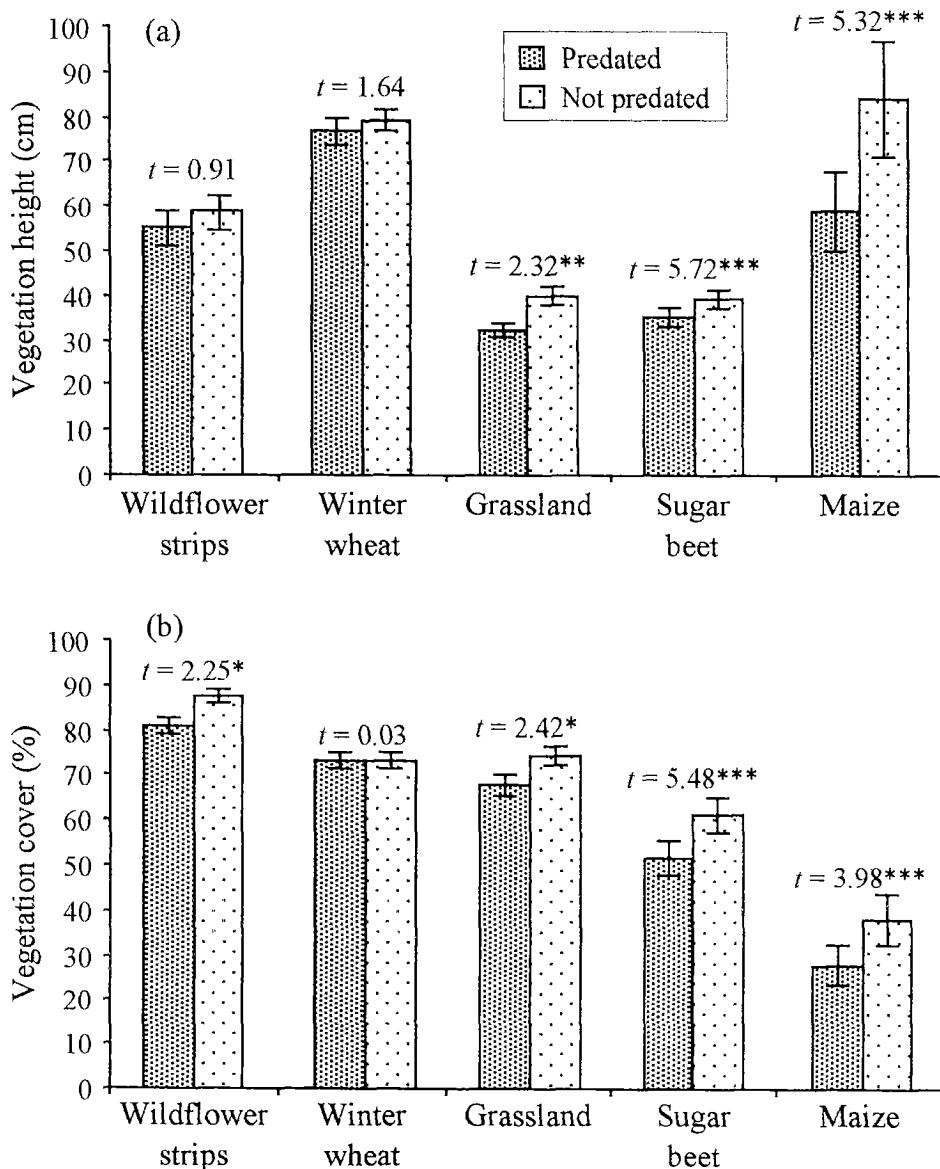

Fig. 1: Effects of vegetation structure on the predation risk of artificial nests; vegetation height (a) and cover (b; Mean ± SE) of predated and not predated artificial nests separated for the different crop types. Paired comparisons on a weekly base; t-test; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
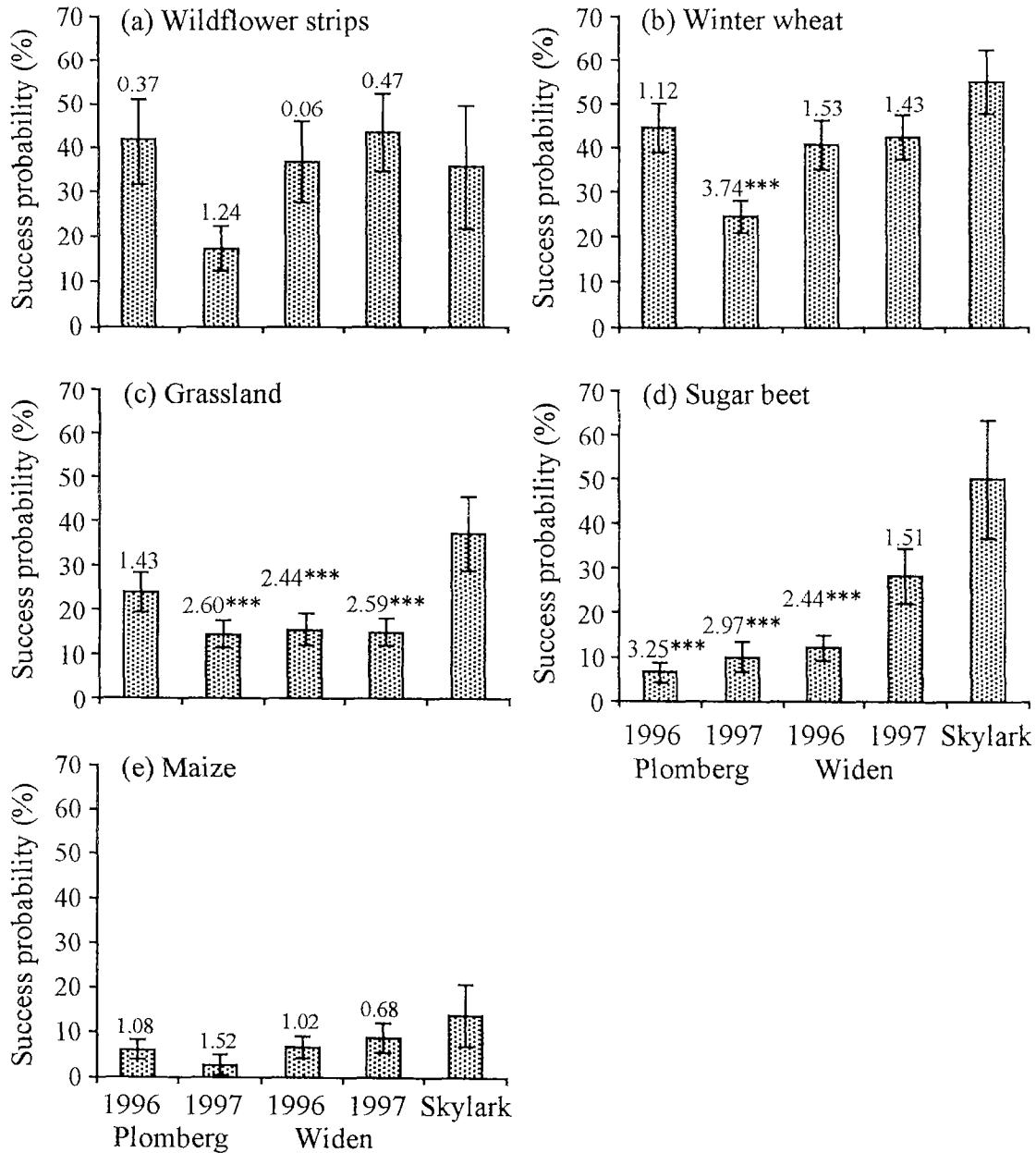
Fig. 2: Comparison of the hatching probabilities (Mean ± SE) of skylark nests with the success probabilities of artificial nests for a two-week period in the two study areas in 1996 and 1997 and separated for the different crop types; numbers are z-values; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

The intensity of predation by the various predator groups differed between the crop types, and also between years and areas (Fig. 3). A log-linear model revealed that both interaction terms *year x crop* ($\chi^2 = 81.3$; *d.f.* = 6; $P < 0.0001$) and *year x area* ($\chi^2 = 219.9$; *d.f.* = 24; $P < 0.0001$) were highly significant, indicating the predation pressure by the various predator groups varied between both year and crop, area and year respectively. In both years, the proportion of nests predated by rodents and corvids was higher in the Widen area than in Plomberg area. In the Widen area, the proportions taken by larger mammals and unidentified predators were correspondingly smaller. In both study areas, more nests were predated by rodents in 1996 than in 1997, but fewer by unidentified predators. In addition fewer nests were predated by corvids and larger mammals in the Widen area in 1996 than 1997, while in the Plomberg the proportion of predated nests by these two groups remained constant. Small rodents were the most frequent predators in wildflower strips and winter wheat in 1996 in both areas, while in all other cases the predator for the majority of nests remained unknown.

Within the crop types, vegetation height and cover influenced the predation rate of the various predator groups (Fig. 4). One obvious trend in the data was that corvids were restricted to those sites with short and low vegetation. For the other predator groups there was little evidence that cover or height of vegetation influenced the intensity of predation in a consistent way.

For each predator group, the predation rate in the different crops was independent of the nest location (all $G < 8.9$; *d.f.* = 6; $P > 0.1$).
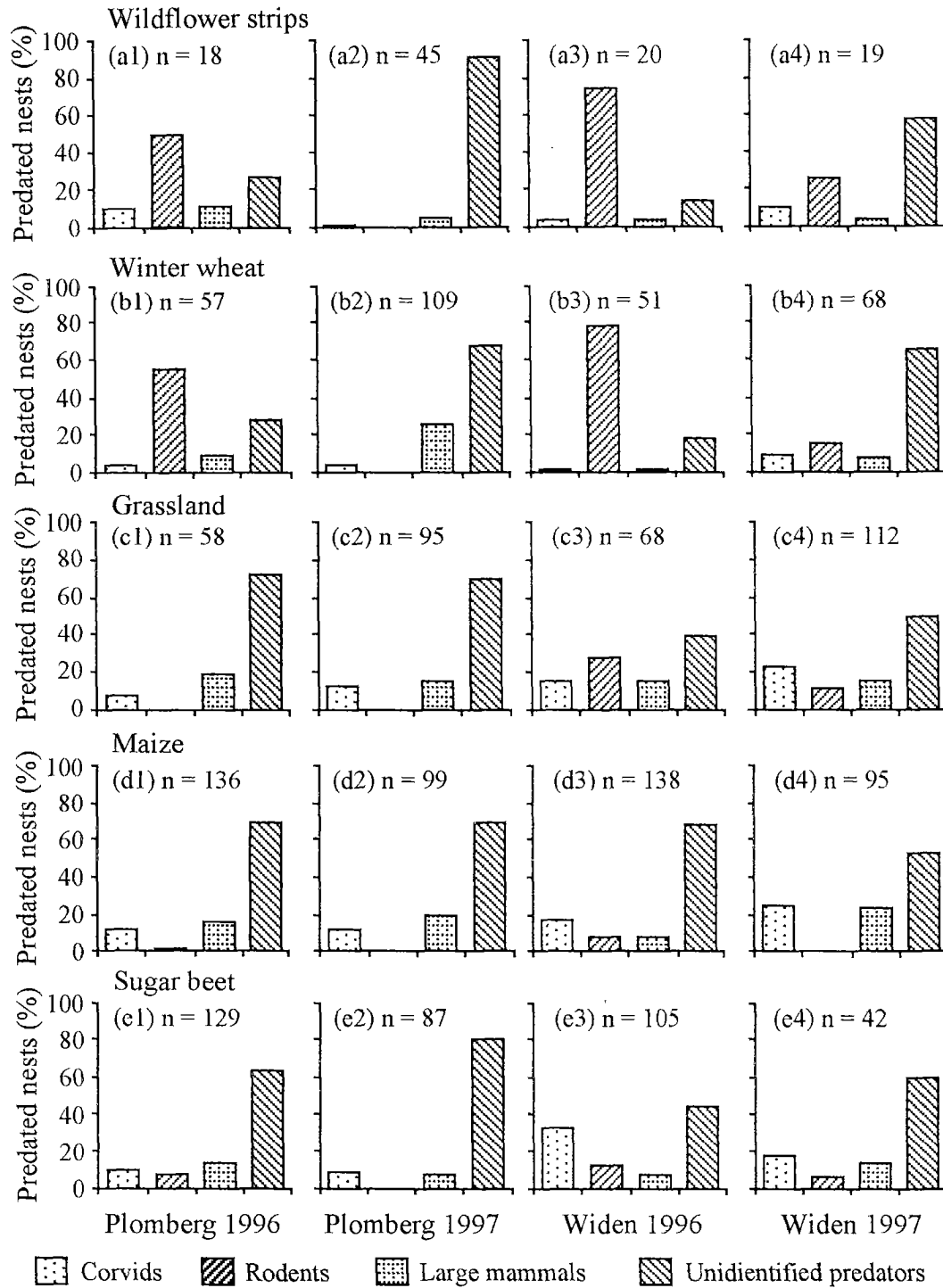
Fig. 3: Differences in the predation rate (% of predated nests) by the various predator groups in the five crop types, two study areas in 1996 and 1997.
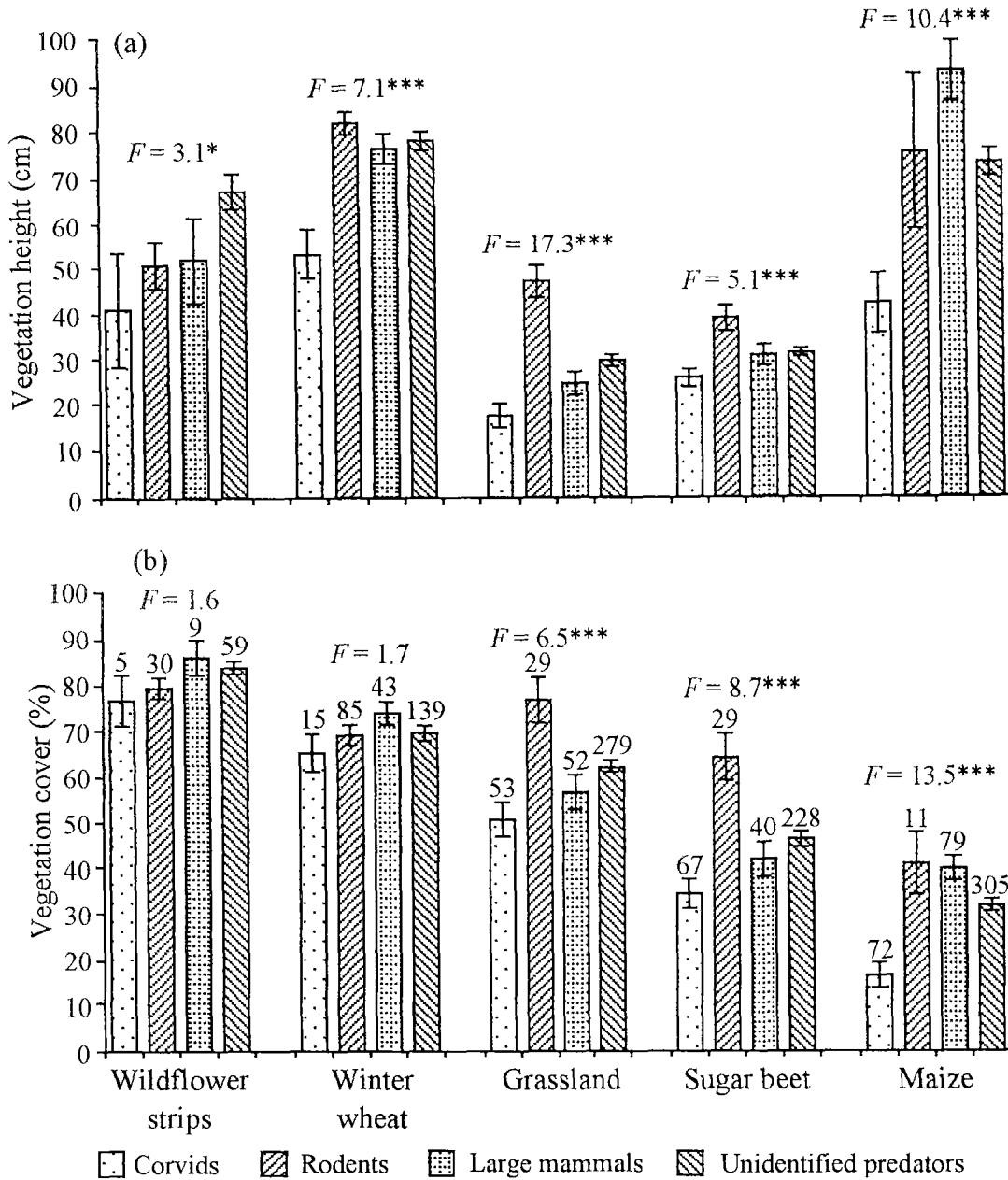
Fig. 4: Influence of vegetation structure on the predation rate of the various predator groups. Vegetation height (a; Mean ± SE) and cover (b; Mean ± SE) of the crop types separated for the predator groups; One-way ANOVA; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; Number of nests are given in figure (b).

Discussion

The high predation rate in the first week of exposure, and the consecutive decrease in the predation rate suspects that the construction of the artificial nests attracted predators, perhaps because of the scent produced due to the paraffin-filled eggs or by the disturbance of the vegetation associated with the nest construction. Predator species are known to be able to remember nest sites and also to locate nests from human activities (i.e. corvids, Sonerud & Fjeld 1987; Gotmark, Neergard & Ahlund 1990). However, the temporal predation pattern could not be explained in terms of trained individuals returning to artificial nests. Evidence was found occasionally (pers. observations), that the temporal predation pattern is also valid within the first week of exposure, e.g. most nests were predated shortly after their construction and the nest sites were therefore no more attractive for predators for several days.

The variation in breeding success and also in the importance of the various predator groups between the study areas, years and crop types is a striking feature of the data. There was no evidence, that predation pressure was higher in the Widen area, which has more wildflower strips and other linear structures as well as boundary lines, than in the Plomberg area. There, the success probability was higher in 1996 than 1997; especially in wildflower strips and winter wheat. Only nests in sugar beet contrast this trend; the slight increase in the success probability may be explained by the later beginning of the experiment, so that the nests were better concealed by vegetation. Probably badgers, perhaps only one or two individuals, caused many of the nest losses in the Plomberg area in 1997; telltale signs were often found nearby the nest, such as heavily damaged vegetation and latrines. A different and less distinct pattern was found in the Widen area, where success probabilities were similar in the two years, except in the case of sugar beet, wildflower strips and maize, where survival was higher in 1997. For nests in sugar beet and maize, this was also probably because of the later beginning of the experiment in the second year.

The increase in the success probabilities in wildflower strips in the Widen area from 1996 to 1997 may be linked with a collapse in small rodent density caused by harsh winter

conditions, which could be confirmed by counting occupied mouse-holes between October 1996 and March 1997 by Buner (1998). Small rodent were apparently more affected in the Plomberg area than in the Widen area, probably due to different soil types.

Skylarks can achieve a high breeding success in winter cereals (Donald & Vickery in prep.; Chapter 1); and it has been suggested that cereal fields are generally not attractive for predators because of a low prey abundance. However, this suggestion is contradicted by our findings with artificial nests. We observed a strong temporal pattern, with small rodents causing most nest losses when grains were available, e.g. from mid-June when vegetation is clearly too high for nesting skylarks.

In each year, corvids predated more nests in the Widen area than in the Plomberg area, reflecting that flocks of crows were larger and more common in the Widen area. Schultz (1991) also found differences in the relative importance of predator groups in different crop types; corvids were restricted to low and sparse vegetation such as there in winter wheat and oilseed rape field after harvesting, or in recently cropped ley grass or newly germinated crops (this study).

For the majority of nests, the predators could not be identified because the eggs had disappeared completely. As neither corvids nor rodents could have removed the eggs fixed by wire, and also because the vegetation structure associated with nests predated by the unknown predators was different from that of those predated by corvids (Fig. 4), we assume that most of the unidentified predators were in fact larger mammals such as canids or mustelids. If this assumption is correct, then large mammals were the most important nest predators, and corvids as well as rodents were of minor importance. Other work has also shown that large mammals including wild boar, badger, and foxes are the most important nest predators in an open agricultural used region (Schultz 1991).

The degree of concealment of nests is known to affect the rate of predation (Major & Kendal 1996). In general, nests located in denser vegetation suffer lower predation rates than those in more open sites (Bowman & Harris 1980; Yahner & Scott 1988; Møller 1989; Matessi & Bogliani 1999), a finding which is confirmed in this study. The search efficiency

of predators is lower in higher and denser crops and some predators, such as corvids are unable to search for food in such areas. Huhta, Jokimäki & Helle (1998) have pointed out the difficulties of assessing the visibility of nests to different predators. In our case the measured vegetation parameters - height and cover - proved to be useful measures of vegetation structure, possibly because nearly three-quarters of the nests were predated by larger mammals.

In contrast to studies with skylark nests (Daunicht 1998; Donald *et al.* 1998; Chapter 1), the experiment with artificial nests provided no evidence that nesting success is affected by the distance from a field edge. This may be a result of a bias associated with artificial eggs; for example, the scent of eggs filled with paraffin is possibly so strong that a nest in 30 m distance from a field border can easily be located by predators from the field border.

There was some evidence that foxes use wildflower strips and field boundaries as travel lines and hunting sites (from cameras set up to document the night activities; unpubl. data). The differences in vegetation structure could also partly explain the generally higher levels of predation observed in this experiment than for skylarks. In grassland, sugar beet, and maize, the particularly higher predation rate of the artificial nests is possibly caused by nest construction in low and sparse vegetation - in grassland immediately after mowing, in sugar beet and maize in the first week after germination - which is not used by skylarks for nesting. The differences in winter wheat are possibly caused by the extended experimental period, with a higher intensity of predation by small rodents later in the season when seeds are available. Differences in success probabilities between skylark and artificial nests are biggest in the Plomberg area in 1997. As we have no surveyed skylark nests in the Plomberg area, we can not be certain whether the observed decrease in success probability is a bias in the method or a real trend. This points out the difficulties in assessing success probabilities of birds from artificial nests; it may be valid when vegetation structure and type, the time of nesting, the year and the area are similar. In addition, nest density and egg characteristics should also be taken into account (Major & Kendal 1996). Few data are available concerning the importance of different predator species as predators of skylarks nests. Evidence was rarely found for nest predation by small rodents, as in nearly all cases

eggs and nestlings disappeared completely without any signs, such as egg shell fragments. I suggest that canids and mustelids are the most important nest predators, because the risk of predation was found to be higher during nestling stage than during incubation and egg laying and furthermore nests close to a field border suffer higher predation risk (Chapter 1).

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