PALACKÝ UNIVERSITY OLOMOUC

FACULTY OF SCIENCE

DEPARTMENT OF ZOOLOGY AND LABORATORY OF ORNITHOLOGY

Effects of nest predators on ground nesting birds in intensively used arable fields

Ph.D. Thesis

Libor Praus

Supervisor: doc. Mgr. Karel Weidinger, Dr.

OLOMOUC 2015

BIBLIOGRAFICAL IDENTIFICATION:
Author`s first name and surname: Libor Praus
Title: Effects of nest predators on ground nesting birds in intensively used arable fields
Type of thesis: Ph.D. Thesis
Department: Department of Zoology and Laboratory of Ornithology, Palacký University
Supervisor: doc. Mgr. Karel Weidinger, Dr.
Study programme: P1527 Biology
Study field: Zoology
Year of presentation: 2015

Abstract

Agricultural intensification may increase an impacts of predators on the reproductive performance of declining populations of farmland birds. Still, there is little definitive evidence of nest success and predator identity in intensive arable fields. In order to clarify whether nest predators really contribute to declines in farmland ground nesting birds, I used video-monitoring to identify nest predators and quantify nest success in the Skylark (*Alauda arvensis*) and Lapwing (*Vanellus vanellus*). Both species share common nesting habitats in sparsely vegetated arable fields, but their life histories suggest different vulnerabilities to nest predation. Results showed very low nest success in the Skylark, but relatively high success in the Lapwing. Skylark nests were vulnerable to all local predators, while it seems that Lapwings can avoid avian predators. The species composition of predators and patterns in nest predation rates mostly differed from those reported from Western Europe.

Because of expected differences in predator identity and nest survival among nesting habitats and regions, I further quantified nest success and identified nest predators for a high-density population of Skylarks as well as Woodlarks (*Lulllula arborea*) breeding in more natural heath and grassland habitats in the Netherlands. Populations of both species co-occur in this area and their nests are similar targets for local predators; even so their nest predators might differ, because these larks differ in the selection of their nest sites. My results suggest that Skylark nests located in open sites were preyed upon mainly by red foxes (*Vulpes vulpes*), while the main predators of Woodlark nests, located generally closer to trees, were Carrion Crows (*Corvus corone*).

Changes in agricultural practices, especially shifts from spring-sown to autumn-sown crops, can limit the number of breeding attempts of Skylarks. Under these circumstances, Skylarks are forced to shift to different breeding sites or habitats. In spite of the seasonal shift in nest sites in my study, nest predation rates did not show a clear seasonal trend; however, the proportion of predation attributed to birds decreased along with vegetation growth. My results suggest that the recently increasing area of maize fields in particular provide an attractive, yet risky, nesting habitat for Skylarks, especially late in the season when autumn-sown crops are too dense.

Nest proximity to field edges may also have a negative influence on breeding productivity, with nests placed closer to edges experiencing higher rates of nest predation. I found that Skylarks seem to avoid areas close to field edges in spite of the comparatively low predation cost associated with nesting there.

Variation in nest predation risk during the breeding period may be an important source of natural selection on parental behaviour. Skylark females spent more time attending clutches in the early morning and evening, with more frequent recesses during the afternoon. Moreover, this diurnal variation was dependent on (i.e. interacted with) ambient temperature and vegetation characteristics at the nest site (height and concealment). This suggests that the way incubation time is allotted during the day may be equally as important as the total amount of time spent incubating.

Key words: nest success, nest predation, video-monitoring, *Alauda arvensis*, *Vanellus vanellus, Lullula arborea*, agricultural intensification, edge effect, incubation behaviour

Number of pages and appendices: viii + 43 pages, 6 appendices
Language: English

BIBLIOGRAFICKÁ IDENTIFIKACE:
Jméno a příjmení autora: Libor Praus
Název práce: Vybrané aspekty predace ptačích hnízd v intenzivních polních kulturách
Typ práce: Doktorská disertační práce
Pracoviště: Katedra zoologie a ornitologická laboratoř PřF UP v Olomouci
Vedoucí práce: doc. Mgr. Karel Weidinger, Dr.
Studijní program: P1527 Biologie
Studijní obor: Zoologie
Rok obhajoby práce: 2015

Abstrakt

Krajinné změny spojené s intenzifikací zemědělství mohou zvyšovat negativní vliv predace na hnízdní produktivitu ubývajících ptačích druhů zemědělské krajiny. Přesto dodnes chybí přesnější odhady hnízdní úspěšnosti a identity predátorů pozemních hnízd v intenzivních polních kulturách. V předkládané práci jsem si položil otázku, zda mohou predátoři ptačích hnízd přispívat k poklesu ubývajících druhů polních ptáků. Hnízdní úspěšnost a identitu predátorů jsem sledoval pomocí kontinuálního videomonitoringu. Za svůj hlavní modelový druh jsem si zvolil skřivana polního (*Alauda arvensis*) a doplňkově čejku chocholatou (*Vanellus vanellus*). Oba druhu sdílejí společné hnízdní prostředí v řídce porostlých polích, nicméně jejich odlišné životní styly naznačují rozdílnou zranitelnost hnízdní predací. U skřivaních hnízd jsem zaznamenal vysokou denní míru predace, naopak hnízdní úspěšnost čejek byla relativně vysoká. Skřivani byli zranitelní všemi přítomnými predátory, zatímco čejky svá hnízda dokázaly aktivně ubránit proti ptačím predátorům. Druhové složení predátorů a vzorce hnízdní predace se lišily od studií ze západní Evropy.

Z důvodu očekávaných rozdílů v identitě predátorů a hnízdní úspěšnosti mezi odlišnými hnízdními prostředími a geografickými regiony jsem dále kvantifikoval hnízdní úspěšnost a identitu predátorů také u populace skřivanů polních a skřivanů lesních (*Lullula arborea*) hnízdících ve více přirozeném prostředí atlantských vřesovišť v severním Nizozemsku. Populace obou druhů skřivanů se zde vyskytují na stejném území a jejich hnízda představují podobný typ kořisti pro predátory, nicméně se tyto dva druhy liší výběrem hnízdních stanovišť. Zatímco skřivani polní se vyhýbají okrajům lesa i jednotlivým stromům, skřivani lesní svá hnízda často umísťují pod vzrostlé dřeviny. Mé výsledky naznačují, že hlavní hnízdní predátoři se mohou mezi těmito dvěma blízce příbuznými druhy lišit. Hnízda skřivanů polních umísťovaná v otevřeném prostoru byla častěji predována liškou obecnou (*Vulpes vulpes*), zatímco hlavním predátorem hnízd skřivanů lesních byla vrána černá (*Corvus corone*).

Dnešní převaha ozimých plodin limituje počet hnízdních pokusů skřivanů na jednom stanovišti z důvodu jejich přílišné hustoty v druhé polovině sezóny. Přesto jsem nepozoroval jasný sezónní trend v přežívání hnízd. Nicméně proporce ptačích predátorů klesala ve prospěch savců se zvětšující se výškou vegetace. V druhé polovině května nabývala na významu zejména pole osetá kukuřicí, která představují pro skřivany atraktivní, ale rizikové hnízdní prostředí.

Produktivita skřivaních hnízd může být negativně ovlivněna i blízkostí polních okrajů, kde je očekáván větší pohyb predátorů. Výsledky naznačují, že skřivani skutečně preferují umísťování hnízd spíše ve středu polí, přesto jsem nezaznamenal výrazně zvýšené predační riziko poblíž polních okrajů.

Rozdílné predační riziko může být významným zdrojem selekce vzorců inkubačního chování. Přítomnost samic skřivanů na hnízdě byla silně ovlivněna denním průběhem. Skřivani trávili více času na snůšce ráno a večer, frekvence odletů byla nejvyšší okolo poledne. Denní variabilita inkubačního chování byla ovlivněna a interagovala s teplotou a rozvojem vegetace. To naznačuje, že správné rozvržení inkubačních směn v rámci dne je stejně důležité jako celková intenzita inkubace.

Klíčová slova: hnízdní úspěšnost, predace ptačích hnízd, video-monitoring, *Alauda arvensis*, *Vanellus vanellus*, *Lullula arborea*, intenzifikace zemědělství, okrajový efekt, inkubační chování

Počet stran a příloh: viii a 43 stran, 6 příloh
Jazyk: anglický

I declare that this Ph.D. thesis is my original authorial work under the supervision of doc. Mgr. Karel Weidinger, Dr. which I have worked out by my own, except co-authors contributions to enclosed papers and manuscripts. All the materials and resources are cited with regard to the scientific ethics, copyrights and the laws protecting intellectual property. This thesis or its parts were not submitted to obtain any other or the same academic title.

Olomouc, May 14, 2015 ……………………….

ACKNOWLEDGEMENTS

I would like to express the deepest appreciation to my supervisor Karel Weidinger who genuinly helped me with all the field and lab work and finally brought this thesis into being.

I am also grateful to Arne Hegemann and Irene B. Tieleman for providing an opportunity to join them during field work in the Aekingerzand in northern Netherlands, where also Rob Voesten and Stef Waasdorp were of invaluable help when searching for lark nests and setting up cameras.

I also thank to my friends, especially Jaroslav Koleček, Jindra Sedláček and Martin Vymazal who helped me in the field, laboratory or in any other way. Finally I would like thank to my parents for their unconditional support and patience.

CONTENT

APPENDICES

a) CONTRIBUTIONS

The present thesis is based on the following contributions, which are referred to by their Roman numerals:

I. Praus, L. & Weidinger, K. (2010). Predators and nest success of Sky Larks *Alauda arvensis* in large arable fields. *Bird Study* **57:** 525–530.

II. Praus, L. & Weidinger, K. (2011). Střevlíci (Carabidae) jako potenciální nebezpečí pro mláďata skřivanů polních (*Alauda arvensis*) na hnízdech. *Sylvia* **47:** 91–94.

III. Praus, L. Hegemann, A., Tieleman, B. I. & Weidinger, K. (2014). Predators and predation rates of Skylark *Alauda arvensis* and Woodlark *Lullula arborea* nests in a semi-natural area in the Netherlands. *Ardea* **102:** 87–94.

IV. Praus, L. & Weidinger, K. (2015). Breeding biology of the Skylark *Alauda arvensis* in maize and other crop fields. *Acta Ornithologica* **50:** 1. (*in press*)

V. Praus, L. & Weidinger, K. Complex patterns of incubation behaviour in the Skylark (*Alauda arvensis*) breeding in arable fields. (*Manuscript*)

b) CURRICULUM VITAE

INTRODUCTION

Nearly all bird species face predation, and it is during the breeding season that birds are the most vulnerable, whether as eggs, chicks or parents (Newton 2013). Therefore, nest predation is one of the major selective agents shaping avian life histories (Martin 1995). Nest predation rates are influenced by features of the habitat, the nesting birds themselves, as well as by the numbers and behaviour of predators present, so rates in the same species vary greatly among different areas and times (Newton 2013). Predation rates on nests can be minimized by parents through adequate nest site choice, timing of breeding and parental behaviour (Magnhagen 1991).

Human-induced habitat alterations often result in the loss or degradation of suitable breeding habitats for bird specialists that have specific demands on the environment (Fuller 2012). Because of anthropogenic habitat change, mismatches between habitat preferences and reproductive performance may, in some cases, be attributable to ecological–evolutionary traps in which historical settlement cues become decoupled from their historical outcomes (Martin 1993, Remeš 2000, Chalfoun & Schmidt 2012). Loss of suitable nesting habitat can result in higher nest densities and subsequently higher density-dependent predation rates (Schmidt & Whelan 1999, Misenhelter & Rotenberry 2000, Pescador & Peris 2001), and habitat changes may also force birds to nest in more dangerous habitat types (Donald 2004, Evans 2004, Morris & Gilroy 2008). Moreover, habitat changes can lead to shortened breeding seasons and thus less opportunity for renesting (Chamberlain & Crick 1999, Schmidt & Whelan 1999, Donovan & Thompson 2001). Nest predation can also be influenced by risky parental nesting behaviour, which may affect the amount of time parents spend off the nest at food-poor habitats (Newton 1986, Martin & Ghalambor 1999).

Furthermore, populations of generalist predators not dependent on specific habitat features benefit from anthropogenically modified landscapes (Bossema et al. 1986, Andrén 1994). They can take a wide variety of prey, switching from one prey species to another as opportunities and needs arise. Because the population levels of such predators can be influenced by the total number of all prey types, they are not often greatly affected by shortages of any one prey type (Newton 2013). Nevertheless, it is not possible to conclude that predators have driven the decline of a population of their prey simply by measuring high levels of nest predation, except in extreme cases.

Nest predation is usually higher in open-nesting than in hole-nesting birds (Martin & Li 1992). Ground-nesting birds seem to suffer greater nest predation than off-ground-nesting species in shrub and grassland habitats (Martin 1993). Breeding populations of waders and gamebirds are more likely to be limited by nest predation than ground nesting passerines (Gibbons et al. 2008). Populations of many farmland bird species have declined throughout Western and Central Europe since the advent of agricultural intensification in the 1950s (van Beusekom 2004, Donald et al. 2006, Voříšek et al.

2009, Hayhow et al. 2014). Agricultural intensification has decreased the heterogeneity of farmland by removing semi-natural habitats, increasing field sizes, promoting large scale monocultures, reducing mixed farming and developing practices that maximise yields (Fuller 2012), which has resulted in depressed food availability (Fuller et al. 1995, Hart et al. 2006) and loss of suitable breeding habitats for farmland birds (Hole et al. 2002, Benton et al. 2003, Donald 2004, Donald et al. 2006, Flohre et al. 2011). It has been demonstrated that habitat loss does not fully explain the observed population declines of farmland birds (Evans 2004). It is plausible that nest predation interacts with farmland habitat change and contributes to declines of ground nesting passerines in impoverished agricultural landscapes (Donald 2004, Morris & Gilroy 2008, Gilroy et al. 2011).

The numbers of some farmland avian predators (e.g. corvids *Corvus spp*., harriers *Circus spp*.) have increased over the last decades (Baillie et al. 2006, Šťastný et al. 2006). The same probably applies to most mammalian mesopredators e.g. the stone marten *Martes foina* and red fox *Vulpes vulpes*, as well as alien species such as the american mink *Mustela vison* (Harris et al. 1995, Anděra & Gaisler 2012). All these predators are generalists (Hanski et al. 1991, Newton 2013), and thus predation rates on any particular prey species are likely to be independent of its density. Bird nests are only a supplementary type of prey for almost all predators, but even so nest predation can cause prey population declines. Thus, the combination of habitat loss and invading predator species may act in concert, causing further negative effects on farmland birds. As such, nest predation may be an issue worthy of consideration in the design of measures to aid the recovery of farmland bird species.

It is known that nesting in sparsely vegetated habitats can increase nest predation rates on small passerines (Martin 1993). Increased vegetation height, density and heterogeneity may reduce nest predation rates through increased nest concealment (Newton 2013). However, predation rates are not always related to the degree of visual nest concealment, because some predators use non-visual cues for nest detection (Rangen et al. 1999, Dion et al. 2000), or because a trade-off exists between nest concealment and good visibility from the nest, so that parents can detect approaching predators in time (Götmark et al. 1995, Whittingham & Evans 2004). Specifically, in farmland habitat nest success has been shown to vary among crop types (Weibel 1999, Donald et al. 2002, Eraud & Boutin 2002, Kragten et al. 2008) as well as within individual fields with proximity to tramlines (Donald et al. 2002) or field edges (Weibel 1999, Morris & Gilroy 2008). Although previous studies often implied predator-specific effects on nest survival, there is still little definitive evidence of nest success and predator identity for ground nesting birds of open habitats in different regions or habitats, or between species with different life histories (MacDonald & Bolton 2008, Morris & Gilroy 2008, Teunissen et al. 2008).

In order to clarify whether generalist predators really contribute to population declines in farmland birds, one must first investigate sources of nesting mortality and the relative importance of different nest predators in habitats of conventionally managed arable fields. In the past it was difficult to be certain of nest fates and the identity of predators, but recently identification of nest predators has become more reliable using camouflaged nest video cameras (Ribic et al. 2012), which provide precise nest survival times and nest fates. Therefore I used video-monitoring to quantify nest success, the identity of nest predators and the behaviour of nest-attending adults in ground nesting birds in intensive arable fields and in semi-natural habitats. The results of my research should help elucidate the causal relationships between farmland habitat change and nest predation, which is essential for developing appropriate management options to reverse the population declines of farmland birds.

AIMS OF THE THESIS

A prerequisite for sensible interpretations of nest predation rates is knowledge of nest predators. Hence I first quantified nest fates and nest predator identity in two species breeding in intensively managed arable fields, the Skylark *Alauda arvensis* and the Lapwing *Vanellus vanellus*. Both these species share common nesting habitat; however the Skylark, a small passerine that relies solely on nest crypsis for defence against nest predators, is expected to experience higher predation by possibly different predators in comparison to the Lapwing, a wader who relies on early detection and active nest defence against bird predators. The majority of observed nests were monitored using continuous video surveillance.

Because of expected differences in predator identity and nest survival among nesting habitats and regions, I also further quantified nest success and identified nest predators for a high-density population of Skylarks as well as Woodlarks *Lulllula arborea* breeding in more natural heath and grassland habitats in the Netherlands. Populations of both lark species co-occur in this area and their nests are similar targets for local predators. Yet, the two species differ in the selection of their microhabitats; while Skylarks avoid forest edges and even the proximity of single trees, Woodlarks usually nest close to trees and/or forest edges. Hence I explored whether this different nest site selection within a semi-natural area relates to species-specific vulnerability to nest predation.

Disturbances associated with placing video cameras and nest visits may introduce bias to estimations of nest survival rates and predator identification (Richardson et al. 2009, Ribic et al. 2012). I therefore evaluated the possible effects of the presence of a camera on predation through an artificial nest experiment with dummy cameras in same area where real Skylark nests were studied.

Agricultural intensification has resulted in a reduction of landscape heterogeneity due to the increasing size of individual arable fields and changes in the structure of crop monocultures. I compared characteristics of Skylark breeding biology and daily survival rates in the "extreme" habitat of maize fields, where vegetation may grow about 150 cm during a single nesting cycle, and other crops with more modest vegetation growth rates. I posed the question whether nesting success can be affected by rapid changes in vegetation growth throughout the breeding season.

Not only the selection of particular crops as breeding habitat but also the spatial distribution of nests within arable fields is expected to influence nest predation rates and predator identities, therefore I asked if nest predation rates are affected by the edge effect, when predation rates are expected to decline with increasing distance from field edges.

Apart from selecting safe nesting habitats, birds can minimize nest predation risk through adequate parental behaviour (Ghalambor & Martin 2002, Massaro et al. 2008, Cervencl et al. 2011), e.g. parental activity may respond to variation in nest concealment (Burhans & Thompson 2001, Lima 2009). The uniform habitat of arable fields facilitates studies of parental behaviour by minimizing habitat heterogeneity within individual crop types. Therefore I evaluated variation in Skylark incubation patterns and its plasticity in relation to vegetation characteristics, season, ambient temperature, incubation progress and clutch size.

STUDY SYSTEM

Model species

Eurasian Skylark (*Alauda arvensis*)

The main model species was the Eurasian Skylark (further referred to as ‘Skylark’), a typical ground-nesting passerine that currently relatively abundantly breeds in areas experiencing changing agricultural systems, as well as in open semi/natural habitats across most of Europe and Asia and in the mountains of northern Africa (Donald 2004, Šťastný et al. 2006, Hegemann 2012). However, almost all monitoring programmes have reported declines in Skylark breeding abundance by 25 - 50% since the 1970s across European farmland regions (Robertson & Berg 1992, Fuller et al. 1995, de Carli et al. 1998, Chamberlain & Crick 1999, Reif et al. 2008, Fig. 1). The Skylark population decline has been associated with agricultural intensification, specifically with changes in cropping patterns and increased use of pesticides and fertiliser. A reduced spectrum of cultivated crops and increasing harvesting efficiency has depressed food availability (Hole et al. 2002, Hart et al. 2006, Flohre et al. 2011) and safe breeding sites (Donald 2004). Particularly, in regions dominated by cereal crops a switch from spring-sown to autumn-sown cereals results in the rapid development of tall, dense swards that, from May onwards, restrict nesting opportunities (Donald 2004) and access to food (Morris et al. 2004). Skylarks prefer a breeding vegetation cover of 35–60% and vegetation height not exceeding 50 cm (Toepfer & Stubbe 2001, Donald 2004).

A large proportion of Skylark nests are lost to predators. Probably as a consequence of naturally high nest predation, larks tend to have small clutch sizes (3–5 eggs) and instead make several (up to 6) nesting attempts during the course of a single breeding season. Other possible anti-predator strategies include rapid chick development (9 days from hatching to leaving the nest) and a rapid dispersion of chicks away from the nest site immediately after fledging (Donald 2004). In spite of generally high nest predation rates varying among crop types as well as within individual fields with proximity to tramlines (Donald et al. 2002) or field edges (Weibel 1999, Morris & Gilroy 2008), no study has yet implicated predation as a major driver of Skylark population declines.

Woodlark (*Lullula arborea*)

Of all the larks, the Woodlark shows the greatest affinity to woodland, preferring relatively open, sandy habitats with scattered trees across much of Europe, the Middle East and northwest Africa (Donald 2004). Woodlark ground nests are similar targets for predators as Skylark nests. Yet, the two lark species differ in the selection of their microhabitats: while Skylarks avoid the proximity of trees, Woodlarks usually nest close to trees and/or forest edges. This allowed me to explore if different nest site selection within an area where both lark species co-occur is related to species-specific vulnerability to nest predation.

The Northern Lapwing (*Vanellus vanellus*)

The Northern Lapwing (further referred to as ‘Lapwing’) is a wader species which breeds on cultivated land and other short vegetation habitats throughout Eurasia (Shrubb 2007). It shares common nesting habitat with the Skylark in sparsely vegetated arable fields, but their life-histories suggest different vulnerability to nest predation. Lapwings are a comparatively larger precocial species with a longer incubation period (24 – 29 days), an active social nest defence (Kis et al. 2000) and only one successful brood per season (Schekkerman 2008). The breeding population of the Lapwing in Western and Central Europe has also declined severely in recent decades (Wilson et al. 2001, Žídková et al. 2007, Bellebaum & Bock 2009, Ławicki et al. 2011, Fig. 1).

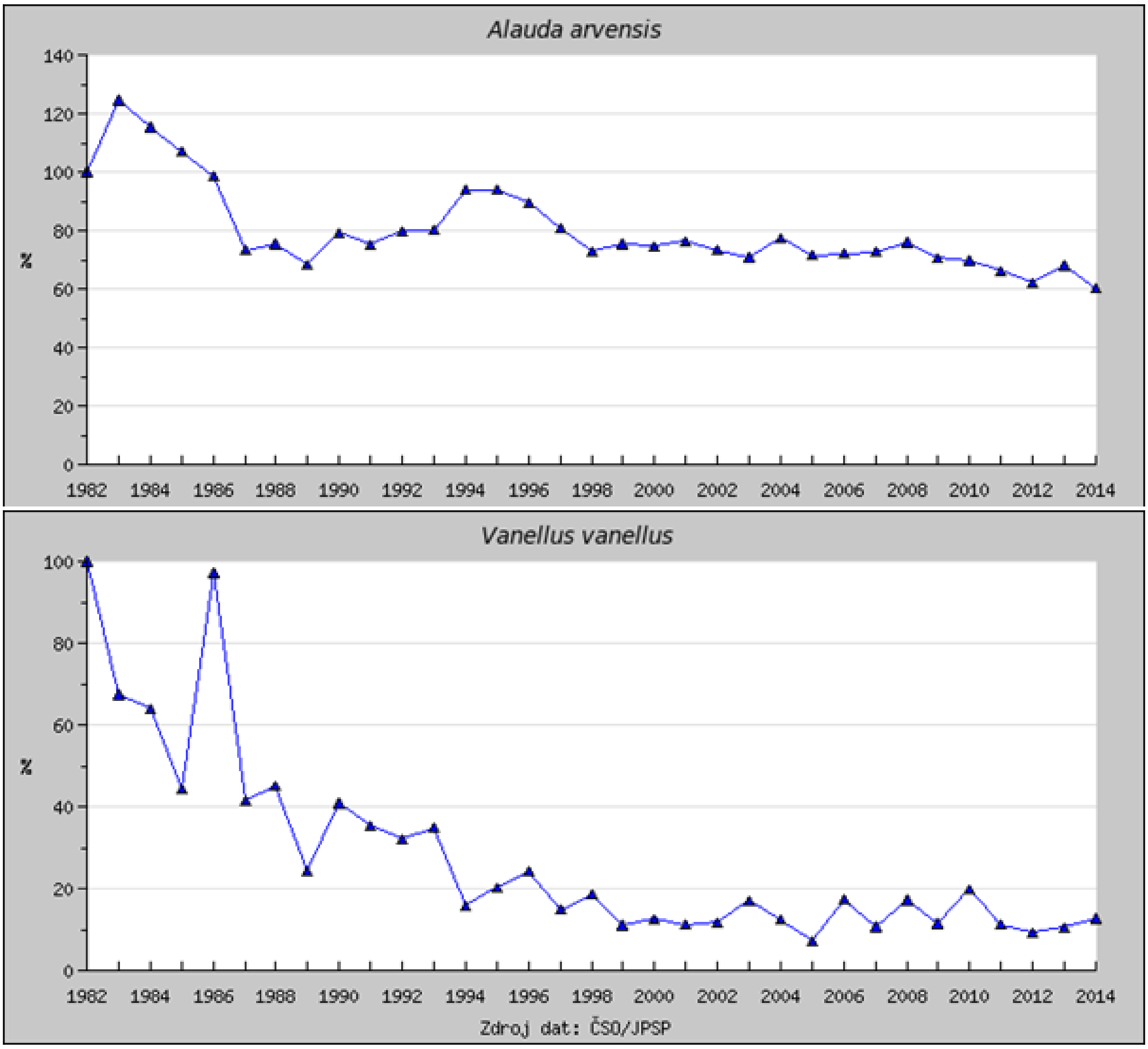


Figure 1. Population trends of Skylarks (*Alauda arvensis*) and Lapwings (*Vanellus vanellus*) in the Czech Republic from 1982-2014 (Czech Society for Ornithology/the Breeding Bird Monitoring Programme).

Study areas

Intensive arable fields (CZ)

The majority of fieldwork was conducted in the northeast part of Chrudim District, the Czech Republic (49° 55.39' N, 15° 59.33' E 49°, altitude 270–500 m). Research was carried out on conventionally-managed intensive arable fields (total study area of c 60 km², mean field size about 50 ha) interspersed with remnants of deciduous woodland and villages (<15% of the total area, Fig. 2). The main crop types were: winter wheat (*Triticum aestivum*) (45%); maize (*Zea mays*) (15%); winter rape (*Brassica napus subsp. napus*) (15%), spring barley (*Hordeum vulgare*) (10%); sugar beet (*Beta vulgaris*) (5%); alfalfa (*Medicago sativa*), opium poppy (*Papaver somniferum*), caraway (*Carum carvi*), pea (*Pisum sativum*) and brown bean (*Vicia faba*) (each ≤2%). Fieldwork was carried out during the breeding seasons 2009-2011.

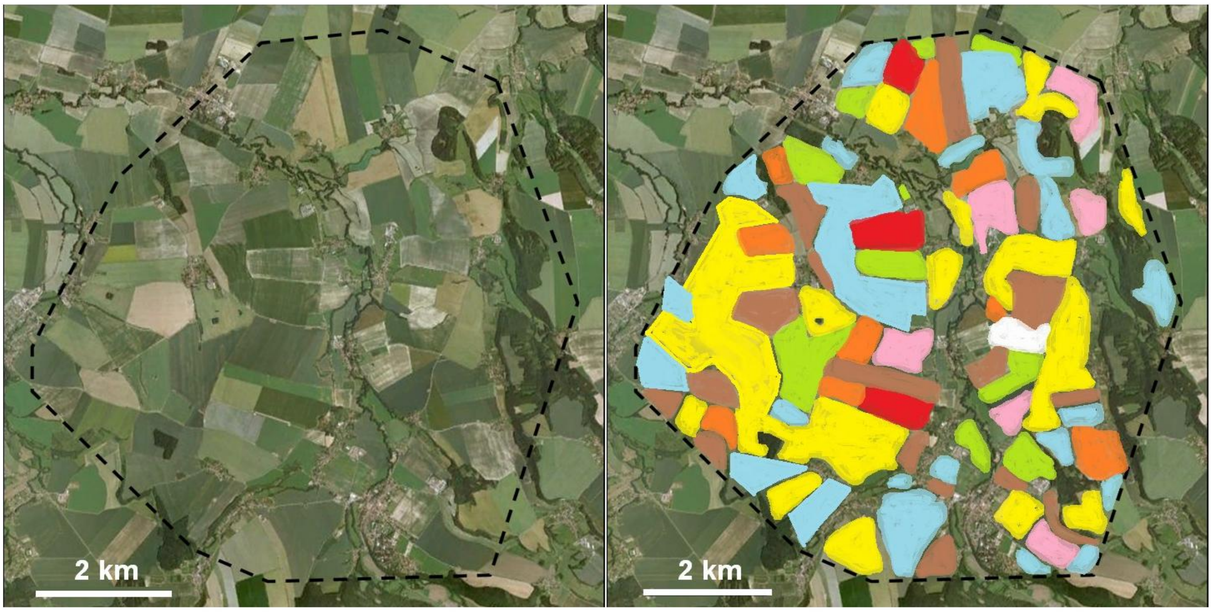


Figure 2. Map of the study area in the Czech Republic. Right map: field crops situation in 2009; yellow: winter wheat, blue: maize, orange: winter rape, green: spring barley, pink: sugar beet, brown: alfalfa, red: opium poppy, white: caraway. (Ortho photo map: www.mapy.cz)

Semi-natural sandy heathland (NL)

I also studied Skylark and Woodlark nesting in the Aekingerzand, part of the National Park Drents-Friese Wold in the northern Netherlands (52°55'N, 6°18'E) (Fig. 3). The study area (c. 400 ha) was characterised by nutrient-poor sandy soil. Dominating vegetation types were heather, *Calluna vulgaris* and *Erica tetralix*, and different succession states of grass, moss and *Juncus* spec. Furthermore, patches of open sand and groups of trees were spread throughout the area, which was surrounded by pine forest. Suitable nesting habitat covered approximately 240 ha for Skylarks and 220 ha for Woodlarks. Fieldwork was conducted from early May to late July in 2012.

Figure 3. Semi-natural habitat of Skylark and Woodlark populations in the Aekingerzand, northern Netherlands, in April 2012. Photo Libor Praus

RESEARCH TOPICS

Chapter 1: PREDATORS AND NEST SUCCESS OF THE SKYLARK AND LAPWING IN ARABLE FIELDS IN THE CZECH REPUBLIC

Skylarks and Lapwings are farmland bird species that are both negatively affected by agricultural intensification (Fig. 1). Both species share common nesting habitat in sparsely vegetated arable fields, but their life histories suggest different vulnerabilities to nest predation. The Skylark is typical small altricial ground nesting passerine with several broods during the season, and relies exclusively on passive anti-predator strategies such as small clutch size with multiple renesting attempts, a short nesting cycle (14 day laying and incubation period, 8 day nestling period) and nest camouflage. In contrast, the Lapwing is comparatively larger precocial species with a longer incubation period (24 – 29 days), an active social nest defence and only one successful brood per season (Schekkerman 2008).

In ***Contribution I.*** we presented novel data on predators of Skylark nests (n = 44) observed in 2009, the first season of our fieldwork. Here we present the complete data set (186 Skylark nest, 18 Lapwing nests) collected during three breeding seasons from 2009-2011. We compare nest predators and nest predation rates of Skylarks and Lapwings exposed to the same predator community in intensively managed arable fields.

METHODS

Fieldwork

Searching for Skylark nests was undertaken from the beginning of the breeding season in the start of April and continued until late July. Roughly, 100 days per year were devoted to searching for nests in the whole study area. We located nests by systematically searching in suitable plots (≤60% mean vegetation coverage); 35% of Skylark nests were found by the flushing of incubating females. Lapwing nests were searched for opportunistically in fields with monitored Skylark nests. The age of nests (first egg = day 0) was estimated from the clutch/brood size and the stage of incubation estimated by egg floatation or by visual clues of nestling development.

Nest survival and fates of Skylark and Lapwing nests were determined by means of continuous video-surveillance. Video-monitoring systems consisted of a video-camera with infrared-emitting diodes, a portable security digital video-recorder (DVR) (Yoko RYK-9107), and a 12V/65(40) Ah deep cycle battery (for details see ***Contribution I.***, Fig. 4). Cameras were placed 0.7–2.0 m from nests (depending on nest visibility) and 2–20 cm above the ground, never exceeding the height of surrounding vegetation. Local natural materials (dry vegetation, stones) were used to mask the camera; all other parts were buried under ground. We set the DVR to record continually with a frequency of 10 frames s −1 at 640 × 480 pixel resolution and medium quality. These settings allowed for 4.5 days of recording on a 16 GB memory card. Cameras were deployed either immediately at the time of nest discovery or within the next 4 days after discovery, avoiding disturbing vegetation or leaving dead-end tracks (to/from the nest). There was usually no response from the birds to the installed recording equipment. All nests were usually visited (80% of cases) every fourth day (mean 3.9, range 1–8) to check nest contents and to change the battery and memory card at video-monitored nests. To keep the time spent at nests short (≤15 min), we offloaded all data in the lab.

About half of our visits took place in the morning (08:00–11:30 Central European Time) and half in the afternoon (12:30–20:30). When a nest was found to be empty, we recorded and photographed its state and searched in the immediate vicinity for signs of nest failure (eggshells, feathers, dead nestlings) or success (live fledglings, droppings, juvenile feathers). We continued video-monitoring of deserted or partially depredated nests with intact egg(s) for at least two 4-day periods, depending on the availability of active nests at that time. For video-monitored nests we determined the exact survival time and nest fate. Time of failure for nests without a video-camera was estimated as the midpoint between the last visit to an active nest with eggs or nestlings and the first negative visit (empty nest, dead chicks or deserted clutch). The exposure time of successful Skylark nests without a video-camera was terminated by the 8th day of chick age on the basis of the mean fledging age of video-monitored nests (8.2 days, range 7–12 days, n=33).

Figure 4. Video-monitoring system in the field: Battery and accessories for camera installation on the left and righ side; Camouflaged nest cameras in arable field and in natural habitat in central pictures. Photo Libor Praus

Data analysis

For nests monitored by video, we viewed the video-recordings backwards to locate any predation events, and to determine the nest fate, timing of the event and the species of nest predator. It is not possible to express nesting success simply as the percentage of all nests that went on to succeed, since nests failing quickly are more likely be missed by the researchers then those that succeed, leading to an overestimate of success (Weidinger 2003). The Mayfield method (Mayfield 1975) and its more complex extensions (e.g. Aebischer 1999, Shaffer 2004) reduce this bias by calculating daily survival rate (DSR) as the probability of survival per day that nests are under observation (nest-days). This allows the derivation of an unbiased estimate of nesting success and to assess the effects of potential covariates.

The exposure period was measured in nest-days since the day of nest discovery with eggs or chicks. Each nest-day was treated as an independent binary observation (survived or failed) and the daily survival rates (DSR) were estimated as the simple ratio of survived to exposed nest-days. We calculated DSR separately for the egg (laying and incubation) and nestling stages (only for Skylarks) of active nests and for deserted (= inactive) nests with eggs. To calculate DSR we considered either nest losses due to predation, or total mortality. Nest survival was estimated as DSR^t where $t = 14$ (egg stage including laying period), 8 (nestling stage) or 22 (total) days for Skylarks and where $t = 28$ (egg stage including laying period) for Lapwings. Egg stage was based on a mean clutch size of 4 eggs for both species and an incubation period of 11 days for Skylarks (Donald 2004, own unpublished data) and 24 days for Lapwing (Hudec & Šťastný 2005) starting with the last egg laid. The limited sample size from the first field season precluded the application of inferential statistics in the preliminary analysis (***Contribution I.***). Here we describe the complete data set and focus on possible patterns in the data; a formal statistical analysis will be the subject of a forthcoming study.

RESULTS

Overall, we found 177 active nests and 9 abandoned clutches of Skylarks (2009: 45, 2010: 82 2011: 59). Skylark nests were found before the commencement of egg laying (37), during laying (61), incubation (62) or the nestling stage (15). The mean age of found nests was 3.2 days (±0.38 SE; day of first egg = 0, minimum = -5, maximum = 21). The earliest Skylark clutch initiation was found on 6 April (2011), the latest on 21 July (2010), with median date = 3 June. The number of monitored nest days during the breeding season showed a unimodal distribution with a peak in late May and early June (Fig. 5.).

Skylark nests experienced a higher overall mortality rate than Lapwing nests (Fig. 6); the major cause of mortality in both species was predation. Daily predation rate was higher in Skylarks (0.084; 95% CI: 0.068-0.096) than in Lapwings (0.011; 0.004-0.027).

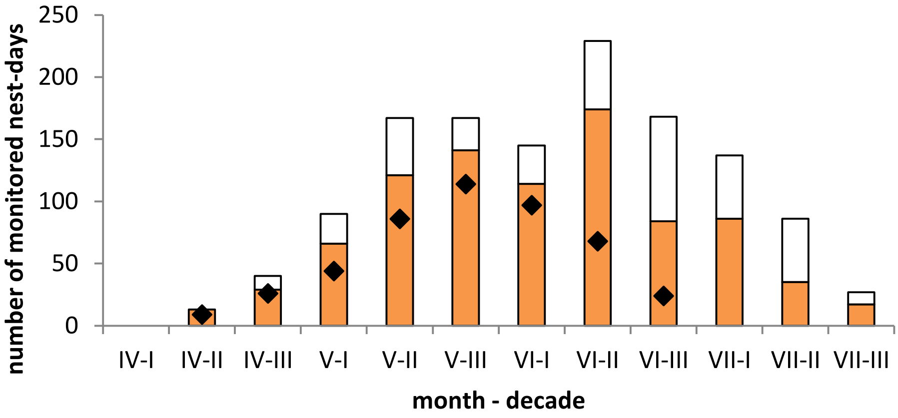


Figure 5. Distribution of monitored active Skylark and Lapwing nest-days over the course of the breeding season (pooled data 2009-2011). Black diamond: number of monitored Lapwing clutch nest-days (n = 18 nests), brown part of bars: number of monitored Skylark nest-days at the egg stage (n = 159 nests), white part of bars: number of monitored Skylark nest-days at the nestling stage (n = 62 nests).

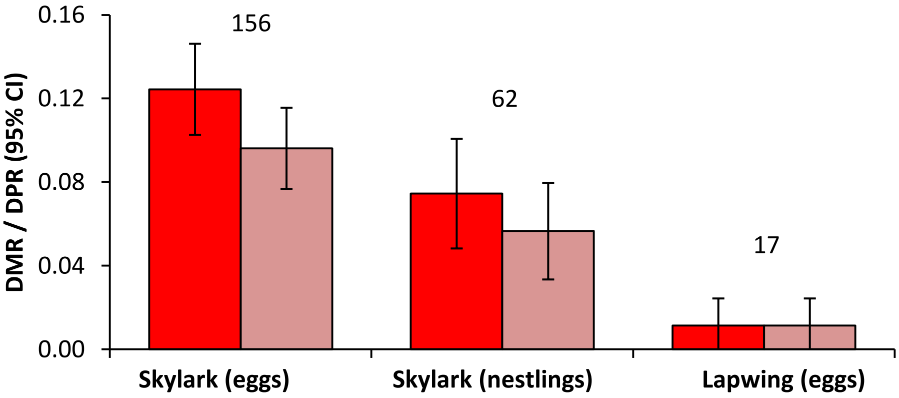


Figure 6. Daily mortality rates (DMR, red bars) and daily predation rates (DPR, pink bars) of Skylark and Lapwing eggs and nestlings (only Skylark), Number of nests is shown above the bars.

Using continuous video-recording, we monitored 161 of 186 found Skylark nests and 18 Lapwing nests. The 104 documented predation events at Skylark nests were caused by: Marsh Harrier (*Circus aeroginosus*) (32), Montagu's Harrier (*Circus pygargus*)(18), stone marten (*Martes foina*) (14), Hooded Crow (*Corvus cornix*) (13), wild boar (*Sus scrofa*) (9), red fox (*Vulpes vulpes*) (8), Common Raven (*Corvus corax*) (2), domestic cat (*Felis silvestris f. catus*) (2), hedgehog (*Erinaceus sp.*) (2), european polecat (*Mustela putorius*) (1), European Magpie (*Pica pica*) (1), Eurasian Jackdaw (*Corvus monedula*) (1) and an unidentified bird of prey (1). Two Lapwing nests were depredated by red fox, and one by wild boar and by stone marten (Fig. 7, 8).

The spatial distribution of predation events (Fig. 9) suggests that results are not based on repeated sampling of the same individual predators, and that the data may successfully be used for further analysis of spatial relationships (see Chapter 5). The identity of predators cannot be inferred from the appearance of depredated nests, because in most cases mammal and bird predators do not leave specific marks and cause similar damage to nests (Fig 10). Nests were vulnerable to the full range of local predators across different locations (crops, vegetation height, and distance) and seasonal timing (Table 1). Nests were under risk of predation at all times of day; mammalian predators were responsible for all nocturnal predation events, while bird predators predominated during daylight (Fig. 11).

Figure 7. Screen shots of video-recorded predators at Skylark nests. Upper line: Marsh Harrier, Montagu's Harrier, Domestic Cat, Common Raven. Central line: Stone Marten, Hooded Crow, Hedgehog, European Magpie. Bottom line: Red Fox, Wild Boar, European Polecat and Eurasian Jackdaw.

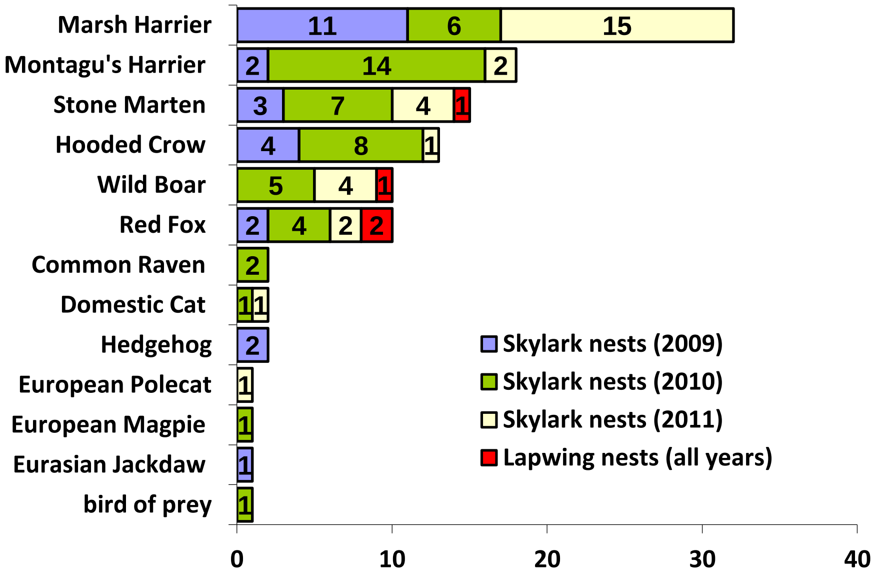


Figure 8. Number and species composition of recorded nest predators at Skylark and Lapwing nests.

Spatial distribution of predation events (Fig. 9) suggests that results are not based on repeated sampling of the same individual predators and that the data are open for further analysis of spatial relationships (see Chapter 5). Identity of predators cannot be inferred from appearance of the depredated nests, because in most cases mammal and bird predators do not leave specific marks and cause similar damage to the nests (Fig 10). Nests were vulnerable to a full range of local predators across different locations (crops, vegetation height, distance) and seasonal timing (Table 1). Nests were under risk of predation at any time of day; mammalian predators were responsible for all nocturnal predation events, while bird predators predominate during daylight (Fig. 11).

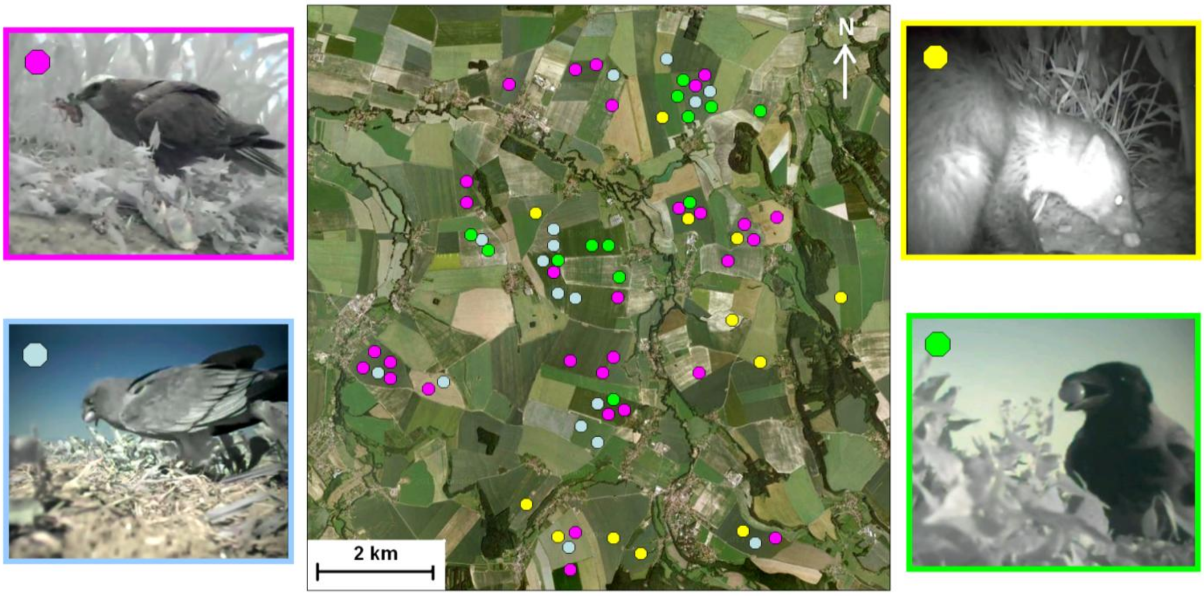


Figure 9. Spatial distribution of predation events by the four most important predators in the study area (pink: Marsh Harrier, blue: Montagu's Harrier, yellow: Stone Marten, green: Hooded Crow.

Table 1. Characteristics (median and range) of predation events at Skylark nests by different predator species.

Predator	Day of the year	Distance from field edge (m)	Vegetation height (m)	n
Marsh Harrier	163; 108-188	110; 26-294	0.29; 0-1.19	32
Montagu' s Harrier	153; 124-185	120; 31-296	0.18; 0.1-0.55	18
Stone Marten	181; 131-205	102; 38-243	0.64; 0.08-1.8	14
Hooded Crow	158; 128-191	123; 24-304	0.2; 0.1-0.29	13
Wild Boar	192; 170-209	44; 1-184	1.1; 0.45-1.95	9
Red Fox	175; 169-189	156; 24-274	0.43; 0.14-1.2	7
Common Raven	173; 164-182	122; 95-149	0.33; 0.2-0.45	2
Domestic Cat	174; 170-178	60; 44-77	0.45; 0.4-0.5	2
Hedgehog	60; 167-180	174; 67-281	0.24; 0.14-0.34	2
European Polecat	173	124	0.9	1
European Magpie	147	147	0.26	1
Eurasian Jackdaw	148	70	0.17	1

Figure 10. Examples of Skylark nests before and after predator visits by the main local predators. From top: Marsh Harrier, Montagu's Harrier, Hooded Crow, Stone Marten, Red Fox and Wild Boar.

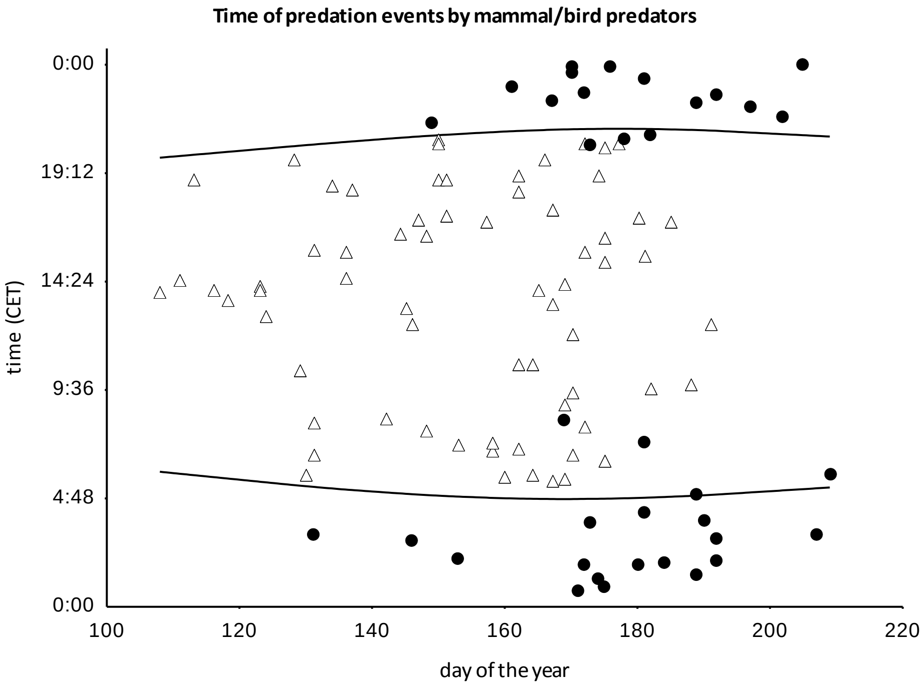


Figure 11. Timing of predation events by bird (white triangles) and mammal (black dots) predators over the course of the nesting season. The lower black line marks the time of sunrise, the upper the time of sunset.

DISCUSSION

Across Western European farmland, the overall Skylark nest success ("Mayfield" estimates) ranges from 0.04 % to 0.40 (Weibel 1999, Donald et al. 2002, Jeromin 2002, Kragten et al. 2008, Kuiper et al. 2015). In this study nest success was quite low (0.07; 95% CI: 0.04–0.11); similar or lower overall nest survival has only been reported from grasslands in the Netherlands due to frequent silage cutting (Kuiper et al. 2015). Lapwings in our study area had relatively high nest success (0.72; 0.49–0.99), which is in agreement with other studies across Europe (MacDonald & Bolton 2008, Teunissen et al. 2008, Roodbergen et al. 2012). The major cause of mortality for both species was predation. Skylark nests were vulnerable to all local predators, while it seems that Lapwings can avoid avian predators. My results are in accordance with a large study of predators of Lapwings clutches in the Netherlands, where the dominant predator was the red fox, while bird predators were responsible only for about 8% of predation events (Teunissen et al. 2008). Until the availability of video-recording data, indirect evidence suggested more frequent predation of Lapwing clutches by bird predators (Berg et al. 1992). Lapwings protect their clutches by aggressively attacking corvids and birds of prey near their nests throughout the incubation period with the same intensity (Kis et al. 2000, Šálek & Šmilauer 2002) and they also rely on egg crypsis as a further strategy against avian nest predators (Šálek & Cepáková 2006). Skylarks rely only on passive nest defence through sitting on the nest (nest attentiveness), thereby hiding the eggs from view and serving to camouflage the nest from predators (Donald 2004).

The distribution of predatory pressure over the course of the day reflected the proportion of total predation by diurnal (birds) and mainly nocturnal (mammals) predator species. A similar distribution of nest predation over a 24-h period was reported for open-cup nests of woodland passerines in same region, where an almost uniform diel distribution of predatory pressure reflected an even proportion of total predation by Jay (diurnal) and marten (mainly nocturnal) species (Weidinger 2009, Weidinger 2010).

The species composition of predators of Skylark nests and patterns in nest predation rates found in our study mostly differ from those reported from Western Europe, where a majority of depredation was due to mammals (Donald 2004, Morris & Gilroy 2008). Our results show that harriers might account for almost 50% (50/103) of total depredation events within our study area. This is unlikely to be a site-specific effect since the local abundance of Marsh Harriers (two breeding pairs in a 55 km^2 area) was representative of the large-scale density for the whole Czech Republic (2.0–3.6 pairs/100 km^2; based on data from Šťastný et al. 2006). Carnivores accounted for about 25% (25/103), corvids for 16.5% (17/105) and wild boars for 9% (9/103) of the total predation.

Video-monitoring of active nests provides an essential method for revealing nest fates and predator identities, and helps towards progress in uncovering life history processes that are connected to the predation of nests. The study presented here demonstrates the potential for future studies of predator-specific effects in farmland breeding birds. At the same time, we caution against the generalisation of site-specific results and unsupported assumptions on predator identity.

Chapter 2: PREDATORS AND PREDATION RATES OF SKYLARK AND WOODLARK NESTS IN A SEMI-NATURAL AREA IN THE NETHERLANDS

Knowledge of predation pressure and the relative importance of lark nest predators in different habitats and across different geographic regions is scarce (Delius 1965, Yanes & Suarez 1995). We quantified nest success and identified nest predators in a high-density population of Skylarks and Woodlarks breeding in a semi-natural heath- and grassland area in the Netherlands characterized by permanently low and sparse vegetation (details in ***Contribution III.***). Populations of both species co-occur in this area and their nests are similar targets for local predators. Of all the larks, the Woodlark shows the greatest affinity to woodland, preferring relatively open, sandy habitats with scattered trees (Donald 2004). Young pine plantations and wooded heaths are especially important Woodlark breeding habitats in Europe (Sitters et al. 1996, Wotton & Gillings 2000, Mallord et al. 2007). Differences in nest site selection between Skylark and Woodlark co-occurring in the same open area allow for an analysis of species-specific vulnerability to nest predation.

METHODS

Fieldwork was conducted from early May to late July in 2012; roughly 80 days were devoted to searching for nests in the whole study area. This period covers the entire breeding season of the local Skylark population (Hegemann 2012) and the period of the second and third broods of Woodlarks (Tieleman et al. unpublished data). A total of 58 Skylark and 40 Woodlark nests were found. A randomly selected subset of these nests (Skylark: n = 37 nests, 247 active nest-days; Woodlark: n = 16, 92) was monitored by continuous video-recording. The field protocol and data analysis were the same as described in Chapter 1.

RESULTS

The overall nest success of all monitored Skylark (Woodlark) nests (58 (40), Mayfield estimate) was 33% (22%; all mortality factors considered) or 43% (25%; only depredation). On video we documented 11 predation events by four species of predators (details in ***Contribution III.***). The principal predators differed between the two lark species – red foxes accounted for 71% of predation events in the Skylark, while corvids accounted for 75% of predation in the Woodlark. The six predation events by red foxes occurred throughout the breeding season, while all three predations by the Carrion Crow (*Corvus corone*) were restricted to the second half of May.

DISCUSSION

The overall nest success of Skylarks in a semi-natural breeding habitat in the northern Netherlands was 33%, and thus within the range of values reported from arable fields throughout Europe (Weibel 1999, Donald et al. 2002, Jeromin 2002, Kragten et al. 2008). Woodlarks had a slightly lower nest success (22%) than Skylarks. One possible drawback of this study is the small study area, which has a similar size as the home ranges of the main predators (Bijlsma 2013). This could account for multiple predation events by a particular predator species/individuals, and the possibly pseudo-replicated data may not be representative of predation patterns at larger spatial scales. Even so, our results suggest that the main nest predators might differ between the two co-occurring lark species. Skylark nests located in more open sites were preyed upon mainly by red foxes, while the main predators of Woodlark nests, located generally closer to trees, were corvids. Because predator-prey systems are locally specific, conclusions from this small isolated area in Western Europe may not be directly applicable to other biogeographical regions. This is well illustrated by the distinctly different composition of nest predators documented from arable fields in the Czech Republic (Chapter 1).

Figure 12. Incubating Skylark (left column) and Woodlark (right column) females and clutches in National park Drents Friese Wold, The Netherlands. Photo Libor Praus.

Chapter 3: RESEARCH DISTURBANCES AND THE RISK OF NEST PREDATION

Placing video-cameras near active bird nests and the disturbances associated with nest visits may introduce bias to estimations of nest survival rates and predator identification (Richardson et al. 2009, Ribic et al. 2012). However, the reported effects of cameras on predation of bird nests are not consistent across studies. The daily predation rate on Skylark nests in Czech arable fields (0.08; see Chapter 1) was higher than average values found in Western European farmland (Weibel 1999, Donald et al. 2002, Jeromin 2002, Kragten et al. 2008, Kuiper et al. 2015). Therefore, we conducted an experiment to evaluate potential bias in our data. A negative effect of observer visits should lead to an increased predation rate on the first days after a nest visit compared to subsequent days (Weidinger 2008). Similarly, a negative camera effect should lead to an increased predation rate on nests monitored by cameras compared to control nests without cameras.

METHODS

During the fieldwork in arable fields in the Czech Republic (see Chapter 1) we kept notes on the time of each nest visit, allowing us to check for a potential observer effect on Skylark nest survival by analysing the relationship between the timing of our visits and the timing of depredation events recorded by video-cameras. We compared daily predation rates between the first and the subsequent days that followed after a nest visit by means of logistic regression, with the day after an observer visit entered as a time-dependent covariate (day 1 vs. subsequent days).

To evaluate the effect of the presence of a camera on predation rates we conducted an artificial nest experiment with dummy cameras. This experiment was run during the breeding season 2011 in same area where real skylark nests were studied (see Chapter 1). Each artificial nest consisted of a shallow depression lined with dry herbaceous material and baited with two Japanese Quail (*Coturnix japonica*) eggs. Nests were placed in sites mimicking those of real Skylark nests. Nests were arranged in pairs, with 100 m between nests in each pair. We placed a dummy camera (a realistic model of the cameras used for video-monitoring, see Chapter 1) and simulated the process of camera deployment with all associated disturbances to the nest surroundings at one of the paired nests. The other paired nest served as a control without a camera. In total, 100 nest pairs were distributed throughout three crop types across 44 fields: cereals (42 nest pairs, 21 fields), sugar beet (24, 7) and maize (34, 16). Two nest pairs separated by 300 m were placed in each field at one time. The exact survival time of control and camera nests was measured using event-recording dataloggers hidden under the nests in the ground. The nests were checked every 5th day and exposed for a total of 15 days.

RESULTS

Daily predation rates were not higher on the first day after an observer visit (0.062, 0.039-0.084 95% CL) compared with subsequent days (0.081, 0.061-0.101 95%CL; Fig. 13). Of the 100 artificial nest pairs, at least one nest was depredated in 65 cases. Of these, a nest with a dummy camera was predated first in 29 cases, whereas a control nest without a camera was predated first in 36 cases (Fig. 13).

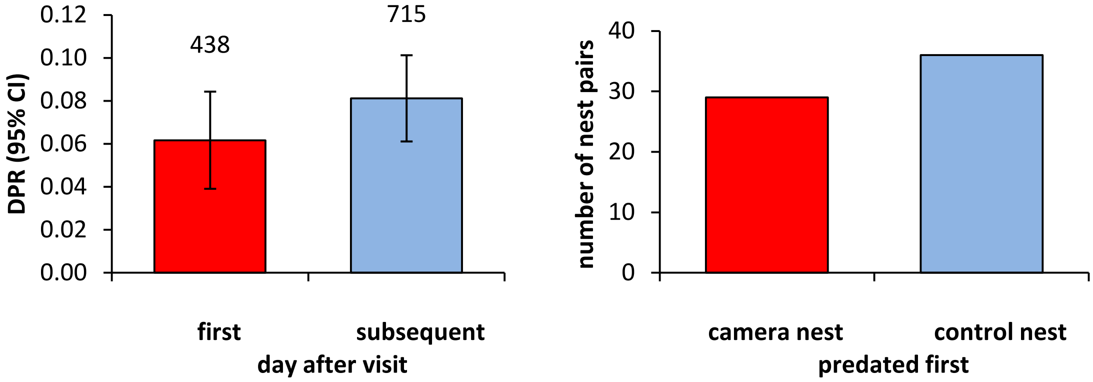


Figure 13. Left chart: a comparison of daily predation rates on active Skylark nests between the first and consecutive days after an observer nest visit (n = nest days). Right chart: a comparison of camera nests predated first and control nests predated first within nest pairs.

DISCUSSION

Although the use of cameras may bias nest predation rates and the species composition of predators (Richardson et al. 2009), this effect is unlikely to be serious in our study of nest predation in arable fields. The marginally lower DPR on the day just after a nest visit as well as at artificial nests with dummy cameras indicate that there are no detectable negative effects of research activities on predation rates. This also supports the suitability of our field protocol, minimising the visible parts of video-equipment and limiting the time spent at nests. In addition, various human artefacts not associated with our research activity (plastic garbage etc.) were common in all fields under study. Most importantly, the observed composition of predators is conservative with regard to the direction of potential bias. Birds of prey, the dominant predators in this study, are known to display neophobia to human artefacts (such as cameras), while carnivore predators, which could have potentially been over-represented because of an attraction to monitored nests (human trails, infrared illumination), were less frequent. The absence of a temporal relationship between the timing of nest visits and the timing of depredation events indicates that overall nest survival in this study was not seriously influenced through altered depredation risk. Previous studies of shrub-nesting passerines in this study area have come to the same conclusions (Weidinger 2008). Yet, we caution against the generalisation of these site-specific results and unsupported assumptions on predator-specific observer effects.

Chapter 4: HABITAT CHARACTERISTICS OF ARABLE FIELDS AND THEIR EFFECTS ON SKYLARK BREEDING BIOLOGY AND NEST PREDATION RATES

Changes to farmland habitats have caused declines in habitat quality throughout the breeding season within bird home ranges (Gilroy et al. 2010). Furthermore, rapid and marked changes of intensive farmland ecosystems may lead to a disconnection between the habitat selection decisions made by breeding birds and the underlying patterns of habitat quality (Gilroy et al. 2011). Skylarks prefer a vegetation cover of 35–60% and vegetation heights up to 50 cm (Toepfer & Stubbe 2001, Donald 2004). Shifts from spring-sown to autumn-sown cereals thus limits the availability of sparsely vegetated plots and consequently the number of breeding attempts of Skylarks in many areas of arable land (Toepfer & Stubbe 2001, Donald 2004). Therefore, Skylarks experiencing multiple breeding opportunities during the course of a season are forced to shift to different breeding sites or habitats (Gilroy et al. 2010, Brambilla et al. 2012). The increasing areas sown by maize are currently becoming a new important nesting habitat for Skylarks in the second half of their breeding season (Brandt & Glemnitz 2013, Saurbrei et al. 2014). Skylarks are capable of nesting on almost bare ground soon after sowing of maize, as well as in fully grown crops, probably because the typical vegetation coverage does not exceed 50% (Schläpfer 1988, Toepfer & Stubbe 2001).

Here, We describe the vegetation characteristics of areas with Skylark nests and explore whether predation rates and predator composition vary systematically over the course of the nesting season with respect to rapid vegetation growth.

As most Skylark nests were found in maize fields (Table 2), we analysed breeding biology and nest survival separately for this "extreme" habitat and for a comparative set of nests from other crops in ***Contribution IV***.

METHODS

Searching for nests and subsequent monitoring followed the general field protocol described previously (for details see Chapter 1). The height of vegetation at the nest site (m) and the degree of nest cover (scored as: 1, well visible from above; 2, intermediate; 3, completely covered from above) were measured and the nest was photographed during each nest visit. The degree of field vegetation cover in a 20 m radius around the nest during the laying period was classified according to four categories: (1: 0–25 % vegetation cover, 2: 26 – 50%, 3: 51–75%, 4: 76–100%).

RESULTS

Skylarks placed nests in a wide variety of habitats (Fig. 14). Of a total 186 Skylark nests, 92 nests were found in maize fields, while the rest were found in nine other crops. The number of nests found in individual crops was not proportional to the proportion of those crops in the study area (Table 2).

The mean crop height during the first egg laying was 0.27 ± 0.032 m (mean ± SE; n= 58, range 0-1.6 m, Fig. 15). Details of nest site selection in maize fields with respect to crop growth and a comparison of breeding biology in maize fields vs. others crops are given in ***Contribution IV.***

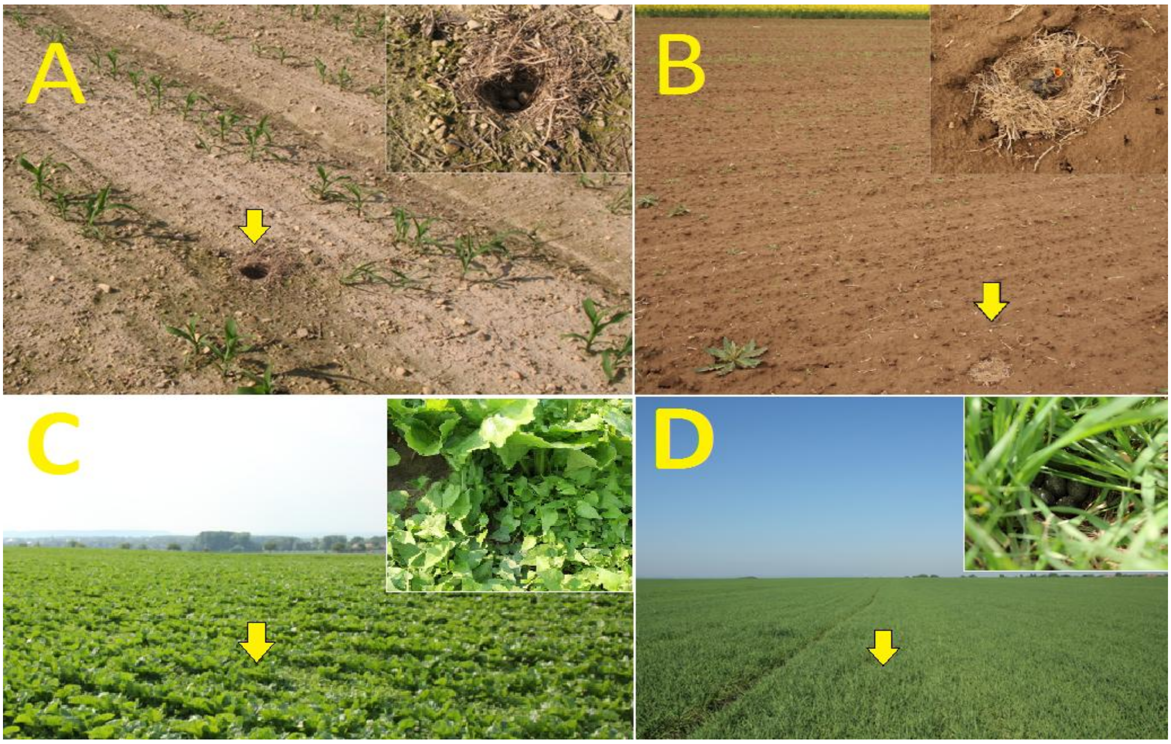


Figure 14. Examples of the variability in Skylark nest placement. A: maize, 7. 6. 2010; B: opium poppy, 16. 5. 2011; C: sugar beet, 1. 6. 2011; D: spring barley, 9. 5. 2011.

Table 2. The distribution of Skylark nests found among crops and the proportion of the total arable land in the study area covered by these crops.

Crop	Found nests		Arable land
	n	%	%
winter wheat	11	5.9	45
maize	92	49.5	15
winter rape	0	.	15
spring barley	9	4.8	10
sugar beet	32	17.2	5
alfalfa	10	5.4	≤2
opium poppy	20	10.8	≤2
oilseed caraway	3	1.6	≤2
pea	4	2.2	≤2
brown bean	3	1.6	≤1
potatoes	2	1.1	≤1

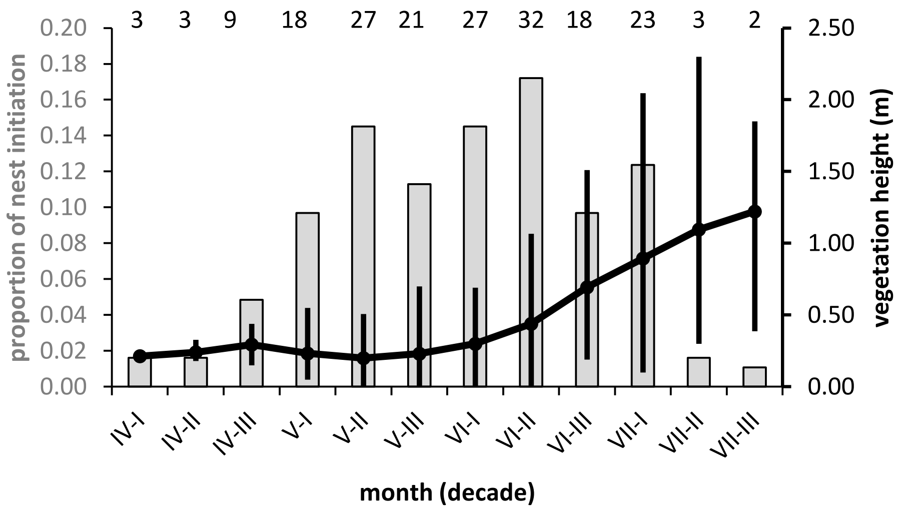


Figure 15. Seasonal changes in the mean (black dots) and range (black vertical line) of vegetation height (m) at monitored Skylark nests. Grey bars show the proportion of Skylark nest initiations (n = number of nests).

The overall nest predation rate of Skylarks did not show a clear trend over the course of the nesting season (Fig. 16). However, the proportion of bird (vs mammal) predation decreased over the course of season, along with vegetation growth (Fig. 17).

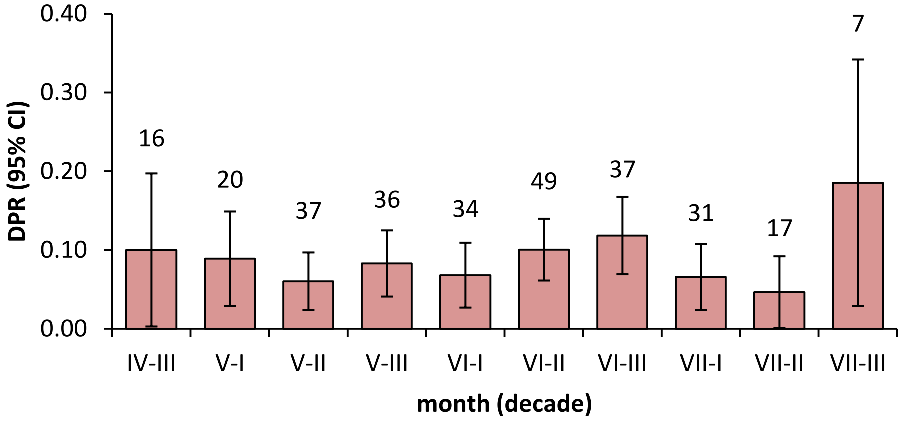


Figure 16. Daily predation rates of Skylark nests over the course of the nesting season (pooled data from 2009-2011, n = nests).

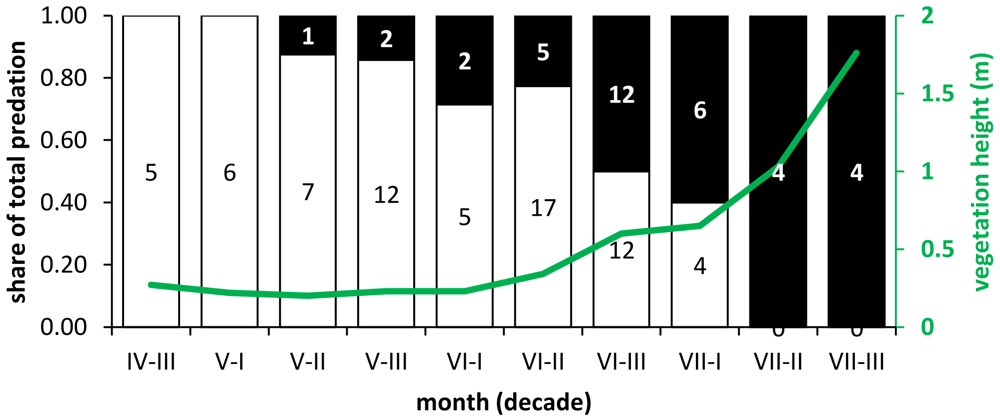


Figure 17. Proportion of bird (white) and mammal (black) predation events over the course of the nesting season (n = depredated nests, pooled data from 2009-2011). Green line: mean vegetation height (m) at predation time.

DISCUSSION

The number of Skylark nests found in each crop type was not proportional to the proportion of those crops in the study area. Despite the fact that these results might not be representative of the whole landscape, we believe they are valid for the crops well represented in our data (maize, sugar beet). Because we searched for nests visually, our data could be potentially biased towards poorly-concealed nests that in turn might be more vulnerable to visually guided predators (Gotmark et al. 1995, Weidinger 2002). Nevertheless, 26% (49/186) of active nests were found by the flushing of incubating birds, and these nests did not differ in vegetation characteristics from nests found directly by visual searching (unpublished data). Nest predation rates of Skylark nests did not show a clear trend over the nesting season; however, the proportion of bird predation decreased over the course of season, along with vegetation growth. This marked seasonal trend in predator composition probably results from the seasonal development of vegetation in the fields selected for nesting. The sparse but high vegetation of maize fields might provide suitable hiding and foraging sites for mammalian predators in late June and July (Panek & Bresinski 2002, Schley & Roper 2003), thus increasing their predation upon late Skylark nests located in such fields. The comparatively low vegetation height of all crops early in the season makes early nests more visible for bird predators and more accessible for their aerial attacks. The very low nest success found in this study suggests that none of the various crops provides safe nesting habitat. Both sparsely vegetated fields early in the season and wide row crops late in the season offer an attractive, yet risky, nesting habitat for Skylarks, especially late in the season when autumn-sown crops are too dense (Donald 2004).

Chapter 5: SPATIAL DISTRIBUTION OF SKYLARK NESTS WITHIN ARABLE FIELDS: EDGE EFFECTS AND PREDATION

Skylark nest success has been shown to vary according to field size, as well as within individual fields with proximity to tramlines (Donald et al. 2002) or field edges (Weibel 1999, Morris & Gilroy 2008). Crop monocultures on large arable fields reduce landscape heterogeneity on large scales; therefore, the importance of field edges as foraging and nesting habitats has increased during the last decades (Weibel 1999, Perkins et al. 2002, Vickery et al. 2002). However, nest proximity to field edges may decrease nesting productivity through increased rates of nest predation along field edges and other linear habitat structures (Morris & Gilroy 2008). This is because some predators tend to move/fly along linear structures such as tracks and the borders between fields (Lariviere 2003, Šálek et al. 2009).

Here, we asked whether Skylarks place nests proportionally to the available area within individual fields, or if they favour certain zones according to the distance from a field edge. Next we asked whether nest predation rates and predator composition vary according to the distance from a field edge. We hypothesized adaptive nest spacing within fields, with most of the available area along field edges being avoided due to the expected high risk of predation.

METHODS

Searching for nests and their subsequent monitoring followed the general field protocol described previously (see Chapter 1). We recorded all observer tracks inside each field parcel during nest searching and the coordinates of each discovered nest using a handheld Garmin Oregon 300 GPS (Fig. 18). This enabled us to quantify the spatial distribution of our nest searching effort through the proportion of tracks at a particular distance from a field edge as well as the spatial distribution of found nests. Parcel size, nearest distance to a field edge, woodland and settlement, and the length of tracks were measured using the Quantum GIS application (http://www.qgis.org). To analyse nest site preferences in relation to the distance from a field edge we applied the Manly resource selection design I (habitat use and availability are measured at the population level - animals are not identified, Manly et al. 2002). Distances and track lengths were grouped into edge-distance classes that represented discrete "habitats". The Manly selection ratio uses relative density as a measure of habitat selection (density-based selection ratio; Wi): Wi = proportion of utilized area / proportion of available area; Wi < 1 categories negatively selected, Wi = 1 no selection, Wi > 1 categories positively selected. Statistics were calculated using the Adehabitat package in R software (R version 3.0.0, AdehabitatHS Package 2011). Daily predation rates were calculated (see Chapter 1) for nests located in each edge-distance class.

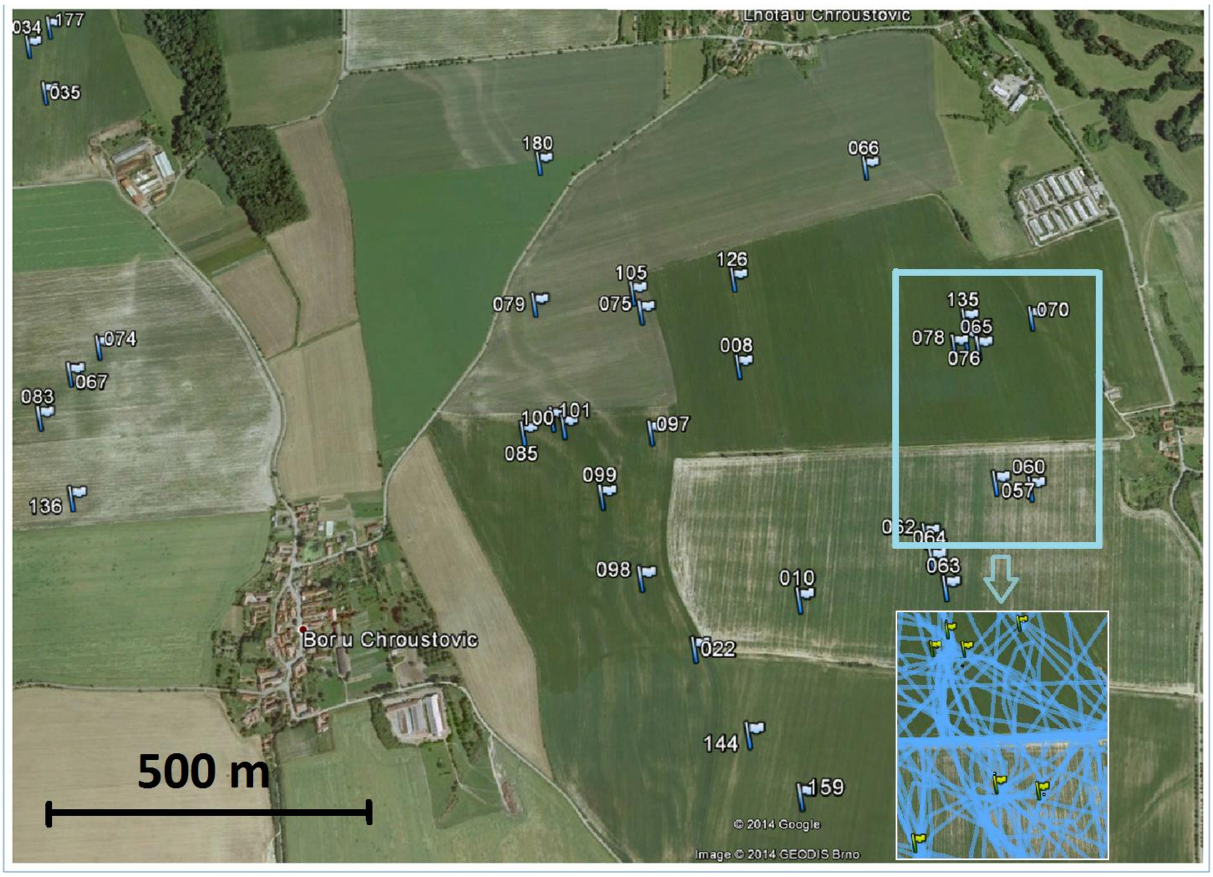


Figure 18. An example of monitored fields with locations (blue flags) of active Skylark nests found. Blue inset: an example of GPS recorded searching tracks used to quantify the searching effort with respect to the distance from a field edge. (Ortho photo map: Google Earth)

RESULTS

The spatial distribution of our nest searching effort was roughly proportional to the available area, with the exception of a lower effort close to field edges (Fig. 19). However, even after correction for this bias Skylarks were found to avoid areas close to field edges (<20 m) for nest placement (wi = 0.127 ±0.089 95% CI). In contrast, field interior areas more than 200 m from field edges were preferred for nest placement (wi = 1.437 ±0.201) (Fig. 20). Nest predation rates were only slightly and non-significantly higher along field edges (Fig. 21). The proportion of bird/mammal predation did not vary systematically with the distance from a field edge (Fig. 22).

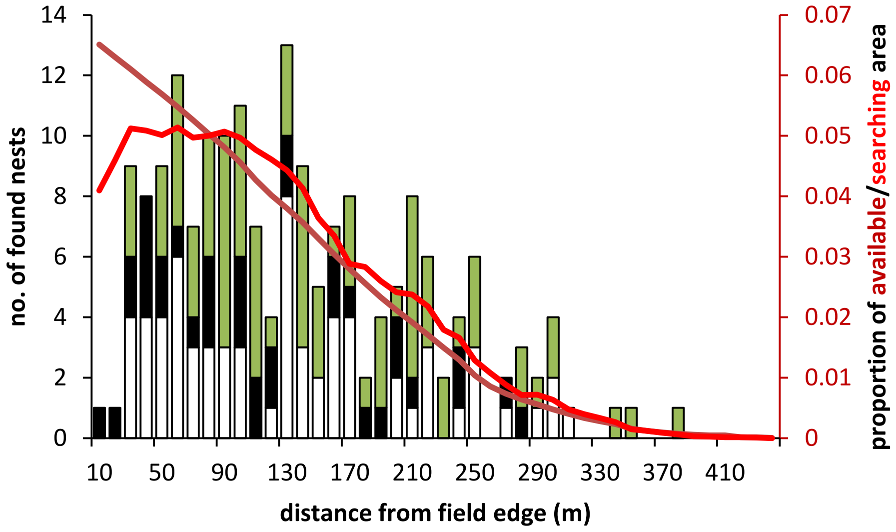


Figure 19. Distribution of Skylark nests (stacked bars: white - nests depredated by birds, black - nests depredated by mammals, green – no predation) according to the distance from a field edge. Red line: distribution of the searching effort, brown line: distribution of the available area within fields.

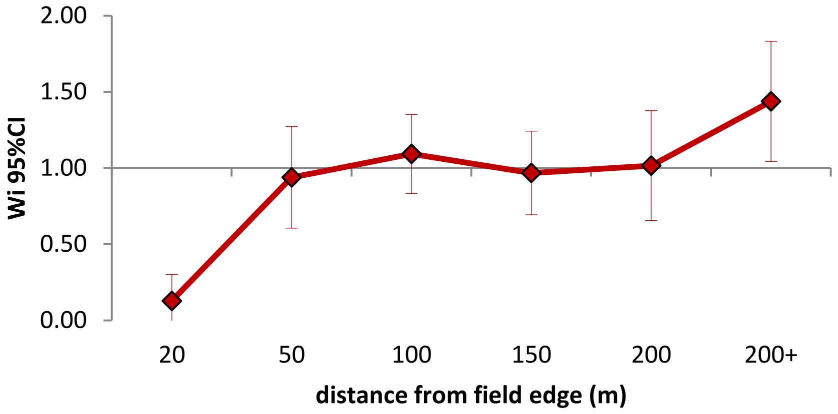


Figure 20. Manly's selection ratios (Wi; 95% CI) for Skylark nest placement within individual fields. Wi < 1 indicates categories negatively selected, Wi = 1 no selection and Wi > 1 categories positively selected.

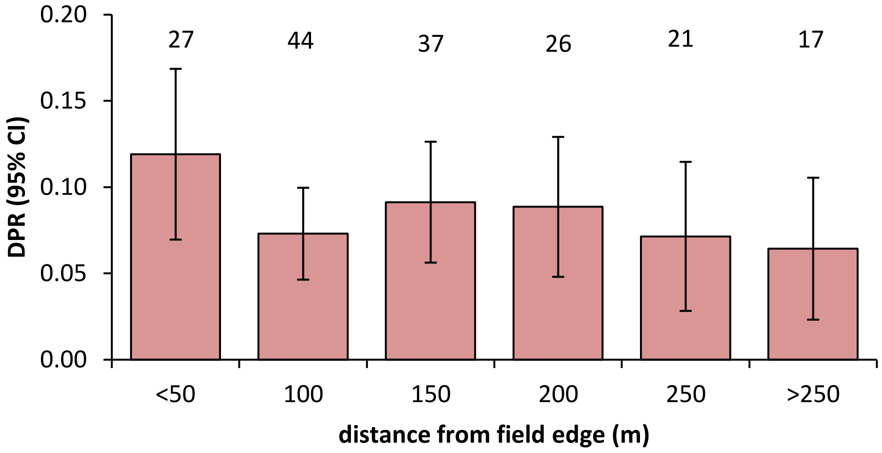


Figure 21. Daily predation rates of Skylark nests according to the distance from a field edge (n = nests).

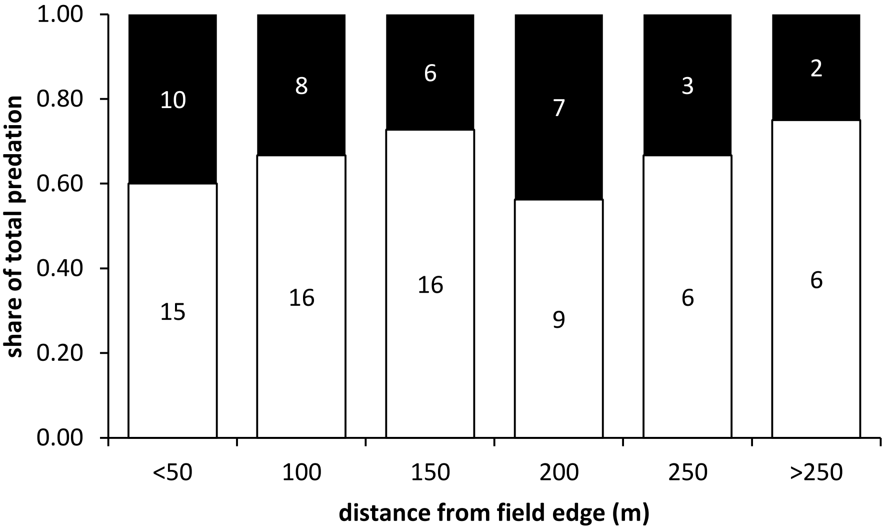


Figure 22. Proportion of predation events by birds (white) and mammals (black) according to the distance from a field edge (n = depredated nests).

DISCUSSION

Skylarks favoured nest locations in the less accessible area of the field interior compared to the more accessible areas close to the edge. This pattern cannot be accounted for by the spatial distribution of the nest searching effort. A significant negative influence on nest productivity, with Skylark nests placed closer to edges experiencing higher rates of nest predation, has been reported from the UK (Donald et al. 2002), where mammals were the dominant nest predators in arable fields (Morris & Gilroy 2008). In contrast, here we found only slightly increased nest predation rates along field edges, and both mammals and birds contributed to nest predation in similar proportions across all edge-distance classes. This pattern can be tentatively explained by the composition of local nest predators (see Chapter 1). The dominant bird predators (harriers, crows) probably use the entire area of fields as a foraging zone approximately uniformly, irrespective of field edges (Underhill-Day 1985, Vogrin 1998, Hudec & Šťastný 2005). Contrary to expectations (e.g. Šálek et al. 2009) we found mammalian predators in the interior of large fields (Table 1), which suggests extensive home ranges and high mobility (Harris et al. 1995, Genovesi et al. 1997, Anděra & Geisler 2012).

In conclusion, Skylarks seem to avoid areas close to field edges in spite of the comparatively low predation costs associated with nesting there. This avoidance of field edges or preference for field interiors might reflect past selection pressures not detected in present-day arable field habitats.

Chapter 6: INCUBATION AND FEEDING BEHAVIOUR OF SKYLARKS WITH NESTS IN ARABLE FIELDS

Adequate parental care plays an important role in the reproductive success of most bird species (Stearns 1992). However, parental care is also costly to the parents in terms of time and energy as well as risk to their own survival (Coleman & Gross 1991). Many studies have shown that intraspecific variation of incubation behaviour is affected by ambient temperature (Hötker 1990, Tieleman et al. 2008, Kovařík et al. 2009), food supply (Zimmerling & Akney 2005, Barnett & Briskie 2010) including allofeeding rates (Pearse et al. 2004), nest predation risk (Ghalambor & Martin 2002, Massaro et al. 2008, Cervencl et al. 2011) and the success of previous nesting attempts (Chalfoun & Martin 2010).

Predators use parental activity to find nests, exerting a predation cost that constrains the rates at which parents can visit nests to incubate their clutch and feed their young. Therefore, variation in predation risk during the egg and nestling periods may be an important source of natural selection on the behaviour and life history strategies of parents (Martin et al. 2000).

Incubation in Skylarks is undertaken by the female alone, and usually begins with the laying of the last egg (Donald 2004). The length of incubation period is quite variable, lasting between 10 and 13 days, with an average of 11 days (Delius 1965, Donald 2004). This short incubation period is supposed to be an adaptation to reduce the likelihood of the nest being predated (Donald 2004).

Here we present a descriptive account of incubation behaviour and examples of feeding behaviour at Skylark nests. A detailed analysis of the factors influencing between/within-day variation in Skylark incubation behaviour is presented in ***Contribution V***.

METHODS

Continuous video-monitoring of nests (see Chapter 1) provided a large amount of video footage. To analyse incubation behaviour and feeding rates we used video-records from days without heavy rain disturbances by agricultural operations, and midway between observer visits. The sampling unit of daylong parental activity was a 24-hour period starting at midnight, taken from continuous recordings of the entire nesting cycle. We sampled recordings to cover the whole breeding season (late April-late July) and all stages of incubation. The day of incubation (day 1 = the 1st day after clutch completion) was determined from a combination of egg floatation and known laying dates. We also took care to sample nests over the full range of crop heights and concealment levels.

We reviewed 24-hour video-recordings in the lab to determine the following variables: nest attentiveness, number of on/off bouts and duration of on/off bouts. Nest attentiveness was defined as the proportion of the total time female was incubating during the working day or during the 24-hour period (including overnight). The working day (*sensu* Shaw & Creswell 2014) is the period from the first morning departure from the nest to the last evening arrival to nest prior to overnight incubation.

A complete analysis of video-recordings of feeding behaviour still awaits processing. Here we analysed six daylong recordings of two nests to illustrate feeding rates at different chicks ages.

RESULTS

In total, 75 complete daily samples of incubation behaviour were analysed (2009: n=14; 2010: n=24; 2011: n=37) from 55 nests (2009: n = 11; 2010: n = 18; 2011: n = 26), with 1114.38 h during the active daylight period and 2150/2075 individual on/off bouts. Nest attentiveness was 0.81 (per 24 hour) or 0.69 (per working day) (Fig. 23), and varied markedly during the course of the working day (Fig. 24). The length of the working day lasted on average 14.87 h (range 11.87 – 17.07 h).

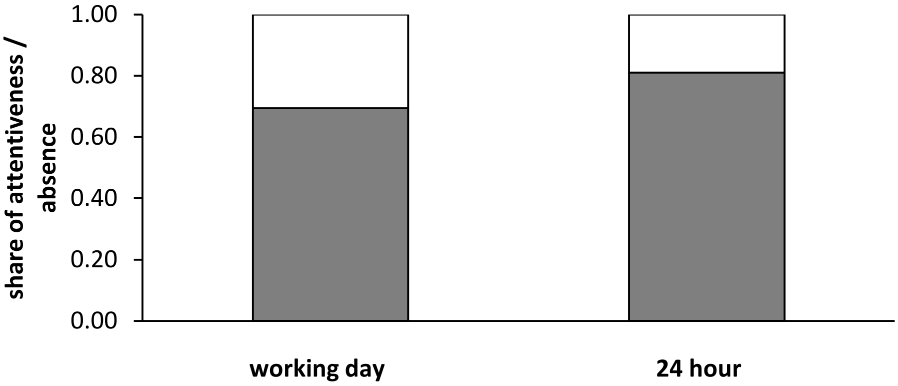


Figure 23. Nest attentiveness(grey part of bars) in Skylark females, calculated for either a working day (from the first morning departure to the last evening arrival) or a 24-h period, n = 75 daylong samples from 55 nests.

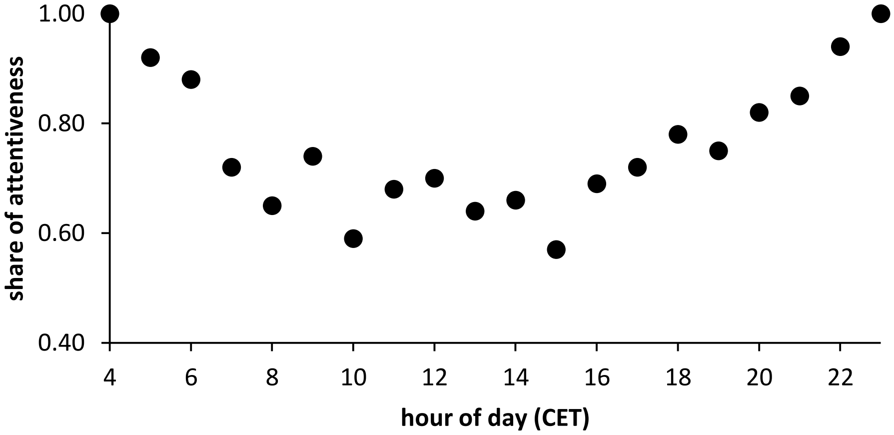


Figure 24. Variation in nest attentiveness during the day (n = 75 daylong samples).

The earliest morning departure from the nest was recorded at 04:23 CET (0.45 h before sunrise) the latest was at 07:41 (2.67 h after sunrise). The earliest evening arrival to roosting was at 18:18 (2.84 h before sunset), the latest was at 21:44 (0.85 h after sunset). Daily activity began mostly after sunrise (on average 1.0 h after sunrise) and ended around sunset (on average 0.05 h before sunset) (Fig. 25). Skylark females did not leave the nest during the hours of darkness.

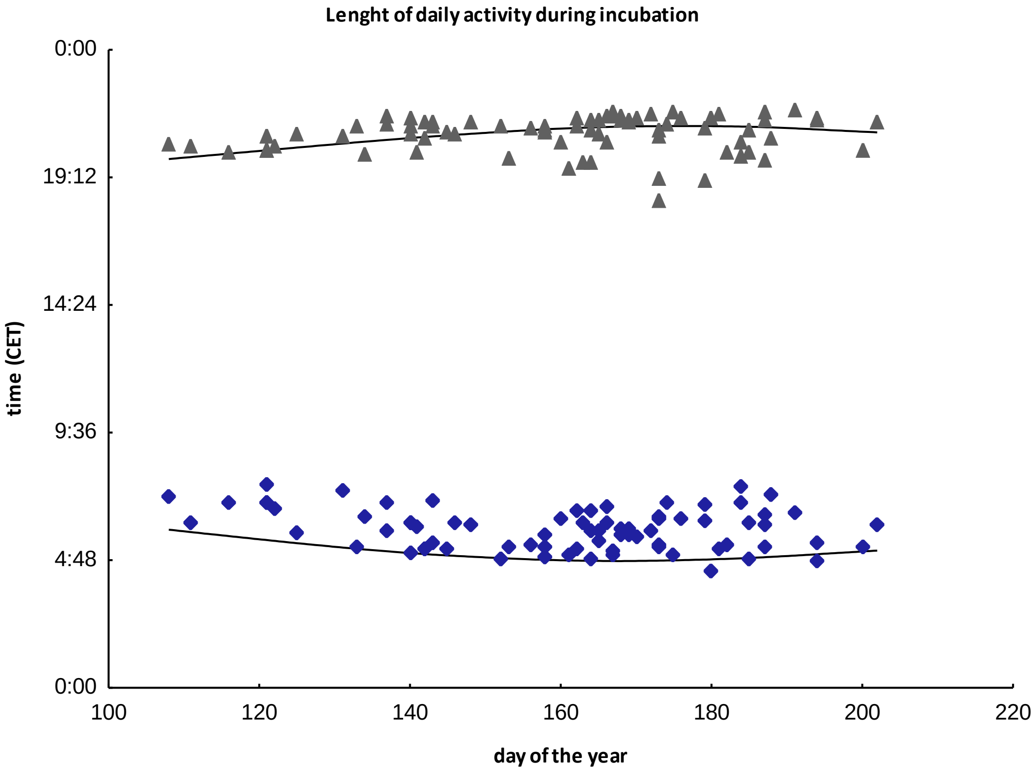


Figure 25. Time of the first morning departure from the nest (blue diamonds) and last evening arrival to the nest (grey triangles) during incubation over the course of the nesting season. The lower black line marks the time of sunrise, upper the time of sunset (n = 75 daylong samples from 55 nests).

Skylark females took on average 28.67 ± 1.02 (SE) departures per working day (n = 75 daylong samples from 55 nests). The frequency of departure rates peaked in the middle of the daylight period (Fig. 26). Number of on/off bouts during one day distinctively varied between individual females (Fig. 27). The average on-bout duration was 22.37 ± 0.37 min (mean ± SE; n = 2075) and average off-bout duration was 9.52 ±0.20 min (n = 2150). On-bouts were longer at the start and the end of daily activity, whereas the length of off-bouts was relatively stable with a marked decline at the end of daily activity (Fig. 28).

Female nest attentiveness decreased markedly from the incubation to nestling stage and further with the increasing age of nestlings (Fig. 29). Feeding rates increased with nestling age (Fig. 30).

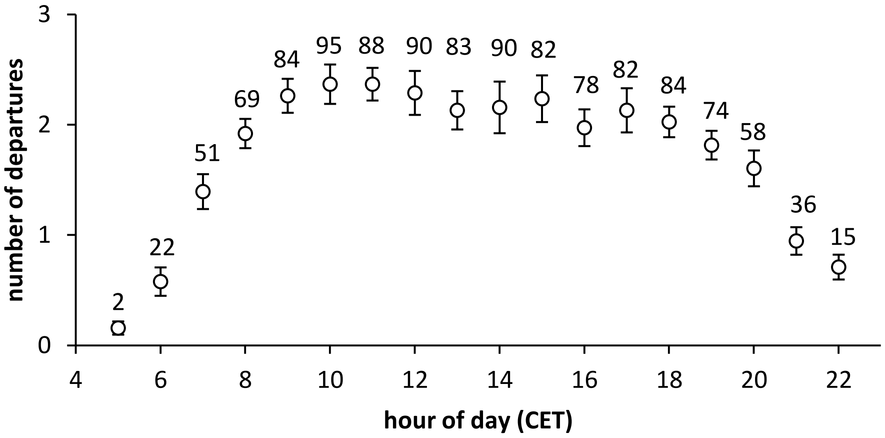


Figure 26. Variation in the number of incubation nest departures during the day (mean ± SE). The number of departures is given for each 1-hour period.

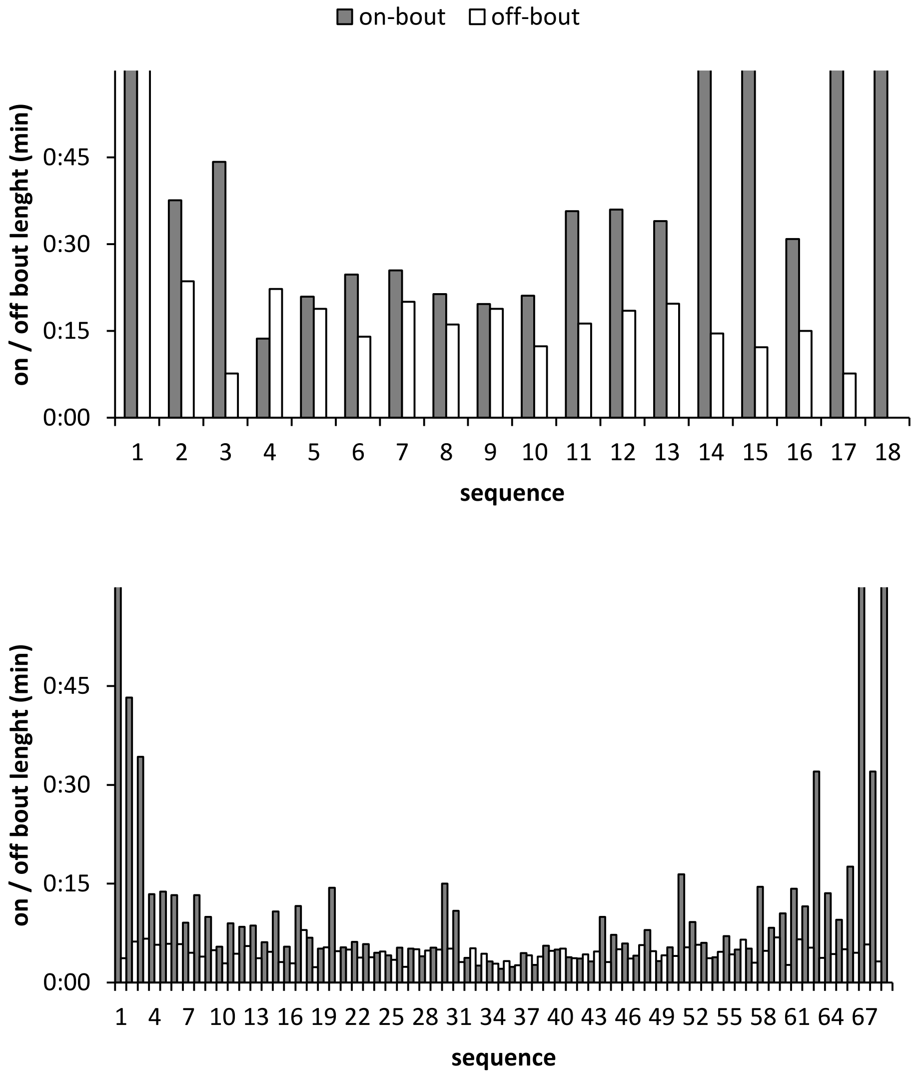
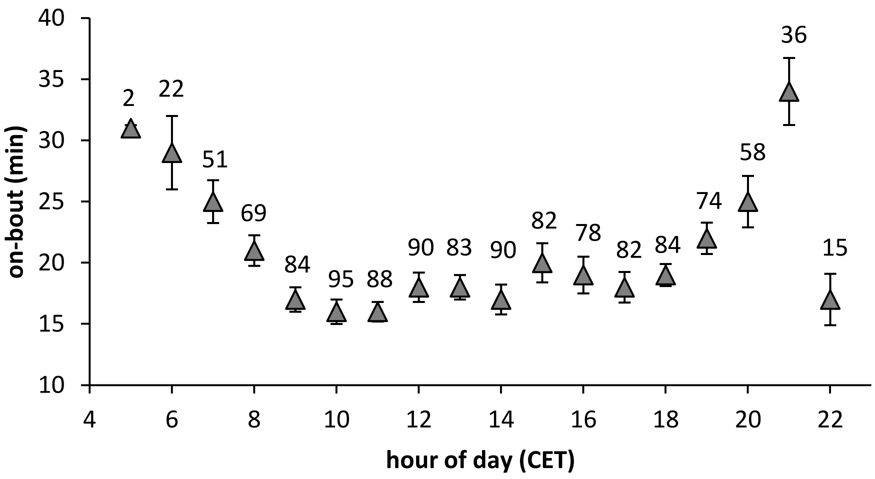


Figure 27. An example of extreme daily samples of incubation behaviour from two nests with the lowest/highest number of on/off bouts.



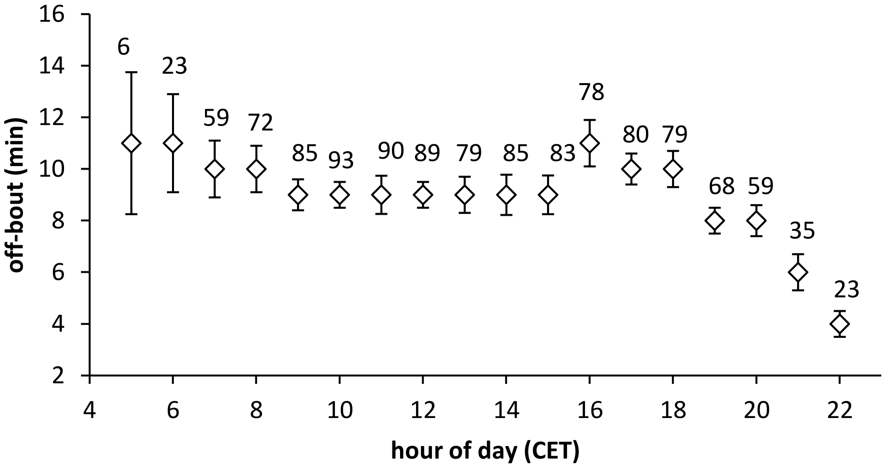


Figure 28. Variation in incubation on-bout (grey triangles) and off-bout (white diamonds) duration during the day (mean ± SE). The number of on/off bouts is given for each 1-h period.

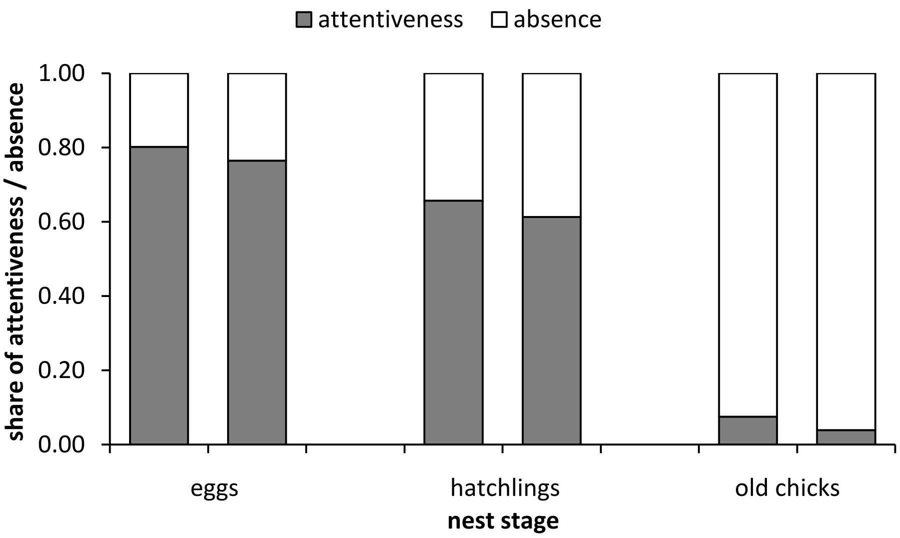


Figure 29. Examples of the attentiveness/absence of Skylark females during the working day at two nests, each sampled in three stages of nesting: clutch incubation, feeding hatchlings, feeding chicks at the age of 8 days.

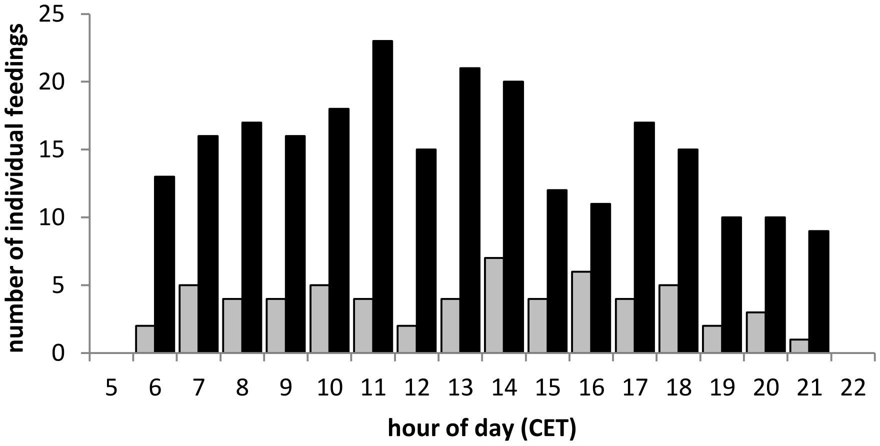


Figure 30. An example of variation in feeding rates during the day at one nest with hatchlings (grey columns) and the same nest just before fledging (black columns).

DISCUSSION

The basic characteristics of the incubation behaviour of Skylark females were similar to patterns found in other small passerines (Skutch 1962, Conway & Martin 2000, Chalfoun & Martin 2007, Kovařík et al. 2009, Davis & Holmes 2012). Mean on- and off- bout duration and average number of daily departures was also very similar to the incubation rhythm of other small open nesting passerines (Norment 1995, Rauter & Rayer 1997, Joyce et al. 2001, Kovařík et al. 2009). The complete absence of incubation feeding in our data set is in accordance with the high rates of nest predation found in this study (Ghalambor & Martin 2002, Matysioková et al. 2011). Apart from ambient temperature, the habitat characteristics (vegetation at the nest site), the day of incubation and clutch size had only weak effects on the mean daylong values of nest attentiveness and duration of on/off bouts (***Contribution V.***). This might indicate a narrow window for adjustments of incubation behaviour determined by the inherent physiological demands of parents and embryos in small passerines (Deeming 2002).

The incubation attentiveness was strongly affected by the time of day. Females spent more time attending clutches in the early morning and evening, with more frequent recesses during the afternoon. Moreover, this diurnal variation was dependent on (i.e. interacted with) ambient temperature and vegetation characteristics at the nest site (crop height and nest concealment). This suggests that the way incubation time is allotted during the day may be equally as important as the total amount of time spent incubating.

CONCLUSIONS

- Video-monitoring of active nests was an important method to reveal nest fates and predator identities.
- Nest success in intensive arable fields was very low in Skylarks, but relatively high in Lapwings. Skylark nests were vulnerable to all local predators, while it seems that Lapwings can avoid avian predation. Species composition of predators of Skylark nests and patterns in nest predation rates mostly differed from those reported from Western Europe, where the majority of depredation has been attributed to mammals. Our data show that Harriers account for almost half of total depredation events on Skylark nests in the Czech Republic.
- A distinctly different composition of nest predators was found in a semi-natural area in the Netherlands, where the main nest predators differed between co-occurring Skylarks and Woodlarks, possibly because differences in nest site selection.
- The high predation rate on Skylark nests was a consequence of sampling nests from risky plots (crops), not a consequence of disturbances associated with the research.
- Nest predation rates in Skylarks did not show a clear trend over the course of nesting season. The proportion of predation by birds decreased over the course of season, along with vegetation growth. The very low nest success found in arable fields suggests that none of the various crops provide safe nesting habitat. Both sparsely vegetated fields early in the season and wide row crops late in the season offer an attractive, yet risky, nesting habitat for Skylarks.
- Skylarks seem to avoid areas close to field edges in spite of the comparatively low predation cost associated with nesting there. This avoidance of field edges or preference for field interiors might reflect past selection pressures not detected in the present-day arable field habitats.
- The incubation behaviour of Skylarks nesting in arable fields was basically similar to what is known about passerine species with comparable life histories. Incubation behaviour was rather stable on a daily basis, yet it markedly varied within the day. This suggests the way incubation time is allotted during the day may be equally as important as the total amount of time spent incubating.
- Farmland ground nesting birds could be made less vulnerable to nest predation by managing habitats to ensure nests will be better hidden from predators or located in locations less favoured by predators.
- To better understand the role nest predation might play in population declines of farmland birds, I propose continued research on spatial and temporal variation in predator-specific nest predation rates, predator behaviour and their interactions with habitat. Manipulative field experiments will be essential for obtaining causal explanations of the patterns found.

REFERENCES

Aebischer, N. J. (1999). Multi-way comparisions and generalized linear models of the nest success: extensions of the Mayfield method. *Bird Study* **46:** 22–31.

Anděra, M. & Gaisler, J. (2012). *Savci České republiky*. Academia, Praha.

Andrén, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71:** 355–366.

Baillie, S. R., Marchant, J. H., Crick, H. Q. P., Noble, D. G., Balmer, D. E., Coombes, R. H., Downie, I. S., Freeman, S. N., Joys, A. C., Leech, D. I., Raven, M. J., Robinson, R. A. & Thewlis, R. M. (2006). *Breeding birds in the wider countryside: Their conservation status 2005*. BTO, Thetford.

Barnett, C. A. & Briskie, J. V. (2010). Silvereyes *Zosterops lateralis* increase incubation attentiveness in response to increased food availability. *Ibis* **159:** 169–172.

Bellebaum, J. & Bock, Ch. (2009). Influence of ground predators and water levels on Lapwing *Vanellus vanellus* breeding success in two continental wetlands. *J. Ornithol.* **150:** 221–230.

Benton, T. G., Vickery, J. A. & Wilson, J. D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* **18:** 182-188.

Berg, Å., Lindberg, T. & Källebrink, K. G. (1992). Hatching success of Lapwings on farmland: differences between habitats and colonies of different sizes. *J. Anim. Ecol.* **61:** 469–476.

Bijlsma, R. G. (2013). Trends en broedresultaten van roofvogels in Nederland in 2012. *De Takkeling* **21:** 5–48.

Bossema, I., Roëll, A. & Baeyens, G. (1986). Adaptations to interspecific competition in five corvid species in The Netherlands. *Ardea* **74:** 199–210.

Brambilla, M., Falco, R. & Negri, I. (2012). A spatially explicit assessment of within-season changes in environmental suitability for farmland birds along an altitudinal gradient. *Anim. Conserv.* **15:** 638–647.

Brandt, K. & Glemnitz, M. (2014). Assessing the regional impacts of increased energy maize cultivation on farmland birds. *Environ. Monit. Assess.* **186:** 679–697.

Burhans, D. E. & Thompson, F. R. (2001). Relationship of songbird nest concealment to nest fate and flushing behavior of adults. *Auk* **118:** 237–242.

Cervencl, A., Esser, W., Meier, M., Oberdiek, N., Thyen, S., Wellbrock, A. & Exo, K. M. (2011). Can differences in incubation patterns of Common Redshanks *Tringa totanus* be explained by variations in predation risk? *J. Ornithol.* **152:** 1033–1043.

Chalfoun, A. D. & Martin, T. E. (2007). Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis. *Anim. Behav*. **73:** 579–585.

Chalfoun, A. D. & Martin, T. E. (2010). Parental investment decisions in response to ambient nest-predation risk versus actual predation on the prior nest. *Condor* **112:** 701–710.

Chalfoun, A.D. & Schmidt, K. A. (2012). Adaptive breeding-habitat selection: is it for the birds? *Auk* **129:** 589–599.

Chamberlain, D. E. & Crick, H. Q. P. (1999). Population declines and reproductive performance in Skylarks *Alauda arvensis* in different regions and habitats of the United Kingdom. *Ibis* **141:** 38–51.

Coleman, R. M. & Gross, R. M. (1991). Parental investment theory: The role of past investment. *Trends Ecol. Evol.* **6:** 404–406.

Conway, C. J. & Martin, T. E. (2000). Evolution of passerine incubation behavior: Influence of food, temperature, and nest predation. *Evolution* **54:** 670–685.

Davis, S. K. & Holmes, T. G. (2012). Identification of Sprague's Pipit nest predators. Pp. 67–76 in Ribic, C. A., Thompson, F. R., & Pietz, P. J. *Video-surveillance of nesting birds*. University of California Press, London.

de Carli, E., Fornasari, L., Bani, L. & Bottoni, L. (1998). Trend in distribution, abundance and habitat features of Skylark *Alauda arvensis* in northern Italy. *Game and Wildlife* **15:** 387–396.

Deeming, D. C. (2002). *Avian incubation: Behaviour, Environment and Evolution*. Oxford University Press, Oxford.

Delius J. D. (1965). A population study of Skylarks *Alauda arvensis*. *Ibis* **107:** 466–492.

Dion, N., Hobson, K. A. & Lariviere, S. (2000). Interactive effects of vegetation and predators on the success of natural and simulated nests of grassland songbirds. *Condor* **102:** 629–634.

Donald, P. F. (2004). *The Skylark*. T & AD Poyser, London.

Donald, P. F., Evans, A. D., Muirhead, L. B., Buckingham, D. L., Kirby, W. B. & Schmitt, S. I. A. (2002). Survival rates, causes of failure and productivity of Skylark *Alauda arvensis* nests on lowland farmland. *Ibis* **144:** 652–664.

Donald, P. F., Sanderson, F. J, Burfield, I. J. & van Bommel, F. P. J. (2006). Further evidence of continent-wide impacts of agricultural intensification on european farmland birds 1990-2000. *Agr. Ecosyst. Environ.* **116:** 189–196.

Donovan, T. M. & Thompson, F. R. (2001). Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. *Ecol. Appl*. **11:** 871–882.

Eraud, C. & Boutin, J. M. (2002). Density and productivity of breeding Skylarks *Alauda arvensis* in relation to crop type on agricultural lands in western France. *Bird Study* **49:** 287–296.

Evans, K. L. (2004). The potential for interactions between predation and habitat change to cause population declines of farmland birds. *Ibis* **146:** 1–13.

Flohre, A., Fischer, C., Aavik, T., Bengtsson, J., Berendse, F., Bommarco, R., Ceryngier, P., Clement, L. W., Dennis, C., Eggers, S., Emmerson, M., Geiger, F., Guerrero, I., Hawro, V., Inchausti, P., Liira, J., Morales, M. B., Oñate, J. J., Pärt, T., Weisser, W. W., Winqvist, C., Thies, C. & Tscharntke, T. (2011). Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids and birds. *J. Appl. Ecol*. **21:** 1772–1781.

Fuller, R. J. (2012). *Birds and habitats: relationships in changing landscapes*. Cambridge University press, Cambridge.

Fuller, R. J., Gregory, R. D., Gibbons, D. W., Marchant, J. H., Wilson, J. D., Baillie, S. R. & Carter, N. (1995). Population declines and range contractions among lowland farmland birds in Britain. *Conserv. Biol.* **9:** 1425–1441.

Genovesi, P., Sinibaldi, I. & Boitani, L. (1997). Spacing patterns and territoriality of the stone marten. *Canad. J. Zool.* **75:** 1966–1971.

Ghalambor, C. K. & Martin, T. E. (2002). Comparative manipulation of predation risk during incubation reveals variability in the plasticity of parental responses. *Behav. Ecol.* **13:** 101–108.

Gibbons, D. W., Amar, A., Anderson, G. Q. A., Bolton, M., Bradbury, R. B., Eaton, M. A., Evans, A. D., Grant, M. C., Gregory, R. D., Hilton, G. M., Hirons, G. M. J., Hughes, J., Johnstone, I., Newbery, P., Peach, W. J., Ratcliffe, N., Smith, K. W., Summers, R. W., Walton, P. & Wilson, J. D. (2008). *The predation of wild birds in the UK: a review of its conservation impact and management*. RSPB Research Report no. 23. RSPB, Sandy, UK.

Gilroy, J. J., Anderson, G. Q. A., Grice, P. V., Vickery, J. A. & Sutherland, W. J. (2010). Mid-season shifts in the habitat associations of Yellow Wagtails *Motacilla flava* breeding in arable farmland. *Ibis* **152:** 90–104.

Gilroy, J. J., Anderson, G. Q. A., Vickery J. A., Grice, P. V. & Sutherland, W. J. (2011). Identifying mismatches between habitat selection and habitat quality in a ground-nesting farmland bird. *Anim. Conserv.* **14:** 620–629.

Gotmark, F., Blomqvist, D., Johansson, O. C. & Bergkvist, J. (1995). Nest site selection: a trade-off between concealment and view of the surroundings? *J. Avian Biol*. **26:** 305–312.

Hanski, I., Hansson, L. & Henttonen, H. (1991). Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.* **60:** 353–367.

Harris, S., Morris, P., Wray, S. & Yalden, D. (1995). *A review of British mammals: population estimates and conservation status of British mammals other than cetaceans*. JNCC, UK.

Hart, J. D., Milsom, T. P., Fisher, G., Wilkins, V., Moreby, S. J., Murray, A. W. A. & Robertson, P. A. (2006). The relationship between Yellowhammer breeding performance, arthropod abundance and insecticide applications on arable farmland. *J. Appl. Ecol.* **43:** 81–91.

Hayhow, D. B., Conway, G., Eaton, M. A., Grice, P. V., Hall, C., Holt, C. A., Kuepfer, A., Noble, D. G., Oppel , S., Risely, K., Stringer, C., Stroud, D. A., Wilkinson, N. & Wotton, S. (2014). *The state of the UK's birds 2014*. RSPB, BTO, WWT, JNCC, NE, NIEA, NRW & SNH, Sandy, Bedfordshire.

Hegemann, A. (2012). *Strive to survive: The Skylark's ecology and physiology in an annual-cycle perspective*. PhD Thesis. University of Groningen, Netherlands.

Hole, D. G., Whittingham, M. J., Bradbury, R. B., Anderson, G. Q. A., Lee, P. L. M., Wilson, J. D. & Krebs, J. R. (2002). Widespread local House Sparrow extinctions – Agricultural intensification is blamed for the plummeting populations of these birds. *Nature* **148:** 931–932.

Hötker, H. (1990). *Der Wiesenpieper: ANTHUS PRATENSIS*. Die neue Brehm-Bücherei, Wittenberg Lutherstadt.

Hudec, K. & Šťastný, K. (2005). *Fauna ČR Ptáci 2/I*. Academia, Praha.

Jeromin, K. (2002). *Zur Ernährungsökologie der Feldlerche ALAUDA ARVENSIS L. 1758 in der Reproduktionsphase*. PhD Thesis. Christian-Albrechts-Universität Kiel, Deutschland.

Joyce, E. M., Sillet, T. S. & Holmes, R. T. (2001). An inexpensive method for quantifying incubation patterns of open-cup nesting birds, with data for Black-throated Blue Warblers. *J. Field Ornithol.* **72:** 369-379.

Kis J., Liker A. & Székely T. (2000). Nest defence by Lapwings: Observations on natural behaviour and an experiment. *Ardea* **88:** 155–163.

Kovařík, P., Pavel, V. & Chutný, B. (2009). Incubation behaviour of the Meadow Pipit (*Anthus pratensis*) in an alpine ecosystem of Central Europe. *J. Ornithol.* **150:** 549–556.

Kragten, S., Trimbos, K. B. & de Snoo, G. R. (2008). Breeding Skylarks *Alauda arvensis* on organic and conventional arable farms in the Netherlands. *Agricult. Ecosyst. Environm*. **126:** 163–167.

Kuiper, M. W., Ottens, H. J., van Ruijven, J., Koks, B. J., Snoo, G. R. & Berendse, F. (2015). Effects of breeding habitat and field margins on the reproductive performance of Skylarks (*Alauda arvensis*) on intensive farmland. J. Ornithol. (*in press*; DOI 10.1007/s10336-015-1159-8).

Lariviere, S. (2003). Edge Effects, predator movements, and the travel-lane paradox. *Wildlife S. B.* **31:** 315–320.

Ławicki, Ł., Wylegała, P., Batycki, A., Kajzer, Z., Guentzel, S., Jasiński. M., Kruszyk, R., Rubacha, S. & Żmihorski, M. (2011). Long-term decline of grassland waders in western Poland. *Vogelwelt* **132:** 101–108.

Lima, S. L. (2009). Predators and the breeding birds: behavioral and reproductive flexibility under the risk of predation. *Biol. Rev.* **84:** 485–513.

MacDonald, M. A. & Bolton, M. (2008). Predation on wader nests in Europe. *Ibis* **150:** 54–73.

Magnhagen, C. (1991). Predation risk as a cost of reproduction. *Trends Ecol. Evol.* **6:** 183–186.

Mallord, J. W., Dolman, P. M., Brown, A. & Sutherland, W. J. (2007). Nest-site characteristics of Woodlarks *Lullula arborea* breeding on heathlands in southern England: are there consequences for nest survival and productivity? *Bird Study* **54:** 307–314.Manly, B. F. J.,

McDonald, L. L., Thomas, D. L., McDonald, T. L. & Erickson, W. L. (2002). *Resource Selection by Animals. Statistical Design and Analysis for Field Studies.* Kluwer Academic Publishers Dordrecht.

Martin, T. E. (1993). Nest predation and nest sites. *Bio-Science* **43:** 523–532.

Martin, T. E. (1995). Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.* **65:** 101–127.

Martin, T. E. & Li, P. (1992). Life history traits of open- versus cavity-nesting birds. *Ecology* **73:** 579–592.

Martin, T. E. & Ghalambor, C. K. (1999). Males feeding females during Incubation I. Required by microclimate or constrained by nest predation? *Amer. Nat.* **153:** 131–139.

Martin, T. E., Scott, J. & Menge, C. (2000). Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc. R. Soc. Lond.* B **267:** 2287–2293.

Massaro, M., Starling-Windhof, A., Briskie, J. V. & Martin, T. E. (2008). Introduced mammalian predators induce behavioural changes in parental care in an endemic New Zealand bird. *Plos One* **3:** e2331.

Matysioková, B., Cockburn, A. & Remeš, V. (2011). Male incubation feeding in songbirds responds differently to nest predation risk across hemispheres. *Anim. Behav.* **82:** 1347–1356.

Mayfield, H. F. (1975). Suggestions for calculating nest success. *Wilson Bull.* **87:** 456–466.

Misenhelter, M. D. & Rotenberry, J. T. (2000). Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. *Ecology* **81:** 2892–2901.

Morris, A. J., Holland, J. M., Smith, B. & Jones, N. E. (2004). Sustainable arable farming for an improved environment (SAFFIE): managing winter wheat sward structure for Skylarks *Alauda arvensis*. *Ibis* **146:** 155–162.

Morris, A. J. & Gilroy, J. J. (2008). Close to the edge: predation risks for two declining farmland passerines. *Ibis* **150:** 168–177.

Newton, I. (1986). *The Sparrowhawk*. Poyser, Calton.

Newton, I. (2013*). Bird populations*. W. Collins, London.

Norment, Ch. J. (1995). Incubation patterns in Harris`s Sparrow and White-crowned Sparrows in the Northwest territories , Canada. *J. Field Ornithol*. **66:** 553–563.

Panek, M. & Bresinski, W. (2002). Red fox *Vulpes vulpes* density and habitat use in a rural area of western Poland in the end of 1990s, compared with the turn of 1970s. *Acta Theriol.* **47:** 433–442.

Pearse, A. T., Cavitt, J. F. & Cully, J. F. (2004). Effects of food suplementation on female nest attentiveness and incubation mate feeding in two sympatric wren species. *Wilson Bull*. 116: 23 – 30.

Perkins, A. J., Whittingham, M. J., Morris, A. J. & Bradbury, R. B. (2002). Use of margins by foraging Yellowhammers *Emberiza citrinella*. *Agric. Ecosyst. Environ*. **93:** 413–420.

Pescador, M. & Peris, S. (2001). Effects of land use on nest predation: an experimental study in Spanish croplands. *Folia Zool.* **50:** 127–136.

Rangen, S. A., Clark, R. G. & Hobson, K. A. (1999). Influence of nest-site vegetation and predator community on the success of artificial songbird nests. *Can. Zool.* **77:** 255–261.

Rauter, C. & Reyer, H. U. (1997). Incubating pattern and foraging effort in the female Water Pipit *Anthus spinoletta*. *Ibis* **139:** 441–446.

Reif, J., Voříšek, P., Šťastný, K., Bejček, V. & Petr, J. (2008). Agricultural intensification and farmland birds: new insights from a central European country. *Ibis* **150:** 569–605.

Remeš, V. (2000). How can maladaptive habitat choice generate source-sink population dynamics? *Oikos* **91:** 579-582.

Ribic C. A., Thompson F. R. & Pietz P. J. (2012). *Video-surveillance of nesting birds*. University of California Press, London.

Richardson, T. W., Gardali, T. & Jenkins, S. H. (2009). Review and meta-analysis of camera effects on avian nest success. *J. Wildlife Manage.* **73:** 287–293.

Robertson, J. & Berg, A. (1992). Status and population changes of farmland birds in southern Sweden. *Ornis Svec.* **2:** 119–130.

Roodbergen, M., Werf, B. & Hötker, H. (2012). Revealing the contributions of reproduction and survival to the Europe-wide decline in meadow birds: review and meta-analysis. *J. Ornithol.* **153:** 53–74.

Saurbrei, R., Ekschmitt, K., Volters, W., Gottschalk, T. K. (2014). Increased energy maize production reduces farmland bird diversity. *GCB Bioenergy* **6:** 265–274.

Schekkerman, H. (2008). *Precocial problems; Shorebird performance in relation to wheather, farming and predation*. PhD Thesis. University of Groningen, Netherlands.

Schläpfer, A. (1988). Populationsökologie der Feldlerche *Alauda arvensis* in der intensiv genutzen Agrarlandschaft. *Ornithol. Beob.* **85:** 309–371.

Schley, L. & Roper, T. J. (2003). Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. *Mammal. Rev.* **33:** 43–56.

Schmidt, K. A. & Whelan, C. J. (1999). Seasonal fecundity in songbirds: can abandonment, renesting, and double brooding ameliorate high nest predation and brood parasitism? *Conserv. Biol.* **13:** 46–57.

Shaffer, T. L. (2004). A unified approach to analyzing nest success. *Auk* **121:** 526–540.

Shaw, P. & Creswell, W. (2014). Latitudinal variation in day lenght and working day lenght has a confounding effect when comparing nest attentiveness in tropical and temperates species. *J. Ornithol.* **155:** 481–489.

Shrubb, M. (2007). *The Lapwing*. Poyser, London.

Sitters, H. P., Fuller, R. J., Hoblyn, R. A., Wright, M. T., Cowie, N. & Bowden, C. G. R. (1996). The Woodlark *Lullula arborea* in Britain: population trends, distribution and habitat occupancy. *Bird Study* **43:** 172–187.

Skutch, A. F. (1962). The constancy of incubation. *Willson Bull*. **74:** 115–152.

Stearns, S. C. (1992). *The Evolution of Life Histories*. Oxford University Press, London.

Šálek, M. & Cepáková, E. (2006). Do Northern Lapwings *Vanellus vanellus* and Little Ringed Plovers *Charadrius dubius* rely on egg crypsis during incubation? *Folia Zool.* **55:** 43–51.

Šálek, M. & Šmilauer, P. (2002). Predation of Northern Lapwing *Vanellus vanellus* nests: the effect of population density and spatial distribution of nests. *Ardea* **90:** 51–60.

Šálek, M., Kreisinger, J., Sedláček, F. & Albrecht, T. (2009). Corridor vs. hayfield matrix use by mammalian predators in an agricultural landscape. *Agric. Ecosyst. Environ.* **134:** 8–13.

Šťastný, K., Bejček, V. & Hudec, K. (2006). *Atlas hnízdního rozšíření ptáků v České republice*. Aventinum, Praha.

Teunissen, W., Schekkerman, H., Willems, F. & Majoor, F. (2008). Identifying predators of eggs and chicks of Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa* in the Netherlands and the importance of predation on wader reproductive output. *Ibis* **150:** 74–85.

Tieleman, I. B., van Noordwijk, H. J. & Williams, J. B. (2008). Nest site selection in a hot desert: Trade-off between microclimate and predation risk? *Condor* **110:** 116–124.

Toepfer, S. & Stubbe, M. (2001). Territory density of the Skylark (*Alauda arvensis*) in relation to field vegetation in central Germany. *J. Ornithol.* **142:** 184–194.

Underhill-Day, J. C. (1985). The food of breeding Marsh Harriers *Circus aeruginosus* in East Anglia. *Bird Study* **32:** 199 - 206.

van Beusekom, R., Huigen, P., Hustings, F., de Pater, K. & Thissen, J. (2004). *Rode Lijst van de Nederlandse broedvogels*. Tirion Uitgevers B. V., Baarn.

Vickery, J. A., Carter, N. & Fuller, R. J. (2002). The potential value of managed cereal field margins as foraging habitats for farmland birds in the UK. *Agric. Ecosyst. Environ.* **89:** 41–52.

Vogrin, M. (1998). Abundance and habitat selection of breeding *Corvus corone cornix* on agricultural land in Central Slovenia. *Acta Zool. Lituan.* **8:** 127–130.

Voříšek, P., Klvaňová, A., Brinke, T., Cepák, J., Flousek, J., Hora, J., Reif, J., Šťastný, K. & Vermouzek Z. (2009). Stav ptactva České republiky 2009. *Sylvia* **45:** 1–38.

Weibel, U. M. (1999). *Effects of wildflower strips in an intensively used arable area on Skylarks (Alauda arvensis).* PhD Thesis. Swiss Federal Institute of Technology, Zurich, Switzerland.

Weidinger, K. (2002). Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. *J. Anim. Ecol.* **71:** 424–437.

Weidinger, K. (2003). Hnízdní úspěšnost. Co to je a jak se počítá. *Sylvia* **39:** 1–24.

Weidinger, K. (2008). Nest monitoring does not increase nest predation in open-nesting songbirds: inference from continuous nest-survival data. *Auk* **125:** 859–868.

Weidinger, K. (2009). Nest predators of woodland open-nesting songbirds in central Europe. *Ibis* **151:** 352–360.

Weidinger, K. (2010). Foraging behaviour of nest predators at open-cup nests of woodland passerines. *J. Ornithol.* **151:** 729–735.

Whittingham, M. J. & Evans, K. L. (2004). A review of the effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis* **146:** 210–220.

Wilson, A., Vickery, J. A. & Browne, S. J. (2001). Numbers and distribution of Northern Lapwings *Vanellus vanellus* breeding in England and Wales in 1998. *Bird Study* **48:** 2–17.

Wotton, S. R. & Gillings, S. (2000). The status of breeding Woodlarks *Lullula arborea* in Britain in 1997. *Bird Study* **47:** 212–224.

Yanes, M. & Suarez, F. (1995). Nest predation patterns in ground nesting passerines on the Iberian Peninsula. *Ecography* **18:** 423–428.

Zimmerling, J. R. & Akney, C. D. (2005). Variation in incubation patterns of Red-winged Blackbirds nesting at lagoons and ponds in Eastern Ontario. *Wilson Bull.* **117:** 280–290.

Žídková, L., Marková, V. & Adamík, P. (2007). Lapwing *Vanellus vanellus* chick ringing data indicate a region-wide population decline in the Czech Republic. *Acta Zool*. **56:** 301–306.

CONTRIBUTION I.

Praus, L. & Weidinger, K. (2010). Predators and nest success of Sky Larks *Alauda arvensis* in large arable fields. *Bird Study* **57:** 525–530.

Bird Study (2010) **57,** 525–530

Predators and nest success of Sky Larks *Alauda arvensis* in large arable fields in the Czech Republic

LIBOR PRAUS* and KAREL WEIDINGER
Department of Zoology and Laboratory of Ornithology, Faculty of Science, Palacky University, tr. Svobody 26, CZ-771 46 Olomouc, Czech Republic

Capsule Nest failure owing to a range of predators was high, but the level and specificity of nest depredation cannot be generalised.

Aims To determine fates and predators of Sky Lark nests in conventionally managed arable fields in the Czech Republic.

Methods Sky Lark nests in large fields (mainly Maize, Sugar Beet and Opium Poppy) were monitored by means of continuous video surveillance.

Results Primary nest fates of 42 active nests were fledging (13), depredation (22), desertion (5), nestling death (1), and flooding (1). The overall nest success (Mayfield estimate) was 17% (all mortality factors considered) or 27% (only depredation). Depredation events were caused by Marsh Harrier *Circus aeruginosus* (11), Hooded Crow *Corvus cornix* (4), Stone Marten *Martes foina* (3), Montagu's Harrier *Circus pygargus* (2), Red Fox *Vulpes vulpes* (2), Hedgehog *Erinaceus* sp. (2) and Eurasian Jackdaw *Corvus monedula* (1). Successful nests were only slightly more away from field edge than depredated nests; nests taken by birds tended to be closer to field edge than those depredated by mammals. The possible reasons for the absence of a clear edge effect include comparatively large field parcels (about 50 ha) and location of nests far from field edge (median = 195 m).

Conclusion Nest survival and composition of nest predators are site-specific and contingent upon the study method and may not be simply generalised.

INTRODUCTION

Sky Larks *Alauda arvensis* are one of the most abundant and widespread of ground-nesting farmland birds (Donald 2004). No other passerine in Europe shows such a strong association with arable land (Reif *et al.* 2008). Sky Lark populations have declined over past decades across much of western Europe and these declines have coincided temporally and spatially with a rapid intensification in farming (Erhard & Wink 1987, Chamberlain & Crick 1999). Therefore, Sky Larks are commonly included among top indicators of loss of biodiversity in agriculture landscapes (Gregory *et al.* 2005). Nest depredation, the principal cause of low nesting success in most passerines, usually accounts for over 70% of all failures of Sky Lark nests (Weibel 1999, Donald *et al.* 2002). Yet, the question of whether nest depredation may have increased as a result of farmland habitat changes, has rarely been addressed (Evans 2004) and no studies have reported depredation as a major driver of population decline for Sky Larks (Donald 2004). Nevertheless, nest success has been shown to vary among crop types (Weibel 1999, Donald *et al.* 2002, Eraud & Boutin 2002, Kragten *et al.* 2008) as well as within individual fields with a proximity to tramlines (Donald *et al.* 2002) or field edges (Weibel 1999, Morris & Gilroy 2008).

Although previous studies often implied predator-specific effects on nest survival, there is little definitive evidence of nest predator identity in farmland birds (MacDonald & Bolton 2008, Teunissen *et al.* 2008). We are aware of only one video surveillance study of any ground-nesting passerine in crop fields (Morris & Gilroy 2008). Because predator–prey systems are locally specific, conclusions from one area may not be directly applicable to other regions (Thompson 2007).

*Correspondence author. Email: prabor@centrum.cz

Agricultural landscapes have developed differently in the western and eastern parts of Europe over the past 50 years. Temporary decline in the intensity of agriculture around 1990 is the likely reason why populations of farmland birds, including Sky Larks, have declined at a slower rate in central and eastern Europe compared with western Europe (Donald *et al.* 2001; see Reif *et al.* [2008] for details on the Czech Republic). Contrary to the well-documented population trends, data on breeding performance and nest predators in the former socialist eastern and central European countries are lacking (Shurulinkov 2005, Erdös *et al.* 2009).

Here we report on breeding success and nest predators of Sky Larks in intensively managed arable fields in the Czech Republic. The results should help to asses whether predictors of Sky Lark nest success identified in western European farmlands can be generalised to other regions.

METHODS

Study area and field methods

The study was conducted in the northeast part of Chrudim District, the Czech Republic (49° 54′ N, 15° 59′ E, altitude 270–460 m) in 2009. The study area of 55 km^2 was characterised by predominance of conventionally managed arable land (>80% of total area, mean parcel size about 50 ha), interspersed with remnants of deciduous woodland (<5% of total area) and villages. Main crop types were: Winter Wheat *Triticum aestivum* (50%); Maize *Zea mays* (25%); Sugar Beet *Beta vulgaris*, Lucerne *Medicago sativa* and Spring Barley *Hordeum vulgare* (each 5%); Opium Poppy *Papaver somniferum*, Oilseed Winter Rape *Brassica napus subsp. napus*, Caraway *Carum carvi*, Pea *Pisum sativum* and Sunflower *Helianthus annuus* (each ≤2%).

Fieldwork was carried out from early April to late July; roughly 100 days were devoted to nest searching in the whole study area. This period covers the breeding season of Sky Larks in the Czech Republic (from end of March to end of July [Hudec 1983]). Sky Larks avoid fields with dense coverage and tall vegetation (Toepfer & Stubbe 2001); therefore, we located nests by systematically searching only the ground of sparse and low-vegetated fields (≤60% coverage and ≤60 cm vegetation height). Searches for nests were conducted mainly in Winter Wheat (during April), Maize, Opium Poppy and Sugar Beet (all from May to July). We did not keep systematic observations of adult birds, but we opportunistically searched in places where birds were flushed. Age of nestlings was estimated from their development; stage of incubation was estimated by egg floatation. First-egg laying date was back-calculated from brood size and hatch date or clutch size and commencement of incubation. Position of each discovered nest was determined with a global positioning system; nearest distance to field edge, woodland and settlement were measured from orthophotomaps. Height of vegetation at the nest site (m) and the degree of nest cover (scored as: 1, well visible from above; 2, intermediate; 3, completely covered from above) were measured and the nest was photographed at each nest visit.

During field work we kept notes on occurrence of potential nest predators, including direct observation (corvids, raptors), occupation of potential breeding sites (completely known only for Marsh Harrier *Circus aeruginosus*) and records of trails and feaces (carnivorous mammals).

Video monitoring

Video monitoring systems consisted of a video camera (40 × 35 mm) with nine infrared-emitting diodes, a portable security digital video recorder (DVR) (Yoko RYK-9107), and a 12V/65Ah deep cycle battery. The DVR was housed in a weatherproof plastic box (125 × 95 × 50 mm) and connected to the camera by a 5-m cable and to the battery by a 1-m cable. All outer parts of the system were camouflaged by brown-green spotted painting. The camera was mounted on a piece of wire that was inserted in the ground and allowed the adjustment of camera position. Cameras were placed 0.7–2.0 m from nests (depending on nest visibility) and 2–20 cm above the ground, never exceeding the height of surrounding vegetation. We used local natural material (dry vegetation, stones) to mask the camera; all other parts (box, battery, cables) were buried under ground. We set the DVR to record continually with a frequency of 10 frames s^{-1} at 640 × 480 pixel resolution and a medium quality. These settings allowed for 4.5 days of recording on a 16 GB memory card. Cameras were deployed either immediately at the time of nest discovery (22 nests), on the same day after a period of 2–5 hours (11 nests) or within the next 4 days after discovery (10 nests). Deployment of the video system by two people took about 20 minutes. We avoided disturbing vegetation or leaving dead-end tracks (to/from the nest). Also, we postponed deployment of the camera (or subsequent nest visits) in the case of rain or when the nest was exposed to another human disturbance (agricultural operations). We visited the nests usually

(70% cases) every fourth day to check nest content and to change the battery and memory card; the rest of the nest visits were at 1- to 3-day intervals. To keep the time spent at nests short (≤15 min), we offloaded all data in the lab. About half of our visits took place in the morning (08:30–10:30 Central European Time) and half in the afternoon (14:30–17:30). When a nest was found to be empty, we recorded and photographed its state and searched in the immediate vicinity for signs of nest failure (eggshells, feathers, dead nestlings) or success (alive fledglings, droppings, juvenile feathers). We continued video monitoring of deserted or partially depredated nests with intact egg(s) for at least two 4-day periods, depending on availability of active nests at that time.

Data analysis

When the nest checked was empty or when some eggs/nestlings were missing we viewed the recordings backward to find the event and to determine the nest fate, timing of the event and the species of nest predator. Although the exact survival times and nest fates were available, the limited sample size precluded sensible application of the methods suitable for continuous survival data (e.g. Weidinger 2008). Instead, we measured the exposure period in nest-days where each nest-day was treated as an independent binary observation (survived or failed). We estimated the daily survival rate (DSR) as a simple ratio of survived to exposed nest-days. With the present type of data this method is equivalent to the conventional logistic (Aebischer 1999) or logistic-exposure (Shaffer 2004) models without covariates. Contrary to these methods applied to ordinary nest-visitation data (i.e. interval survival data) the survival time in this study was known and did not need to be estimated from the length of nest visit intervals. In this way we estimated DSR separately for the egg (laying and incubation) and nestling stage of active nests, and for deserted (= inactive) nests with eggs. For the active nests we considered either nest losses owing to predation, or combined mortality.

Given the limited sample size we performed only simple univariate analyses; we focused on indicating possible patterns in the data rather than on formal statistical testing. We examined an edge effect on nest survival by means of logistic regression (*sensu* Aebischer 1999; with scale adjustment for over-dispersion) with distance to field edge entered as a single continuous nest-level covariate. We checked for potential observer effects on nest survival by analysing the relationship between timing of observer visits and timing of depredation events. We compared DSR among the four days that followed after a nest visits by means of logistic regression with day entered as either a categorical (day 1 vs. subsequent days) or continuous time-dependent covariate. Lowered DSR on the day just after nest visit would indicate attraction of predators by observer presence at the nest, while DSR gradually increasing from the first to the forth day after observer visit would indicate a vanishing effect of tracks left by observer at the nest (for detailed reasoning see Weidinger [2008]).

RESULTS

In all, 44 nests (42 active nests and two abandoned nests with fresh intact eggs) were found in 16 different fields representing seven crop types: Maize (19 nests, five fields), Sugar Beet (12, 4), Opium Poppy (7, 2), Lucerne (2, 2), Caraway (2, 1), Spring Barley (1) and Pea (1). Median age of nests at discovery was 4 days (day 1 = first-egg laying date); the nests were found before commencement of egg laying (5), during laying (8), incubation (28) or nestling stage (1). Nests found by accidental flushing of incubating birds ($n = 15$) were similar in vegetation characteristics (difference ± se; vegetation cover score: 0.01 ± 0.26; vegetation height: –0.07 ± 0.12 cm) to nests found directly by visual search ($n = 27$). The electronic supplementary data file details all nest depredation events.

The median laying date was 3 June (24 April–5 July, $n = 42$), size of completed clutches was 3.86 ± 0.12 se (2–5, $n = 35$), number of hatchlings was 3.53 ± 0.19 se (2–4, $n = 15$) and number of fledglings was 3.31 ± 0.33 se (1–4, $n = 13$). Primary nest fates of the 42 active nests were: fledging (13); complete depredation (17); partial depredation (5); desertion (5); nestling death (1); and flooding (1). Almost all (26/29) nest losses occurred during the egg stage. Overall nest success was 17% (all mortality factors considered) or 27% (only predation considered; Table 1).

Video monitoring of 43 nests (342 active nest-days and 106 abandoned nest-days) documented 38 primary nest fates and seven secondary depredations on nests previously deserted or partially depredated, yielding a total of 25 documented depredation events at 23 nests (see supplementary data which is available on the supplementary content tab of the article's Informaworld page at http://dx.doi.org/10.1080/00063657.2010.506208). In all, seven species (four birds, three mammals) were recorded depredating Sky Lark nests: Marsh Harrier (11 events, 11 nests), Hooded Crow *Corvus cornix* (4, 3), Stone Marten *Martes foina* (3, 3), Montagu's Harrier *Circus pygargus* (2, 2),

Table 1. Survival rates of active (primary depredation, all mortality) and abandoned (secondary depredation) Sky Lark nests in crop fields in the Czech Republic.

Mortality factor	Total nests	Failed nests	Exposure nest-days	DSR[a]	95% CI		Nest survival[b]	95% CI	
Nesting stage									
Primary predation									
Eggs	42	21	245	0.914	0.872	0.946	0.29	0.15	0.46
Nestling	16	1	120	0.992	0.954	1.000	0.94	0.69	1.00
Total	43	22	365	0.940	0.910	0.962	0.25	0.13	0.42
Total[c]	–	–	–	–	–	–	0.27	0.10	0.46
Secondary predation									
Eggs (abandoned)	13	7	118	0.941	0.882	0.976	–	–	–
All mortality factors									
Eggs	42	26	245	0.894	0.848	0.930	0.21	0.10	0.36
Nestling	16	3	120	0.975	0.929	0.995	0.82	0.55	0.96
Total	43	29	365	0.921	0.888	0.946	0.16	0.07	0.30
Total[c]	–	–	–	–	–	–	0.17	0.06	0.34

[a]Daily survival rate; [b]nest survival = DSR^t, where t = 14 (eggs), 8 (nestlings) or 22 (total) days; [c]calculated as the product of nest survival for the egg and nestling stage, respectively.

Hedgehog *Erinaceus* sp. (2, 2), Red Fox *Vulpes vulpes* (2, 2) and Eurasian Jackdaw *Corvus monedula* (1, 1). Appearance of the depredated nests did not provide any useful cues to determine the species or class of the predator. Predation by birds and mammals was restricted to day (05:34–20:34) and night (21:24–03:43), respectively. The median distance from Sky Lark nests depredated by Marsh Harrier to the nearest occupied harrier nest was 3.5 km (0.3–4.5 km, *n* = 11).

Daily nest survival rate (considering predation losses) did not change appreciably with distance to field edge: DSR (logit scale) = 2.3647 (± 0.6710 se) + 0.0024 (± 0.0039 se) × distance (m). Correspondingly, successful nests (*n* = 13) were, on average, only slightly further away from field edge (difference ± se: 31 ± 25 m) than depredated nests (primary predation, *n* = 22). Nests depredated by birds (*n* = 17) differed little from those depredated by mammals (*n* = 7) in vegetation cover score (difference ± se: 0.34 ± 0.41), but tended to be closer to field edge (difference ± se: –76 ± 34 m).

Daily survival rate (considering depredation losses during the egg stage) was non-significantly higher on the first day after observer visit compared with subsequent days (difference ± se, logit scale: 0.3855 ± 0.4268) and did not show a trend across the four days in between nest visits (regression slope ± se, logit scale: –0.0412 ± 0.1425).

DISCUSSION

The overall nest success (Mayfield estimate) in this study (17%) was lower than the average values found in the UK (23–40% [Wilson *et al.* 1997, Chamberlain & Crick 1999, Donald *et al.* 2002]), Germany (22% [Jeromin 2002]) and Switzerland (22% [Weibel 1999]). However, our estimate is based on single-year data and it falls at the lower end of annual variation reported from elsewhere (e.g. 18–38% [Weibel 1999], 16–30% [Donald *et al.* 2002]); more data are needed to assess an 'average' nest success in our study area.

At least 76% (22/29) of primary nest losses were caused by depredation, which is in agreement with other Sky Lark studies (Weibel 1999, Donald *et al.* 2002). About 72% (18/25) of all depredation events were attributable to birds, which is in stark contrast with a study from the UK (Morris & Gilroy 2008), where all depredation was caused by mammals. While corvids were traditionally suspected as primary nest predators of ground-nesting farmland birds across Europe, the recent video evidence from western Europe revealed carnivorous mammals as the principal nest predators of waders (MacDonald & Bolton 2008, Teunissen *et al.* 2008) as well as passerines (Morris & Gilroy 2008). Yet, we showed that raptors (Harriers) might account for as much as 52% (13/25) of total depredation events within our study area. This is unlikely to be a site-specific effect as the local abundance of Marsh Harriers (two breeding pairs in a 55 km area) was representative of the large-scale density for the whole Czech Republic (2.0–3.6 pairs/100 km^2; based on data from Šťastný *et al.* 2006). Corvids and carnivores each accounted for about 20% (5/25) of total nest depredation events. Predation by foxes was low, despite their local abundance (inferred from hunting statistics) and frequently reported effects on farmland birds (Tryjanowski *et al.* 2002, MacDonald & Bolton 2008). Unlike foxes, predators like martens (López-Martín *et al.* 1992, Virgós & García 2002) and hedgehogs (Micol *et al.* 1994) are thought to require more complex habitat structure and their activity is supposed to be concentrated along field edges and linear habitats (Šálek *et al.* 2009). Surprisingly, we documented their nest depredations and occurrence (based on trails and faeces) even in central part of large crop fields (>300 m from edge).

Contrary to some previous studies (Weibel 1999, Donald 2004, Morris & Gilroy 2008) we did not find depredation rates to vary with distance to field edge. The possible reasons include comparatively large size of field parcels (about 50 ha in this study versus e.g. 12 ha in a UK study [Vickery *et al.* 2002]), small number of monitored nests and their location rather far from field edge (median = 195 m, minimum = 30 m). The edge effect on nest success in crop fields is presumably a result of increased mammalian nest depredation near edges, but the principal predators in our study were birds. Moreover, nests depredated by birds tended to be closer to field edge than those depredated by mammals.

Breeding performance of Sky Larks varies markedly among crop types (Wilson *et al.* 1997, Weibel 1999, Donald *et al.* 2002), but the number of Sky Lark nests found in each crop type was not entirely proportional to the distribution of crops in the study area. Despite the fact that our results might not be representative of the whole landscape, we believe they are valid for the crops well represented in our sample (Maize, Sugar Beet). Because we searched for nests visually, our sample could be potentially biased towards poorly concealed nests that in turn might be more vulnerable to visually guided predators. Nevertheless, 36% (15/42) of active nests in our sample were found by accidental flushing of incubating birds and these nests did not differ in vegetation characteristics from nests found directly by visual search. Moreover, nests depredated by birds were not less concealed than those depredated by mammals.

Although the use of cameras may bias nest depredation rates and species composition of predators (Richardson *et al.* 2009), this effect is unlikely to be serious in this study, for several reasons. We minimised the visible parts of video equipment (see Methods), while various human artefacts not associated with research activity (plastic garbage, cans, etc.) were common on all fields under study. Most importantly, the observed composition of predators is conservative with regard to the direction of potential bias. Predators potentially under-represented because of neophobia to human artefacts (cameras) – raptors – dominated in our sample of video records, while predators potentially over-represented through attraction to the monitored nests (human trails, infrared illumination) – carnivores – were less frequent. The absence of a temporal relationship between timing of our nest visits and timing of depredation events indicates that overall nest survival in this study was not seriously influenced through changed depredation risk (Weidinger 2008). All cases of 'spontaneous' (unexplained) nest desertion occurred more than 12 hours (i.e. night hours on the next day or later) after our last nest visit. Contrary to potential bias (see earlier) video monitoring allowed us to eliminate the problem of uncertain nest fates in estimating nest survival (Manolis *et al.* 2000, Weidinger 2007).

To conclude, we showed that video surveillance represents an efficient tool to study nest success and nest predators of a farmland breeding passerine. This study of Sky Larks revealed a distinctly different composition of nest predators than studies of farmland birds in other regions or an earlier study of woodland passerines in the same area (Weidinger 2009). Identification of principal predators is vital for causal interpretation of observed nest depredation rates as well as for efficient conservation of populations threatened by nest depredation (Gibbons *et al.* 2007). Yet, we caution against generalisation of site-specific results and unsupported assumptions on predator identity.

ACKNOWLEDGEMENTS

This work was supported by the Ministry of Education of the Czech Republic (grant no: MSM 6198959212). We would like to thank Peter Adamík, James Gilroy and Simon Gillings for comments on the manuscript.

REFERENCES

Aebischer, N.J. 1999. Multi-way comparisions and generalized linear models of the nest success: extensions of the Mayfield method. *Bird Study* **46:** 22–31.

Chamberlain, D.E. & Crick, H.Q.P. 1999. Population declines and reproductive performance of Skylarks *Alauda arvensis* in different regions and habitats of the United Kingdom. *Ibis* **141:** 38–51.

Donald, P.F. 2004. *The Skylark.* T & AD Poyser, London.

Donald, P.F., Evans, A.D., Muirhead, L.B., Buckingham, D.L., Kirby, W.B. & Schmitt, S.I.A. 2002. Survival rates, causes of failure and productivity of Skylark *Alauda arvensis* nests on lowland farmland. *Ibis* **144:** 652–664.

Donald, P.F., Green, R.E. & Heath, M.F. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. Lond. B.* **268:** 25–29.

Eraud, C. & Boutin, J.M. 2002. Density and productivity of breeding Skylarks *Alauda arvensis* in relation to crop type on agricultural lands in western France. *Bird Study* **49:** 287–296.

Erdös, S., Báldi, A. & Batáry, P. 2009. Nest-site selection and breeding ecology of Sky Larks *Alauda arvensis* in Hungarian farmland. *Bird Study* **56:** 259–263.

Erhard, R. & Wink, M. 1987. Veränderungen des Brutvogelbestandes im Großraum Bonn: Analyse der Rasterkartierung 1975 und 1985. *J. Ornithol.* **128:** 477–484.

Evans, K.L. 2004. The potential for interactions between predation and habitat change to cause population declines of farmland birds. *Ibis* **146:** 1–13.

Gibbons, D.W., Amar, A., Anderson, G.Q.A., Bolton, M., Bradbury, R.B., Eaton, M.A., Evans, A.D., Grant, M.C., Gregory, R.D., Hilton, G.M., Hirons, G.M.J., Hughes, J., Johnstone, I., Newbery, P., Peach, W.J., Ratcliffe, N., Smith, K.W., Summers, R.W., Walton, P. & Wilson, J.D. 2007. The predation of wild birds in the UK: a review of its conservation impact and management. RSPB Research Report no. 23., RSPB, Sandy, UK.

Gregory, R.D., van Strien, A.J., Voříšek, P., Gmelig Meyling, A.W., Noble, D.G., Foppen, R.P.B. & Gibbons, D.W. 2005. Developing indicators for European birds. *Phil. Trans. R. Soc. Lond. B.* **360:** 269–288.

Hudec, K. (ed). 1983. *Fauna ČSSR*, Ptáci 3. Academia, Prague, Czech Republic.

Jeromin, K. 2002. Zur Ernährungsökologie der Feldlerche (*Alauda arvensis* L. 1758) in der Reproduktionsphase. PhD Thesis, Christian-Albrechts-Universität, Kiel.

Kragten, S., Trimbos, K.B. & de Snoo, G.R. 2008. Breeding Skylarks (*Alauda arvensis*) on organic and conventional arable farms in the Netherlands. *Agric. Ecosyst. Environ.* **126:** 163–167.

López-Martín, J.M., Ruiz-Olmo, J. & Cahill, S. 1992. Autumn home range and activity of a Stone Marten (*Martes foina* Erxleben, 1777) in Northeastern Spain. *Misc. Zool.* **16:** 258–260.

MacDonald, M.A., Bolton, M. 2008. Predation on wader nests in Europe. *Ibis* **150:** 54–73.

Manolis, J.C., Andersen, D.E. & Cuthbert, F.J. 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. *Auk* **117:** 615–626.

Micol, T., Doncaster, C.P. & Mackinlay, L.A. 1994. Correlates of local variation in the abundance of Hedgehogs *Erinaceus europaeus*. *J. Anim. Ecol.* **63:** 851–860.

Morris, A.J. & Gilroy, J.J. 2008. Close to the edge: predation risks for two declining farmland passerines. *Ibis* **150:** 168–177.

Reif, J., Voříšek, P., Šťastný, K., Bejček, V. & Petr, J. 2008. Agricultural intensification and farmland birds: new insights from a central European country. *Ibis* **150:** 569–605.

Richardson, T.W., Gardali, T. & Jenkins, S.H. 2009. Review and meta-analysis of camera effects on avian nest success. *J. Wildl. Manage.* **73:** 287–293.

Shaffer, T.L. 2004. A unified approach to analyzing nest success. *Auk* **121:** 526–540.

Shurulinkov, P. 2005. On the breeding biology of Skylark *Alauda arvensis cantarella* (Aves: Passeriformes) in West Bulgaria. *Acta Zool. Bulg.* **57:** 207–216.

Šálek, M., Kreisinger, J., Sedláček, F. & Albrecht, T. 2009. Corridor vs. hayfield matrix use by mammalian predators in an agricultural landscape. *Agric. Ecosyst. Environ.* **134:** 8–13.

Šťastný, K., Bejček, V. & Hudec, K. 2006. *Atlas hnízdního rozšíření ptáků v České republice.* Aventinum, Prague, Czech Republic.

Teunissen, W., Schekkerman, H., Willems, F. & Majoor, F. 2008. Identifying predators of eggs and chicks of Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa* in the Netherlands and the importance of predation on wader reproductive output. *Ibis* **150:** 74–85.

Thompson, F.R. 2007. Factors affecting nest predation on forest songbirds in North America. *Ibis* **149:** 98–109.

Toepfer, S. & Stubbe, M. 2001. Territory density of the Skylark (*Alauda arvensis*) in relation to field vegetation in central Germany. *J. Ornithol.* **142:** 184–194.

Tryjanowski, P., Goldyn, B. & Surmacki, A. 2002. Influence of the Red Fox (*Vulpes vulpes* Linnaeus 1758) on the distribution and number of breeding birds in an intensively used farmland. *Ecol. Res.* **17:** 395–399.

Vickery, J., Carter, N. & Fuller, R.J. 2002. The potential value of managed cereal field margins as foraging habitats for farmland birds in the UK. *Agric. Ecosyst. Environ.* **89:** 41–52.

Virgós, A. & García, F.J. 2002. Patch occupancy by Stone Martens *Martes foina* in fragmented landscapes of central Spain: the role of fragment size, isolation and habitat structure. *Acta Oecol.* **23:** 231–237.

Weibel, U.M. 1999. Effects of wildflower strips in an intensively used arable area on Skylarks (*Alauda arvensis*). PhD thesis, Swiss Federal Institute of Technology, Zurich, Switzerland.

Weidinger, K. 2007. Handling of uncertain nest fates and variation in nest survival estimates. *J. Ornithol.* **148:** 207–213.

Weidinger, K. 2008. Nest monitoring does not increase nest predation in open nesting songbirds: inference from continuous nest-survival data. *Auk* **125:** 859–868.

Weidinger, K. 2009. Nest predators of woodland open-nesting songbirds in central Europe. *Ibis* **151:** 352–360.

Wilson, J.D., Evans, J., Browne, S.J. & King, J.R. 1997. Territory distribution and breeding success of Skylarks *Alauda arvensis* on organic and intensive farmland in southern England. *J. Appl. Ecol.* **34:** 1462–1478.

(MS received 25 June 2010; revised MS accepted 1 July 2010)

Predators and nest success of Sky Larks *Alauda arvensis* in large arable fields in the Czech Republic

Supplementary File

Summary of video recorded Sky Lark nest depredation events and characteristics of the depredated Sky Lark nests in crop fields in the Czech Republic. Mammalian predators are shown in boldface.

Event Predator[a]	Date (d.m.)	Time (CET)	Crop[b]	Area (ha)	Height[c] (m)	Cover[c]	Edge[d] (m)	Forest[d] (m)	Settlement[d] (m)
Primary predation									
Marsh Harrier	31.05.	18:55	Maize[1]	47.5	0.18	2[f]	240	820	550
Marsh Harrier	02.06.	07:12	Maize[1]	47.5	0.11	1[f]	140	710	740
Hooded Crow[1]	06.06.	17:09	Maize[1]	47.5	0.11	2	120	700	490
Hooded Crow	16.06.	15:30	Maize[1]	47.5	0.20	3[f]	130	620	300
Hedgehog	16.06.	22:22	Maize[1]	47.5	0.14	3	190	1020	450
Marsh Harrier	11.06.	06:59	Maize[2]	11.6	0.22	2[f]	90	270	890
Marsh Harrier	24.06.	20:20	Maize[2]	38.2	0.25	3	150	310	240
Marsh Harrier	26.06.	20:34	Maize[3]	38.2	0.26	3[f]	100	330	400
Marsh Harrier	29.06.	17:16	Maize[4]	50.1	0.40	2[f]	140	2290	220
Hedgehog	30.06.	01:53	Maize[4]	50.1	0.34	2[f]	130	250	500
Marten	22.06.	03:43	Maize[5]	86.0	0.32	3	340	400	660
Marsh Harrier	16.06.	05:34	Sugar Beet[7]	75.0	0.25	2[f]	100	1820	1050
Marsh Harrier	18.06.	06:15	Sugar Beet[7]	75.0	0.25	3	200	2070	830
Marsh Harrier	07.07.	09:50	Sugar Beet[8]	53.1	0.16	1	140	1280	430
Red Fox	08.07.	22:21	Sugar Beet[8]	53.1	0.40	1	260	1070	420
Marten[2]	26.05.	02:58	Sugar Beet[9]	53.0	0.12	1	240	330	820
Marten [e]	29.05.	21:24	Lucerne[10]	18.5	0.22	1	90	570	670
Montagu's Harrier	10.05.	05:54	Opium Poppy[12]	48.2	0.16	1[f]	140	840	610
Secondary predation									
Hooded Crow[1]	11.06.	19:07	Maize[1]	47.5	0.13	2	120	700	490
Marsh Harrier	19.06.	06:43	Maize[4]	50.1	0.50	1	190	540	500
Marsh Harrier	18.06.	14:18	Maize[6]	44.3	0.70	3	30	835	580
Hooded Crow	06.07.	12:26	Sugar Beet[8]	53.1	0.20	2	130	1340	280
Red Fox[2]	02.06.	02:10	Sugar Beet[9]	53.0	0.14	1	240	330	820
Eurasian Jackdaw	28.05.	07:52	Lucerne[11]	5.6	0.17	1	230	660	270
Montagu's Harrier	07.06.	06:59	Opium Poppy[12]	48.2	0.32	3[f]	50	860	510

[a] Numerical superscripts indicate double predation of the same nest.

[b] Numerical superscripts indicate individual field parcels.

[c] Vegetation height and cover on the last nest visit before the predation event. Cover was estimated as visibility of the nest from above: 1 – well visible, 2 – intermediate, 3 – completely covered.

[d] Nearest distance to field edge, forest and settlement.

[e] The only predation on nestlings, all other cases refer to nests with eggs.

[f] Nests discovered by incidental flushing of incubating female; remaining nests were found by systematic search.

CONTRIBUTION II.

Praus, L. & Weidinger, K. (2011). Střevlíci (Carabidae) jako potenciální nebezpečí pro mláďata skřivanů polních (*Alauda arvensis*) na hnízdech. *Sylvia* **47:** 91–94.

Střevlíci (Carabidae) jako potenciální nebezpečí pro mláďata skřivanů polních (*Alauda arvensis*) na hnízdech

Ground beetles (Carabidae) as potential predators of Skylark (Alauda arvensis) *nestlings*

Libor Praus & Karel Weidinger

Katedra zoologie a ornitologická laboratoř, PřF UP, tř. Svobody 26, CZ-771 46 Olomouc;
e-mail: prabor@centrum.cz, weiding@prfnw.upol.cz

Praus L. & Weidinger K. 2011: Střevlíci (Carabidae) jako potenciální nebezpečí pro mláďata skřivanů polních (*Alauda arvensis*) na hnízdech**.** *Sylvia 47: 91–94.*

Dne 13. 6. 2010 bylo v kukuřičném poli u obce Mentour na Chrudimsku nalezeno hnízdo skřivana polního (*Alauda arvensis*), které obsahovalo dvě vejce a jedno právě se líhnoucí mládě. K jeho pravému tibiotarsu byl zakouslý černý střevlík (čeleď Carabidae) o velikosti asi 1cm náležící s největší pravděpodobností do rodu *Pterostichus*. Ten způsobil mláděti zranění, které vedlo později k odumření a odpadnutí většiny pravé spodní končetiny. Přes nápadné zaostávání v růstu se mládě díky rodičovské péči dožilo věku osmi dnů a uhynulo až po vyvedení svého později se vylíhlého zdravého sourozence.

The paper describes an unusual case of fatal injury of a Skylark (Alauda arvensis) hatchling by a ground beetle (Carabidae, probably of the genus Pterostichus). The beetle bite caused necrosis and apostasy of the chick's right tarsometatarsus. The young Skylark without a major part of its right leg survived due to parental care until his healthy sibling fledged (eight days later).

Keywords: *Alauda arvensis*, Carabids, farmland birds, nest predation, Skylark

Drobné na zemi otevřeně hnízdící druhy ptáků musí při inkubaci a péči o mláďata odolávat vysokému predačnímu tlaku. To platí plnou měrou i o skřivanech polních (*Alauda arvensis*), u kterých se predace podílí na hnízdním neúspěchu více než ze 70 % (Weibel 1999, Donald et al. 2002). Identita predátorů skřivaních hnízd zůstává často neobjasněna. Přesto mezi doposud spolehlivě zdokumentované konzumenty snůšek a mláďat skřivanů patří poměrně rozsáhlá paleta ptačích i savčích druhů (Donald 2004, Morris & Gilroy 2008, Praus & Weidinger 2010) . Mimo „pravé“ predační události byly v minulosti zaznamenány pouze zcela ojediněle i kuriózní interakce s bezobratlými živočichy (nepočítaje případy parazitóz), které měly za následek zmaření hnízdního pokusu. Z Velké Británie je doloženo zničení snůšky skřivana hlemýžděm zahradním (*Helix pomatia*), který při doplňování svých zásob vápníku narušil radulou vaječné skořápky, což mělo za následek úhyn embryí. Obdobný případ je zdokumentován i ze Švýcarska, kde měl na svědomí porušení skřivaních vajec neurčený druh slimáka (Limacidae) (Donald 2004).

Dne 13. 6. 2010 dopoledne nalezl první z autorů v kukuřičném poli (36 ha, výška porostu 22 cm, vzdálenost od okraje pole 122 m) u obce Mentour (okres Chrudim; kvadrát 6062; koordináty 49°58'N 16°20'E; nadmořská výška 285 m n. m.) hnízdo skřivana polního, které obsahovalo dvě vejce a jedno právě se líhnoucí mládě. K jeho pravé spodní končetině byl zakouslý černý střevlík o velikosti asi 1 cm, s největší pravděpodobností náležící do rodu *Pterostichus* (Hůrka 2005). Na první pohled se zdálo, že je mládě mrtvé. Po přiblížení byly zaznamenány u ptáčete drobné pohyby, proto byl střevlík ihned odstraněn. Při následném ohledání a fotodokumentaci (obr. 1) se ukázalo, že střevlík mláděti způsobil otevřené poranění v oblasti pravého tibiotarsu.

Při druhé kontrole (15. 6.) jsme k hnízdu instalovali videonahrávací zařízení. Na hnízdě se nacházela dvě živá mláďata a jedno vejce. U poraněného ptáčete již zcela chyběla část pravé dolní končetiny pod mezotarzálním kloubem. Obě mláďata byla zvážena (tab. 1) a vrácena do hnízda.

Potřetí jsme hnízdo navštívili 18. 6. Poraněné mládě bylo stále naživu, výrazně však zaostávalo v růstu za svým zdravým sourozencem (tab. 1) a celková tělesná stavba vykazovala asymetrii, kdy osvalení bylo nápadně vyvinuto na levé polovině těla, kterou podpírala zdravá spodní končetina.

Při poslední kontrole 22. 6. navečer leželo handicapované mládě mrtvé v hnízdní kotlince (obr. 2). Díky videozáznamu víme, že k vyvedení zdravého mláděte došlo 21. 6. dopoledne. V té době bylo zraněné mládě stále na živu. Uhynulo až po několika hodinách snahy rodičů vyvést je z hnízda.

Zdokumentovaný případ rozšiřuje známé spektrum možných hrozeb pro skřivaní hnízda. V dostupné literatuře jsou střevlíci doposud popisováni vždy

Obr. 1. Líhnoucí se mládě skřivana polního (*Alauda arvensis*). Poranění pravého tibiotarsu (žlutá šipka) způsobil střevlík, pravděpodobně rodu *Pterostichus.* Foto L. Praus.
Fig. 1. *Skylark (Alauda arvensis) chick hatching. Right tibiotarsus injury (yellow arrow) was caused by a carabid beetle, probably of the genus Pterostichus, Photo by L. Praus.*

pouze v opačné roli – jako poměrně významná složka potravy pro mladé i dospělé skřivany (Poulsen et al. 1998, Smith et al. 2009). Případ napadení mláděte skřivana polního střevlíkem nebyl dosud v literatuře popsán. Naskýtá se otázka, nakolik představuje případ ohrožení malých skřivaních mláďat na hnízdě větším druhem střevlíka přirozenou situaci. Je pravděpodobné, že pokud by byla na hnízdě v době líhnutí přítomna samice, střevlík by mládě nemohl ohrozit. Nelze vyloučit, že za osudnou absenci samice může první z autorů, který se ve vzdále-

Tab. 1. Hmotnostní rozdíly mezi zdravým a handicapovaným mládětem skřivana polního ve snůšce nalezené 13. 6. 2010 v kukuřičném poli u obce Mentour na Chrudimsku.
Table 1. *Body weight differences between the healthy and handicapped Skylark siblings in the nest found in a maize field, Mentour village, eastern Bohemia on 13 June 2010*

datum *date*	věk (dny) *age (days)*	hmotnost (g) *weight (g)*	
		handicapované mládě *handicapped chick*	zdravé mládě *healthy sibling*
15. 6.	2	5,7	11,6
18. 6.	5	7,8	17,8
22. 6.	9	6,9†	vyvedeno *fledged*

†-1 den mrtvé
†- 1 day dead

Obr. 2. Uhynulé mládě skřivana polního ve věku osmi dnů. Část pravé spodní končetiny pod poraněním odumřela a odpadla během prvního dne po vylíhnutí. Foto L. Praus.
Fig. 2. *Injured Skylark chick died at the age of 8 days. Necrotic part of the right leg dropped off the first day after being wounded. Photo by L. Praus.*

nosti do 200 m od hnízda pohyboval asi posledních 20 minut před jeho nálezem. Na druhou stranu samice skřivana nezahřívá vejce ani malá mláďata bez přerušení celý den. Hnízdo během světelné fáze opouští většinou více než třicetkrát a doba jednotlivých absencí se pohybuje i okolo několika desítek minut (Praus, nepubl. data). Navíc větší druhy střevlíků jsou v polích dodnes poměrně běžné (Desender & Alderweireldt 1988, Döring et al. 2003). Domněnku o tom, že jsou mláďata drobných pozemně hnízdících pěvců střevlíky skutečně ohrožena podporuje i zaznamenaný případ pokousání mláďat lindušky luční (*Anthus pratensis*) neurčeným druhem střevlíka na hnízdě v alpínském pásmu Hrubého Jeseníku (Bureš 1997). Popisovaný případ proto nemusí být zcela ojedinělý.

LITERATURA

Bureš S. 1997: High Common Vole *Microtus arvalis* predation on ground-nesting bird eggs and nestlings. *Ibis 139: 173–174.*

Desender K. & Alderweireldt M. 1988: Population dynamics of adult and larval Carabid beetles in a maize field and its boundary. *J. Appl. Entomol. 106: 13–19.*

Donald P. F. 2004: The Skylark. *T. & A. D. Poyser, London.*

Donald P. F., Evans A. D., Muirhead L. B., Buckingham D. L., Kirby W. B. & Smith S. I. A. 2002: Survival rates, causes of failure and productivity of Skylark *Alauda arvensis* nests on lowland farmland. *Ibis 144: 652–664.*

Döring T. F., Hiller A., Wehke S., Schulte G. & Broll G. 2003: Biotic indicators of carabid species richness on organically and conventionally managed arable fields. *Agric., Ecosyst. Environ. 98: 133–139.*

Hůrka K. 2005: Brouci České a Slovenské republiky. *Kabourek, Zlín.*

Morris A. J. & Gilroy J. J. 2008: Close to the edge: predation risks for two declining farmland passerines. *Ibis 150: 168–177.*

Poulsen J. G., Sotherton N. W. & Aebischer N. J. 1998: Comparative nesting and feeding ecology of skylarks *Alauda arvensis* on arable farmland in southern England with special reference to set-aside. *J. Appl. Ecol. 35: 131–147.*

Praus L. & Weidinger K. 2010: Predators and nest success of Sky Larks *Alauda arvensis* in large arable fields in the Czech Republic. *Bird Study 57: 525–530.*

Smith B., Holland J., Jones N., Moreby S., Morris A. J. & Southway S. 2009: Enhancing invertebrate food resources for skylarks in cereal ecosystems: How useful are in-crop agri-environment scheme management options? *J. Appl. Ecol. 46: 692–702.*

Weibel U. 1999: Effects of wildflower strips in an intensively used arable area on Skylarks (*Alauda arvensis*). *PhD thesis, Swiss Federal Institute of Technology, Zurich.*

Došlo 30. září 2010,
přijato 16. února 2011.
Received 30 September 2010;
accepted 16 Feburary 2011.
Editor: P. Adamík

CONTRIBUTION III.

Praus, L., Hegemann, A., Tieleman, B. I. & Weidinger, K. (2014). Predators and predation rates of Skylark *Alauda arvensis* and Woodlark *Lullula arborea* nests in a semi-natural area in the Netherlands. *Ardea* **102:** 87–94.

Predators and predation rates of Skylark *Alauda arvensis* and Woodlark *Lullula arborea* nests in a semi-natural area in The Netherlands

Libor Praus[1,*], Arne Hegemann[2], B. Irene Tieleman[2] & Karel Weidinger[1]

Praus L, Hegemann A. Tieleman B.I & Weidinger K. 2014. Predators and predation rates of Skylark Alauda arvensis and Woodlark Lullula arborea nests in a semi-natural area in The Netherlands. Ardea 102: 87–94.

Predation is a major cause of breeding failure in bird species with open nests. Although many studies have investigated nest predation rates, direct identification of nest predators is sporadic, especially in (semi-)natural habitats. We quantified nest success and identified nest predators in a population of Skylarks Alauda arvensis and Woodlarks Lullula arborea breeding in a protected semi-natural area dominated by heathland and different succession states of grassland on nutrient-poor soil in The Netherlands. We monitored 54 nests by means of continuous video surveillance to determine survival times and predators, and monitored another 44 nests without a camera. Fates of the 58 (40) Skylark (Woodlark) nests were: fledging 41 (27), depredation 13 (12), egg desertion 1 (0) and nestling death 3 (1). The overall nest success of all monitored nests (58 (40), Mayfield estimate) was 33% (22%; all mortality factors considered) or 43% (25%; only depredation). Predators of Skylark nests were Red Fox Vulpes vulpes (5), Carrion Crow Corvus corone (1) and European Adder Vipera berus (1). Woodlark nests were depredated by Carrion Crow (2), Eurasian Jay Garrulus glandarius (1) and Red Fox (1). Results suggest that the main nest predators might differ between the two co-occurring lark species; Skylark nests located in more open sites were preyed upon mainly by Red Fox, while the main predators of Woodlark nests, located generally closer to trees, are corvids.

Key words: Alauda arvensis, Lullula arborea, nest predators, nest success, video monitoring

[1]Department of Zoology and Laboratory of Ornithology, Faculty of Science, Palacky University, 17. listopadu 50, 771 46 Olomouc, Czech Republic;
[2]Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands;
*corresponding author (praus@szm.cz)

Predation is a major cause of nest failure for many birds and hence it is an important source of natural selection that shapes avian behaviour and life-history traits (Martin 1995). Nest predation has been suggested to be the primary cause of losses across a wide range of bird species, habitats, and geographic regions, accounting on average for 80% of nest losses (Ricklefs 1969, Martin 1993). In particular, breeding populations of some ground-nesting birds of open habitats, such as waders and galliformes, are highly vulnerable to a wide range of mammalian and avian predators, sometimes to the point of affecting population size (Marcström *et al.* 1988, Tapper *et al.* 1996, Grant *et al.* 1999). By contrast, the evidence that numbers of breeding passerines are limited directly by nest predation is weak (Gibbons *et al.* 2007). Population declines of many ground-nesting passerines of open habitats in Western and Central Europe are primarily caused by loss and degradation of breeding habitat (Donald 2004, Grzybek *et al.* 2008, Menz *et al.* 2009). However, interactions between habitat changes and nest predation rates frequently occur and can obscure the primary causes of bird populations declines (Evans 2004).

Nest predators differ among habitats and species, but some general patterns exist. Red Foxes *Vulpes vulpes*, martens and corvids are among the important nest predators in European woodland (Jędrzejewska & Jędrzejewski 1998, Weidinger 2009, Mallord *et al.* 2012) and in farmland (MacDonald & Bolton 2008, Teunissen *et al.* 2008, Praus & Weidinger 2010). Predation studies in intensive farmland have focused on nest success and nest predator identity of ground-breeding farmland birds (Teunissen *et al.* 2008, Morris & Gilroy 2008, Praus & Weidinger 2010). Some studies have also investigated the nesting success of these species in more natural areas like coastal, steppe and heathland habitats (Auninš *et al.* 2001, Pearce-Higgins & Grant 2002, Wright *et al.* 2009). However, direct evidence of the identity of nest predators in natural habitats is anecdotal and detailed studies are lacking.

The Skylark *Alauda arvensis* and the Woodlark *Lullula arborea* are ground-nesting species of open landscapes that face high predation rates (Donald 2004, Dolman 2010). The Skylark was originally widespread in a variety of open habitats including steppes, natural grasslands, heathlands and saltmarshes, but nowadays the majority of European birds breed in agricultural landscapes, where Skylarks are rapidly declining (EBCC 2012). The Woodlark inhabits semi-natural habitats, especially restocked conifer plantations and lowland heathlands across Europe (Sitters *et al.* 1996, Wotton & Gillings 2000, Mallord *et al.* 2007). Various predators and variable nest predation rates have been identified for Skylark nests in West and Central European farmland (Morris & Gilroy 2008, Praus & Weidinger 2010) and Woodlark nests in lowland heathlands of Great Britain (Dolman 2010). However, information about predation pressure and relative importance of nest predators in different habitats and across different geographic regions is scarce (Delius 1965, Yanes & Suarez 1995).

In this study, we quantified nest success and identified nest predators in a rather high-density population of Skylarks and Woodlarks breeding in a semi-natural heath- and grassland area in The Netherlands. Populations of both species co-occur in this area, but the two species differ in the selection of their nest sites; while Skylarks avoid forest edges and even the proximity of single trees, Woodlarks usually nest close to trees and/or forest edges. Thus our study tentatively allowed us to explore whether different nest site selection within an area relates to species-specific vulnerability to nest predation.

METHODS

We monitored fates and identified predators of lark nests in the Aekingerzand, part of the National Park Drents-Friese Wold in the northern Netherlands (52°55'N, 6°18'E) in 2012. The study area (c. 400 ha) is characterised by nutrient-poor soil. Dominating vegetation types are heather, *Calluna vulgaris* and *Erica tetralix*, and different succession states of grass, moss and *Juncus* spec. Furthermore, patches of open sand and groups of trees are spread through the area which is surrounded by coniferous forest. Suitable nesting habitat covers approximately 240 ha for Skylarks and 220 ha for Woodlarks. Population densities are rather high compared to most modern agricultural areas of Western Europe and the local Skylark (80–100 pairs) and Woodlark (60–80 pairs) populations have been intensively studied since 2006 (Hegemann *et al.* 2010, Hegemann & Voesten 2011). About 500 sheep graze the study area year-round, keeping the vegetation short and succession limited. The National Park is surrounded by intensive farmland with maize, potatoes and cereals as the main crop types, and to a lesser extent by intensive grasslands (Geiger *et al.* 2014).

Fieldwork was conducted from early May to late July; roughly 80 days were devoted to nest searching in the whole study area. This period covers the entire breeding season of the local Skylark population (Hegemann *et al.* 2012, 2013) and the period of second and third broods in Woodlarks (Tieleman *et al.* unpublished data). Although we missed the first Woodlark broods, this does not pose a major problem, because one aim of our study is to compare predation rates and predators between the two species breeding in the same area and at the same time, rather than to obtain season-long estimates of breeding performance. Nests were found either through direct observation of adults returning to the nest or by systematic searches of spots where intense mating behaviour had been observed. Age of nestlings was estimated by visual clues from their development (e.g., opening of eyes, feather development); first-egg laying date was back-calculated from brood size and hatch date, or from clutch size and the stage of incubation estimated by egg floatation.

We found a total of 58 Skylark and 40 Woodlark nests. A randomly selected subset of these nests (Skylark: $n = 37$ nests, 247 active nest-days; Woodlark: $n = 16$, 92) were monitored by continuous video recording. The remaining nests served as control nests without video monitoring. Video systems consisted of a small camouflaged video camera with IR diodes, a portable security digital video recorder (DVR), and a

Figure 1. The typical layout of a video camera (arrow) at one of the monitored nests, here with incubating Woodlark female, 18 May 2012 (Photo Libor Praus).

12V/40Ah deep cycle battery (for details see Praus & Weidinger 2010). We used local natural material (dry moss, stones) to mask the camera; all other parts (DVR, battery, cables) were buried under the ground (Figure 1). We set the DVR to record continually with a frequency of 10 fps at 640 × 480 pixel resolution. These settings allowed for 4.5 days of recording on a 16 GB memory card. Cameras were deployed about 2 days (range 0–4) after nest discovery. We visited the nests usually (80% cases) every fourth day (mean 3.4, range 1–5) to check nest content and to change the battery and memory card; we visited nests with cameras as well as control nests according to the same time schedule (mean 3.0, range 1–6). When a nest was found empty, we searched in the immediate vicinity for signs of nest failure (eggshells, feathers, dead nestlings) or nest success (alive fledglings, droppings).

For video monitored nests we determined the exact survival time, nest fate and the species of nest predator by inspection of video recordings. Survival time of failed nests without a video camera was estimated as a midpoint between the last visit to an active nest (eggs or nestlings) and the first negative visit (empty nest, dead chicks or deserted clutch). Survival time of successful nests without a video camera was terminated by the 8th day of chick age for both Lark species (Skylark mean fledging age 8.6 days, range 7–12 days, $n = 19$ video-monitored nests; Woodlark 9.3 days, range 9–10, $n = 10$); disappearance of younger chicks was considered as predation. The observed mean age of fledging might have been influenced by the disturbance associated with ringing; chicks left the nest within one day after ringing. However, nestlings also regularly fledge at an age of 7 or 8 days, without ringing or other research activities at the nest, especially if ambient temperature is high and nestlings need to escape the direct sunlight (Hegemann *et al.*, unpublished data). Exposure period for all nests was measured in nest-days since the day of discovery of an active nest or since camera deployment (see below). We treated each nest-day as an independent binary observation (survived or failed) and estimated the daily survival rate (*DSR*) as a simple ratio of survived to exposed nest-days. We calculated *DSR* separately for the egg (laying and incubation) and nestling stage. To calculate *DSR* we considered either nest losses owing to predation, or total mortality. Nest survival was estimated as DSR^t where $t = 14$ (egg stage including laying period), 8 (nestling stage) or 22 (total) days for Skylarks and where $t = 15$ (egg stage including laying period), 9 (nestling stage) or 24 (total) days for Woodlarks. Egg stage is based on a mean clutch size of 4 eggs for both species and an incubation period of 11 days for Skylarks (Glutz von Blotzheim & Bauer 1985, own unpublished data) and 12 days for Woodlarks (Nick Horrocks & Stef Waasdorp, pers. comm.) starting with the last egg laid. Duration of nestling stage is based on the video-recordings (see above). The limited sample size precluded

Table 1. Daily survival rates (*DSR*) of Skylark and Woodlark nests in a semi-natural heath- and grassland in the northern Netherlands during the breeding season of 2012.

Species Nesting stage	Total nests	Exposure nest-days	Depredated nests	DSR[1]	95% CL[1]	Total failed nests	DSR[2]	95% CL[2]
Skylark								
Eggs	21	91	4	0.956	0.891–0.988	5	0.945	0.876–0.982
Nestlings	53	259	9	0.965	0.935–0.984	12	0.954	0.921–0.976
Total	58	350	13	0.963	0.937–0.980	17	0.951	0.923–0.972
Woodlark								
Eggs	9	88	5	0.943	0.872–0.981	5	0.943	0.872–0.981
Nestlings	34	123	7	0.943	0.886–0.977	8	0.935	0.876–0.972
Total	40	211	12	0.943	0.903–0.970	13	0.938	0.897–0.967

[1] calculated from the number of depredated nests; [2] calculated from the total number of failed nests

Table 2. Summary of video-recorded Skylark and Woodlark nest depredation events during the 2012 breeding season in a semi-natural heath- and grassland in The Netherlands.

Predator identity	Date (d.m)	Time (CET)	Nesting stage	Nest age (within stage)	Tree[1] (m)
Skylark nests					
Red Fox *Vulpes vulpes*	19.05	05:07	Nestlings	4	310
Red Fox *Vulpes vulpes*	27.05	03:54	Nestlings	3	180
Red Fox *Vulpes vulpes*	03.06	23:45	Nestlings	4	230
Red Fox *Vulpes vulpes*	24.06	03:15	Nestlings	6	45
Red Fox *Vulpes vulpes*	26.06	01:45	Nestlings	5	260
Carrion Crow *Corvus corone*	19.05	21:22	Nestlings	5	30
European Adder *Vipera berus*	22.05	19:40	Nestlings	4	50
Woodlark nests					
Carrion Crow *Corvus corone*	17.05	11:35	Eggs	15	40
Carrion Crow *Corvus corone*	26.05	06:05	Nestlings	8	2
Eurasian Jay *Garrulus glandarius*	29.06	15:02	Eggs	16	2
Red Fox *Vulpes vulpes*	14.05	02:37	Eggs[2]	15	1

[1] Distance to the nearest tree (height ≥ 5 m); [2] Fox took incubating female, unattended eggs were taken later by Carrion Crow

formal statistical analyses, therefore we present only descriptive data. To check for an effect of research disturbance on the risk of nest predation, we compared daily predation rates between samples of nest-days with and without video camera, and between the first day after an observer's visit and subsequent days. Results of these comparisons are presented as odds ratios with 95% confidence limits.

RESULTS

Skylark

Overall, we found 58 Skylark nests at a median age of 17 days (day 1 = first-egg laying date); the nests were found during nest building and egg laying (9), incubation (4) or nestling stage (45). The median back-calculated laying date was 1 June (27 April – 5 July, n = 58). Size of completed clutches was 3.62 ± 0.27 SE (2–5, n = 13) and number of fledglings was 3.37 ± 0.12 SE (2–5, n = 41). Nest fates were: fledging (41), depredation (13), egg desertion (1) and nestling death (3). Overall nest success was 33% (95% confidence limits: CL = 17, 54; all mortality factors considered) or 44% (CL = 24, 64; only predation considered; Table 1). Corresponding values of nest success, calculated as a product of nest survival for the egg and nestling stage were 31% (CL = 8, 64) and 40% (CL = 12, 74), respectively. Fates of the video-monitored nests were: fledging (27), depredation of nestlings (7; Table 2), egg desertion (1) and nestling death (2). Based on the odds ratio (OR), daily predation rate was non significantly lower on the first day after observer visits vs. subsequent days (OR = 0.69; CL = 0.13, 3.64), and on nests with video cameras vs. nests without cameras (OR = 0.51; CL = 0.17, 1.56).

Woodlark

Altogether, we found 40 Woodlark nests at a median age of 20 days; the nests were found during nest building and egg laying (6), incubation (3) or nestling stage (31). The median laying date was 30 April (29 March – 26 June, n = 40). Size of completed clutches was 4.23 ± 0.32 SE (3–6, n = 13) and number of fledglings was 4.00 ± 0.29 SE (2–5, n = 23). Nest fates were: fledging (27), depredation (12) and nestling death (1). Overall nest success was 22% (CL = 7, 45; all mortality factors considered) or 25% (CL = 9, 48; only predation considered; Table 1). Corresponding values of nest success calculated as the product of nest survival for the egg and nestling stage were 23% (CL = 4, 58) and 25% (CL= 4, 61), respectively. Fates of the video-monitored nests were: fledging (11), depredation of nestlings (1; Table 2), depredation of clutches (3; Table 2) and nestling death (1). Based on the odds ratio, daily predation rate was non significantly higher on the first day after observer visits vs. subsequent days (OR = 1.12; CL = 0.4, 3.56), and non significantly lower on nests with video cameras vs. nests without cameras (OR = 0.36; CL = 0.11, 1.13).

Nest predators

We documented on video 11 predation events (one event per nest) by four species of predators (Table 2). The principal predators differed between the two lark species – Red Fox accounted for 71% (5/7) of predation events in Skylark, while corvids accounted for 75% (3/4) of predation in Woodlark. The six predation events by Red Fox occurred throughout the breeding season (14 May – 26 June), while all three predations by Carrion Crow *Corvus corone* were restricted to a shorter period (17–26 May). Foxes accounted for all nocturnal predation events (Table 2).

DISCUSSION

The overall nest success of Skylarks in a semi-natural breeding habitat in the northern Netherlands was 33% and thus within the range of values reported (also using the 'Mayfield method') from arable fields in the UK (23–40%; Wilson *et al.* 1997, Chamberlain & Crick 1999, Donald *et al.* 2002), The Netherlands (27%; Kragten *et al.* 2008), Germany (22%; Jeromin 2002), Switzerland (22%; Weibel 1999) and Czech Republic (17%; Praus & Weidinger 2010). In our study area, Woodlarks had a slightly lower nest success (22%) than Skylarks. The nest success rates we found are also lower than those reported for Woodlarks breeding on heathlands in southern England (47%; Mallord *et al.* 2007). Predation accounted for 76% (13/17) and 92% (12/13) of nest losses in Skylarks and Woodlarks, respectively. These values are in accordance with data from Skylark populations breeding on farmland (generally >70%; Weibel 1999, Donald *et al.* 2002, Praus & Weidinger 2010) and in coastal dunes (>85%; Delius 1965). The second most important cause of nest failure in this study was nestling death. All cases of nestling death in Skylarks (3/53) and Woodlarks (1/34; Table 1) were likely a consequence of predation on parents. Video recordings of one Skylark nest showed that the male kept on bringing food to the 3 days old nestlings after the female had disappeared, but without brooding by the female the nestlings died of hypothermia. We also video-recorded an incubating Woodlark female being taken at night by a fox. The fox did not take the clutch but these remained unattended in the nest for four hours until taken by a Carrion Crow.

No nest with nestlings was deserted after we installed the camera equipment and only one female Skylark did not resume incubation after camera deployment. We are reasonably confident that neither the presence of a camera at the nest, nor the repeated visits associated with the video recording, increased nest predation rate. In fact, there was a non-significant trend in the opposite direction. In both species predation was marginally lower on nests with a camera. Furthermore, in Skylarks it was also marginally lower on the first day after an observer visit to the nest compared to subsequent days. In both cases confidence intervals are wide and do not allow any firm conclusions. Yet, our data are in line with the current opinion that nest cameras do not increase nest predation (Ribic *et al.* 2012).

Combining both lark species, nest predation occurred during darkness in 55% cases, despite the relatively longer daylight periods during the breeding season (68% of recording time). This pattern was mainly attributed to a predominance of predation by Red Foxes which mainly forage at night (Doncaster & MacDonald 1997). Red Foxes accounted for 55% (6/11) of all video recorded predation events. Foxes are known to be the most important predators of wader nests across The Netherlands (Teunissen *et al.* 2008). Nevertheless, bird nests might represent only an alternative prey for foxes, whose foraging behaviour and/or abundance is rather affected by their primary prey-populations of small rodents (Marcström *et al.* 1988, Tomkovich & Zharikov 1998, Kjellander & Nordström 2003). If so, foxes may actively switch to bird nests when the primary prey is scarce. Or alternatively, incidental predation on bird nests may increase as a side effect of increased abundance of the primary prey (Yanes & Suarez 1996). In 2012 Common Vole *Microtus arvalis* and Wood Mouse *Apodemus sylvaticus*, two of the main prey species of Red Foxes (Lloyd 1980), showed relatively high population abundances in Drents-Friese Wold, where our study area is located (Bijlsma 2013).

The second most important nest predators were corvids, accounting for more predation losses in Woodlarks (3/4) than in Skylarks (1/7). This is not unexpected because corvids probably use trees as observation posts, and consequently prey more on Woodlark nests, which are located generally closer to trees than Skylark nests (Table 2). In spite of limited sample size, we documented one case of a European Adder *Vipera berus* preying on Skylark nestlings. This, together with evidence from a broadly similar habitat in southern England (16% of 7 nests; Dolman 2010) suggests that snakes might be locally important predators of lark nests in heathlands. Although the available data suggest that foxes were the main predators during the single study season, a higher sampling intensity over multiple seasons would likely reveal a wider range of nest predator species and may change the importance of different predator species in our study area (e.g., Dolman 2010, Praus & Weidinger 2010).

In summary, nest success of both lark species, intensity of predation and species composition of nest predators in Aekingerzand were similar to what is known from other regions and habitats. We realize that our sample size is limited and our data are mainly based on nests found in the nestling stage, which may influence the robustness of our conclusions. Additionally, we studied only one breeding season and might have missed yearly variation in predation rates. We therefore suggest sampling across years to help address these issues. Monitoring the abundance of predator species identified in this study and the abundance of their primary prey may further help to understand predation patterns. Finally, combining a study on nest predation with tracking of predators foraging behaviour would help to clarify whether foxes actively search for nests or find them incidentally while searching for their primary prey.

ACKNOWLEDGEMENTS

Rob Voesten and Stef Waasdorp were of invaluable help in finding nests and setting up cameras. LP and KW were supported by funding from Palacky University (IGA PrF_2012_021 and IGA PrF_2013_007). Staatsbosbeheer Drents-Friese Wold kindly allowed working in their area. Comments by Rob Bijlsma, John Mallord and an anonymous reviewer greatly improved the earlier draft of this paper.

REFERENCES

Auninš A., Petersen B.S., Priednieks J. & Prins E. 2001. Relationship between birds and habitats in Latvian farmland. Acta Ornithol. 36: 55–64.

Bijlsma R.G. 2013. Trends en broedresultaten van roofvogels in Nederland in 2012. De Takkeling 21: 5–48.

Chamberlain D.E. & Crick H.Q.P. 1999. Population declines and reproductive performance of Skylarks *Alauda arvensis* in different regions and habitats of the United Kingdom. Ibis 141: 38–51.

Delius J.D. 1965. A population study of Skylarks *Alauda arvensis*. Ibis 107: 466–492.

Dolman P. 2010. Woodlark and Nightjahr recreational disturbance and nest predator study 2008 and 2009. Final report to Breckland District Council. University of East Anglia, Norwich.

Donald P.F., Evans A.D., Muirhead L.B., Buckingham D.L., Kirby W.B. & Schmitt S.I.A. 2002. Survival rates, causes of failure and productivity of Skylark *Alauda arvensis* nests on lowland farmland. Ibis 144: 652–664.

Donald P.F. 2004. The Skylark. Poyser, London.

Doncaster C.P. & Macdonald D.W. 1997. Activity patterns and interactions of Red Foxes *Vulpes vulpes* in Oxford city. Journal of Zoology 241: 73–87.

EBCC 2012: Pan-European Common Bird Monitoring Scheme. Available from: http://www.ebcc.info/pecbm.html.

Evans K.L. 2004. The potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146: 1–13.

Geiger F., Hegemann A., Gleichman M., Flinks H., de Snoo G.R., Prinz S., Tieleman B.I. & Berendse F. 2014. Habitat use and diet of Skylarks (*Alauda arvensis*) wintering in an intensive agricultural landscape of the Netherlands. J. Ornithol. 155: 507–518.

Gibbons D.W., Amar A., Anderson G.Q.A., Bolton M., Bradbury R.B., Eaton M.A., Evans A.D., Grant M.C., Gregory R.D., Hilton G.M., Hirons G.M.J., Hughes J., Johnstone I., Newbery P., Peach W.J., Ratcliffe N., Smith K.W., Summers R.W., Walton P. & Wilson J.D. 2007. The predation of wild birds in the UK: a review of its conservation impact and management. RSPB Research Report no. 23. RSPB, Sandy, UK.

Glutz von Blotzheim U.N.& Bauer K.M 1985. Handbuch der Vögel Mitteleuropas, Bd 10, II Passeriformes (1, Teil). Akademische Verlagsgesellschaft, Wiesbaden.

Grant M.C., Orsman C., Easton J., Lodge C., Smith M., Thompson G., Rodwell S. & Moore N. 1999. Breeding success and causes of breeding failure of Curlew *Numenius arquata* in Northern Ireland. J. Appl. Ecol. 36: 59–74.

Grzybek J., Michalak I., Osiejuk T.S. & Tryjanowski P. 2008. Densities and habitats of the Tawny Pipit *Anthus campestris* in the Wielkopolska region (W Poland). Acta Ornithol. 43: 221–225.

Hegemann A., van der Jeugd H.P., de Graaf M., Oostebrink L.L. & Tieleman B.I. 2010. Are Dutch Skylarks partial migrants? Ring recovery data and radiotelemetry suggest local coexistence of contrasting migration strategies. Ardea 98: 135–143.

Hegemann A. & Voesten R. 2011. Can Skylarks Alauda arvensis discriminate a parasite nestling? Possible case of nestling Cuckoo *Cuculus canorus* ejection by its host parents. Ardea 99: 117–120.

Hegemann A., Matson K.D., Both C. & Tieleman B.I. 2012. Immune function in a free-living bird varies over the annual cycle, but seasonal patterns differ between years. Oecologia 170: 605–618.

Hegemann A., Matson K.D., Flinks H. & Tieleman B.I. 2013. Offspring pay sooner, parents pay later: Experimental manipulation of body mass reveals trade-offs between immune function, reproduction and survival. Frontiers Zool. 10: 77.

Jędrzejewska B. & Jędrzejewski W. 1998. Predation in Vertebrate Communities. The Białowieża Primeval Forest as a Case Study. Springer-Verlag, Berlin.

Jeromin K. 2002. Zur Ernährungsökologie der Feldlerche *Alauda arvensis* L. 1758 in der Reproduktionsphase. PhD Thesis, Christian-Albrechts-Universität, Kiel.

Kjellander P. & Nordström J. 2003. Cyclic voles, prey switching in red fox, and roe deer dynamics – a test of the alternative prey hypothesis. Oikos 101: 338–344.

Kragten S., Trimbos K.B. & de Snoo G.R. 2008. Breeding Skylarks *Alauda arvensis* on organic and conventional arable farms in the Netherlands. Agricult. Ecosyst. Environm. 126: 163–167.

Lloyd H.G. 1980. The Red Fox. Batsford, London.

MacDonald M.A. & Bolton M. 2008. Predation on wader nests in Europe. Ibis 150: 54–73.

Mallord J.W., Dolman P.M., Brown A. & Sutherland W.J. 2007. Nest-site characteristics of Woodlarks *Lullula arborea* breeding on heathlands in southern England: are there consequences for nest survival and productivity? Bird Study 54: 307–314.

Mallord J.W., Orsman C.J., Cristinacce A., Butcher N., Stowe T.J. & Charman E.C. 2012. Mortality of Wood Warbler *Phylloscopus sibilatrix* nests in Welsh Oakwoods: predation rates and the identification of nest predators using miniature nest cameras. Bird Study 59: 286–295.

Marcström V., Kenward R.E. & Engren E. 1988. The impact of predation on boreal tetraonids during vole cycles: an experimental study. J. Anim. Ecol. 57: 859–872.

Martin T.E. 1993. Nest predation and nest sites. Bioscience 43: 523–532.

Martin T.E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. Ecol. Monogr. 65: 101–127.

Menz M.H.M., Mosimann-Kampe P. & Arlettaz R. 2009. Foraging habitat selection in the last Ortolan Bunting *Emberiza hortulana* population in Switzerland: final lessons before extinction. Ardea 97: 323–333.

Morris A.J. & Gilroy J.J. 2008. Close to the edge: predation risks for two declining farmland passerines. Ibis 150: 168–177.

Pearce-Higgins J.W. & Grant M.C. 2002. The effects of grazing-related variation in habitat on the distribution of moorland Skylarks *Alauda arvensis* and Meadow Pipits *Anthus pratensis*. Aspects Appl. Biol. 67: 155–163.

Praus L. & Weidinger K. 2010. Predators and nest success of Sky Larks *Alauda arvensis* in large arable fields in the Czech Republic. Bird Study 57: 525–530.

Ribic C.A., Thompson F.R. & Pietz P.J. 2012. Video surveillance of nesting birds. University of California Press, London.

Ricklefs R. E. 1969. An analysis of nesting mortality in birds. Smithson. Contr. Zool. 9: 1–48.

Sitters H.P., Fuller R.J., Hoblyn R.A., Wright M.T., Cowie N. & Bowden C.G.R. 1996. The Woodlark *Lullula arborea* in Britain: population trends, distribution and habitat occupancy. Bird Study 43: 172–187.

Tapper S.C., Potts G.R. & Brockless M.H. 1996. The effect of an experimental reduction in predation pressure on the breeding success and population density of Grey Partridges *Perdix perdix*. J. Appl. Ecol. 33: 965–978.

Teunissen W., Schekkerman H., Willems F. & Majoor F. 2008. Identifying predators of eggs and chicks of Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa* in the Netherlands and the importance of predation on wader reproductive output. Ibis 150: 74–85.

Tomkovich P. S. & Zharikov Y. V. 1998. Wader breeding conditions in the Russian tundras in 1997. Wader Study Group Bull. 87: 30–42.

Weibel U.M. 1999. Effects of wildflower strips in an intensively used arable area on Skylarks *Alauda arvensis*. PhD thesis, Swiss Federal Institute of Technology, Zürich, Switzerland.

Weidinger K. 2009. Nest predators of woodland open-nesting songbirds in central Europe. Ibis 151: 352–360.

Wilson J.D., Evans J., Browne S.J. & King J.R. 1997. Territory distribution and breeding success of Skylarks *Alauda arvensis* on organic and intensive farmland in southern England. J. Appl. Ecol. 34: 1462–1478.

Wotton S.R. & Gillings S. 2000. The status of breeding Woodlarks *Lullula arborea* in Britain in 1997. Bird Study 47: 212–224.

Wright L.J., Hoblyn R.A., Green R.E., Bowden C.G.R, Mallord J.W., Sutherland W. & Dolman P.M. 2009. Importance of climatic and environmental change in the demography of a multi-brooded passerine, the Woodlark *Lullula arborea*. J. Anim. Ecol. 78: 1191–1202.

Yanes M. & Suarez F. 1995. Nest predation patterns in ground-nesting passerines on the Iberian Peninsula. Ecography 18: 423–428.

Yanes M. & Suarez F. 1996. Incidental nest predation and lark conservation in an Iberian semiarid shrubsteppe. Conserv. Biol. 10: 881–887.

SAMENVATTING

Predatie is een van de belangrijkste oorzaken van nestverliezen, vooral bij vogels met open nesten. Toch is er betrekkelijk weinig directe evidentie welke predatoren waar, hoe en wanneer toeslaan. In deze studie staan Boomleeuwerik *Lullula arborea* en Veldleeuwerik *Alauda arvensis* centraal. Beide soorten broeden op de grond in open terrein, maar de Boomleeuwerik doet dat bij voorkeur in de buurt van boomopslag, terwijl de Veldleeuwerik juist bomen en struiken mijdt. Het Aekingerzand op de grens van Friesland en Drenthe, een open heidegebied met een afwisseling van grazige en zandige delen, herbergt een forse dichtheid van beide soorten. In mei–juli 2012 werden hier 58 nesten van de Veldleeuwerik en 40 nesten van de Boomleeuwerik opgespoord. Bij een willekeurige steekproef uit deze nesten werd een gecamoufleerde videocamera bijgeplaatst, waarmee de lotgevallen van het nest *non-stop* werden geregistreerd. De overige nesten fungeerden als controle. Beide sets van nesten werden volgens een zelfde schema gecontroleerd. Op deze wijze werd een antwoord gezocht op de vraag of de keuze van een nestplek van invloed is op soortspecifieke kwetsbaarheid voor predatie.

Het nestsucces van Veldleeuweriken, berekend met de Mayfield-methode, kwam uit op 33%, tegen 22% voor Boomleeuweriken. Bij beide soorten was predatie voor het gros van de verliezen verantwoordelijk. De videocamera's lieten zien dat Vossen *Vulpes vulpes* de belangrijkste predator van de nesten van de Veldleeuwerik waren (altijd 's nachts), terwijl dat bij nesten van de Boomleeuwerik Zwarte Kraaien *Corvus corone* waren (overdag). Jongen die dood in het nest werden aangetroffen, waren vermoedelijk indirect slachtoffer van predatie geworden, doordat de ouder(s) waren gepredeerd. Er werden geen aanwijzingen gevonden dat de plaatsing van camera's bij nesten, noch de daaropvolgende controles van de camera's, hebben geleid tot een stijging van de predatiekans. Hoewel de steekproef aan de kleine kant was (en voornamelijk nesten met jongen betrof) en het onderzoek slechts één broedseizoen omvatte, lijkt het erop dat Veld- en Boomleeuweriken specifieke predatoren hebben, geassocieerd met het type van de nestplaats: respectievelijk open terrein met Vossen en halfopen terrein met Zwarte Kraaien. Een grotere steekproef zou uitsluitsel moeten geven of dit verschil reëel is, en of het ieder jaar in dezelfde mate optreedt. Immers, de dynamiek van predatoren en hun invloed op de slagingskans van leeuweriknesten hangen nauw samen met de talrijkheid van hun hoofdprooi (in het geval van Vossen: muizen). (RGB)

Corresponding editor: Rob G. Bijlsma
Received: 31 January 2014; accepted: 18 June 2014

CONTRIBUTION IV.

Praus, L. & Weidinger, K. (2015). Breeding biology of the Skylark *Alauda arvensis* in maize and other crop fields. *Acta Ornithologica* **50:** 1. (*in press*)

Breeding biology of the Skylark *Alauda arvensis* in maize and other crop fields

LIBOR PRAUS[1]* & KAREL WEIDINGER[1]

[1]Department of Zoology and Laboratory of Ornithology, Faculty of Science, Palacky University,
17. listopadu 50, 771 46 Olomouc, Czech Republic

*Corresponding author, e-mail: libor.praus@gmail.com

Abstract. The Skylark populations are declining in most European agricultural landscapes. Changing crop compositions and seasonal vegetation dynamics have been suggested to influence the breeding success of Skylarks in arable fields. We quantified the breeding performance of Skylarks by means of continuous video surveillance in maize fields (n = 83 nests) and in a pooled sample of other crops, mostly sugar beet, opium poppy and cereals (n = 89 nests), in the Czech Republic, from 2009 to 2011. Skylarks colonized the bare ground of maize fields immediately after sowing and continued to breed there until the end of the breeding season in late July. The vegetation height at the time of laying did not exceed 100 cm, but late broods left nests under maize reaching up to 210 cm. In spite of similar clutch sizes, a lower number of chicks fledged per successful nest in maize fields compared to other crops, as a consequence of the lower hatchability and higher partial nestling mortality. Nest success (based on daily survival rates) was very low ranging from 8% (raw estimate) to 12% (model estimate), while the difference between crops was less than 1%. The nest productivity was less than 0.4 chicks produced per nesting attempt in both crops. At least 84% (maize) and 65% (other crops) of primary nest losses were caused by predation. After controlling for vegetation height, there was little difference in nest survival between crops during the egg stage, but nest survival was marginally lower in maize during the nestling stage. We propose that the recent increasing area of energy cropping fields represented mainly by maize provide an attractive, yet risky, nesting habitat for Skylarks, especially late in the season when autumn-sown crops are too dense. The main factor responsible for the low nesting success is the high rate of nest predation, regardless of vegetation height, as a consequence of shift from mainly avian to mammalian predation towards the end of breeding season.

Key words: *Alauda arvensis*, *Zea mays*, nesting habitat, farmland biodiversity, nest success, crop height

Suggested running title: Breeding biology of the Skylark in crop fields

INTRODUCTION

Farmland bird species, which have benefited historically from the spread of arable land, are now suffering severe population declines. The rate and extent of farmland change, and its negative impact on birds has markedly accelerated within the last decades, since the advent of agricultural intensification in the 1950s (Wilson et al. 2009). Agricultural intensification has decreased the heterogeneity of farmland throughout Europe by removing semi-natural habitats, increasing field sizes, promoting large scale monocultures, reducing mixed farming and developing practices that maximises yields (Nagy et al. 2009, Fuller 2012), which factors ultimately depressed food availability and safe breeding sites for birds (Hole et al. 2002, Donald 2004, Hart et al. 2006, Flohre et al. 2011).

Farmland habitat changes may cause declines in habitat quality throughout the breeding season within a bird’s home range (Gilroy et al. 2010). Birds experiencing multiple breeding opportunities during the course of a season can buffer against these declines by shifting to different breeding sites or habitats (Gilroy et al. 2010, Brambilla et al. 2012). However, the shift from spring-sown to winter-sown cereals limits the number of breeding attempts of ground nesting passeriness in numerous area's of arable land (Donald & Vickery 2001, Toepfer & Stubbe 2001). Contrary, increasing arable areas sown by spring wide row energy crops now represents a new important nesting habitat for farmland birds in the second half of their breeding season (Brand & Glemnitz 2013, Saurbrei et al. 2014). In particular, the cultivation of maize for energy cropping has increased substantially in recent years, with further increases predicted throughout the European Union (Schümann et al. 2010, Čandová 2011), Czech Republic including (2002: 289 265 ha; 2012: 324 441 ha, Czech Statistical Office 2012). Models assessing the impact of increase of maize fields on biodiversity predicts marked population decline in ground nesting farmland passerines with respect to increased energy maize cultivation (Gevers et al. 2011, Engel et al. 2012, Brand & Glemnitz 2013, Saurbrei et al. 2014).

There is strong evidence that especially vegetation coverage and height are important determinants of habitat selection in ground nesting passerines, because vegetation structure affects nest predation risk (Davis 2005, Winter at al. 2005), food availability (Wilson 2001) and possibility also locomotion (Donald 2004). Maize fields are characterized by rapid increase of crop height, yet relatively stable coverage. The pattern of maize growth is typically characterized by a sigmoid curve with slow growth during May, followed by rapid development to final height of about 200 cm during June (Berzsenyi & Lap 2004). This posses chalenge for birds that have to cope with dramatic changes of nesting habitat even during a single nesting cycle.

The Skylark *Alauda arvensis* is the most abundant and widespread passerine of arable land in Europe (Hagemeier & Blair 1997) and one of the few ground-breeding birds inhabiting maize fields. Since the mid 1970s, intensive agriculture practices have resulted in Skylark population declines by 50% across West European farmland (Robertson & Berg 1992, Busche 1994, de Carli et al. 1998, Siriwardena et al. 1998). Skylark populations in Central and East Europe declined by 25% on average in the same period (Rheinwald 1993, Tryjanowski 2000, Reif et al. 2008), possibly due to less intensive agriculture than in West Europe. Skylark territory density is influenced by the vegetation coverage and height, the preferred vegetation cover is 35–60% and the preferred vegetation height does not exceed 50 cm (Toepfer & Stubbe 2001, Donald 2004).

Skylarks start to establish territories in maize fields since early May due to the late sowing date. About 5 territories per 10 ha has been observed in May (J. Koleček in litt.), 7.5 territories in late June and 2-6.5 territories still found in July (Toepfer & Stubbe 2001, Eraud & Boutin 2002). Skylarks are capable of nesting on almost bare ground soon after maize sowing, as well as in fully grown crops, probably because the typical vegetation coverage does not exceed 50% (Schläpfer 1988, Toepfer & Stubbe 2001). During the Skylark nesting cycle (average 23 days) maize can grow by about 150 cm, thus making maize fields one of the most seasonally dynamic breeding habitats. This poses questions about the maximum crop height selected by Skylarks for nest placement and the subsequent crop growth tolerated by already nesting birds to complete the nesting cycle.

Here we report on Skylark breeding biology and nest survival in the "extreme" habitat of maize fields in the Czech Republic, together with comparative breeding data on Skylark nests from other crops. To evaluate an effect of crop type per se, we statistically controlled for seasonal increase in crop heights and seasonal variation in breeding performance.

METHODS

Study area and field methods

The study was carried out on conventionally managed arable fields (total study area of c 60 km², mean field size about 50 ha) interspersed with remnants of deciduous woodland and villages (<15% of the total area) during the breeding seasons from 2009-2011, in the East Bohemia Region, the Czech Republic (49° 55.39' N, 15° 59.33' E, altitude 240-500 m). The main crop types were: winter wheat *Triticum aestivum* (45%); maize *Zea mays* (15%); winter rape *Brassica napus subsp. Napus* (15%), spring barley *Hordeum vulgare* (10%); sugar beet *Beta vulgaris* (5%); alfalfa *Medicago sativa*, opium poppy *Papaver somniferum*, oilseed caraway *Carum carvi*, pea *Pisum sativum* and brown bean *Vicia faba* (each ≤2%).

Searching for nests was undertaken from the beginning of the breeding season in the middle of April and continued until late July. Roughly, 100 days per year were devoted to nest searching in the whole study area (70 days in maize fields). We located nests by systematically searching in suitable plots (≤60% mean vegetation coverage), 35% of sample nests were found by the flushing of incubating females (26% nests in maize). The age of nests (first egg=day 0) was estimated from the clutch/brood size and the stage of incubation estimated by egg floatation or by visual clues of nestling development. The degree of field vegetation cover in a 20 m radius around the nest during the laying period was classified to three categories: (1: 0– 20 % vegetation cover, 2: 21 – 60%, 3: 61–100%). The degree of egg visibility during the laying period to the direct view of an observer standing above the nest was classified to three categories: well visible from above, intermediately covered, and completely covered. Vegetation height above the nest (cm) was measured at each visit.

Videomonitoring

Using continuous video recording, we monitored 161 of 172 found active Skylark nests (81/83 of nests in maize fields and 80/89 nests in other crops). Video systems consisted of a small camouflaged video camera with IR diodes, a portable security digital video recorder, and a 12V/40Ah deep cycle battery (for details see Praus & Weidinger 2010). The system allowed for 4.5 days of recording on a 16 GB memory card. There was usually no response from the birds to the installed recording equipment. We visited all nests usually (80% of cases) every fourth day (mean 3.7, range 1–6) to check nest contents and to change the battery and memory card at nests monitored by video. For video-monitored nests we determined the exact survival time and nest fate. Time of failure for nests without a video camera was estimated as the midpoint between the last visit to an active nest with eggs or nestlings and the first negative visit (empty nest, dead chicks or deserted clutch). The exposure time of successful nests without a video camera was terminated by the 8th day of chick age on the basis of mean fledging age of video-monitored nests (8.2 days, range 7–12 days, n=33). In total, >91% of all exposure time (nest-days) included in the subsequent nest survival analyses was documented on video.

Data analysis

The focal habitat variable in our analyses was the type of crop. Of the total sample of 172 active nests, 83 nests were found in maize fields, while the rest was found in nine other crops (sugar beet: 29, opium poppy: 20, winter wheat: 11, alfalfa: 9, spring barley: 8, pea: 4, oilseed caraway: 3, brown bean: 3, potatoes *Solanum tuberosum*: 2). Because no other crop provided a sufficient sample of nests, we show results separately for maize fields and a pooled sample of the other crops. Only the nests from maize fields comprise a well-defined sample that represents a particular crop throughout the entire nesting season. The composition of the pooled sample does not represent the proportional use of different crops by nesting Skylarks, or the seasonal distribution of nests in different crops. As this precludes a meaningful application of inferential statistics, we focused on describing patterns in the data rather than on formally testing the differences between crop types.

We evaluated the effects of predictor variables on clutch size and brood size by fitting a linear mixed model. The data unit in these analyses was a nest. The fixed effect predictors were crop type (maize vs. other crops; see above), vegetation height (m; linear term) and date of first-egg laying or fledging, respectively (linear and squared term to account for a nonlinear seasonal pattern). Dates were transformed prior to analysis to take variation in phenology between years into account. To do this, we centred dates around the annual medians and then added a constant to ensure that all dates were positive before calculating squared terms.

We modelled daily survival rate (DSR) of nests separately during the egg and nestling stage by fitting a logistic mixed model. Each nest-day of exposure was regarded as an independent binary observation (survived or failed) and represented the data unit in these analyses. The fixed effect predictors were the same as in models of clucth/brood size, except that date and vegetation height refer to individual nest-days rather that to laying/fledging days. For this purpose we extrapolated vegetation height on individual nest-days from the measurements taken on each nest visit.

All models contained a random effect of year (random intercept) for which we estimated the variance component. We present regression coefficients estimated by the full model containing all fixed effect predictor variables that were a priori deemed important, regardless of their formal statistical significance. All models were fitted by procedures implemented in Proc Glimmix (SAS version 9.2; SAS Institute, Inc. 2013). To visualize model outputs we plotted the predicted values of breeding parameters for each crop type against date, while keeping the vegetation height at a fixed value.

In addition to model outputs we present also raw estimates of breeding parameters calculated from the pooled data for both crop types. This ensures direct comparability of our results with those of earlier descriptive studies. Mean clutch size was calculated from the sample of incubated nests checked at least twice in a four day interval. Hatchability of eggs/clutches is defined as the proportion of hatched eggs/complete clutches among those that survived over the incubation period. The daily survival rate was estimated separately for the egg (laying and incubation) and nestling stages as the simple ratio of survived to exposed nest-days. This procedure is eqivalent to an output of logistic regression model (see above) without covariates. Overall nest success was estimated as a product of stage-specific survival, i.e. $(\text{DSR for egg stage})^{14}$ x $(\text{DSR for nestling stage})^{9}$, where exponents were set to the mean length (in days) of the nesting stages. Nest productivity (number of fledglings per nesting attempt) was then estimated as a product of nest success x mean brood size at fledging. Mean values are shown with SE, or with 95% confidence intervals (CI) where indicated.

RESULTS

Timing of breeding

Of the 83 (89) nests in maize (other) fields, 13 (23) nests were found during nest building, 27 (30) during egg laying, 31 (33) during incubation and 12 (3) in the nestling stage. The mean nest age at discovery was 4.3 ±0.6 days for maize (-4 to 21; first egg laying = 0) and 2.2 ±0.4 day (-5 to 17) for other crops. The age of the nest when found slightly decreased throughout the season in both crop samples; linear regression for maize: age = 12.28 (±6.64 SE) – 0.05 (±0.04)*day of the year; day 1 = 1 January, n = 83; other crops: age = 8.16 (±2.56) – 0.04 (±0.02)* day of the year; n = 89. The earliest clutch in maize was initiated on 8 May (2009), the latest on 21 July (2010), the median first egg laying date was 12 June, and the highest number of active nests was present from about 5 to 28 June. Compared to maize, breeding was advanced in other crops; the earliest clutch was initiated on 6 April (2011), the latest on 16 July (2010), the median first egg laying date was 15 May, and the highest number of active nests was present during May (Fig. 1).

Vegetation at nest sites

Median vegetation height above the nest was 9 cm at the time of egg laying (0 – 95; n = 50), 68 cm at the time of hatching (5 – 180 cm; n = 32) and 110 cm at the time of fledging (25 – 215; n = 15) in maize fields vs. 15 cm at the time of egg laying (0 – 45; n = 70), 29 cm at the time of hatching (0 – 68 cm; n = 26) and 38 cm at the time of fledging (0 – 65; n = 18) in other crops (Fig. 2). Vegetation height above the nests in the stage of egg laying slightly increased over the course of nesting season in both crop samples; linear regresion for maize: height = -15.48 (±33.70) + 0.23 (±0.21)*day of the year, day 1 = 1 January, n = 50; other crops, height = -1.16 (±6.75) + 0.13 (±0.05)*day of the year, n = 70. Of 50 nests in maize (vs. 70 nests in other crops), 16% (18%) nests were initiated in fields with vegetation cover under 20%, 80% (54%) nests were initiated in fields with cover from 21 to 60%, and only 4% (20%) nests were placed in fields with cover exceeding 60%. Of these nests, 10% (4%) had no vegetation cover above the nest, 46% (61%) were partially covered and 44% (35%) were completely concealed by vegetation during egg laying.

Clutch and brood size

The size of completed clutches was 3.84 ± 0.10 eggs (4x 2 eggs, 12x 3, 37x 4 and 10x 5) in maize vs. 3.59 ± 0.08 eggs (2x 2 eggs, 24x 3, 36x 4 and 2x 5) in other crops. Mean clutch size slightly increased from April to June and declined thereafter (Fig. 3). A model (Table 1) accounting for annual differences in phenology corroborated a seasonal trend with the largest clutches being laid in about the middle of the season (Fig. 4a). After controlling for laying date and height of vegetation during laying the mean clutch size did not differ between maize vs. other crop fields (Table 1). The mean number of hatchlings was 3.42 ± 0.21 (1x 1, 3x 2, 8x 3, 9x 4; 3x 5) in maize vs. 3.29 ± 0.17 (4x 2, 7x 3, 10x 4) in other crops. Hatchability was 83.7% (n= 98 eggs) and 54.2% (n= 24 clutches) in maize vs. 89.6% (n = 77 eggs) and 66.7% (n = 21 clutches) in other crops. The length of incubation was 10.8 ± 0.17 days (9–12, n = 24; days counted from the first day after clutch completion) in maize vs. 11.1 ± 0.14 days (10–12, n = 21) in other crops. Chicks fledged at a mean age of 9.0 ± 0.25 days (7–10, n = 15, hatching day = age 1) in maize vs. 9.2 ± 0.36 days (7–12, n = 18) in other crops. The mean number of fledglings per successful nest was 2.60 ± 0.32 (4x 1, 3x 2, 3x 3, 5x4) in maize vs. 3.00 ± 0.30 (4x 1, 2x 2, 2x 3, 10x 4) in other crops. A model (Table 1) accounting for annual differences in phenology revealed a pronounced seasonal trend with the largest broods of fledglings in about the middle of the season (Fig. 4b). After controlling for fledging date and height of vegetation during fledging the broods were, on average, markedly smaller in maize compared to other crops (Table 1).

Nesting success and productivity

Documented nest fates in maize (vs. other crops) were: fledging 15 (18) nests, depredation 58 (47), egg desertion 4 (16), egg flooding 3 (4) and nestling death 3 (4). The number of nest depredated by birds/mammals was 27/24 in maize vs. 26/7 in other crops. Daily survival rate of nests was marginally higher during the nestling stage compared to the egg stage in both crop types (Table 2). During the egg stage, DSR was highest in about the middle of the nesting season, increased with vegetation height, but did not differ between maize vs. other crops (Table 2 and 3, Fig. 4c). During the nestling stage, DSR increased with date and was marginally lower in maize vs. other crops (Table 2 and 3, Fig. 4d). Nest productivity (nest success x brood size) derived from the raw data was 0.20 (0.079 x 2.60) fledglings per nest in maize vs. 0.24 (0.078 x 3.00) in other crops. Nest productivity derived from estimates yielded by the models (Table 1 and 2), where covariate values (height, date) were set to crop-specific means found in the data, was 0.32 (0.109 x 2.91) fledglings per nest in maize vs. 0.43 (0.123 x 3.52) in other crops.

DISCUSSION

Skylarks colonized the bare ground of maize fields immediately after sowing at about the beginning of May, and continued to breed there until the end of the nesting season in late July. Vegetation height at the time of clutch initiation was typically from 10 to 30 cm, and the maximum height did not exceed 100 cm throughout the nesting season. Vegetation height during the incubation and nestling stages did not differ markedly between maize and the pooled sample of other crops until about the middle of June (Fig. 2). However, the difference between crops became apparent with the accelerating growth of maize. Nestlings fledged in May and early June left nests under vegetation not exceeding 65 cm in all crops, while those fledged in July did so under maize reaching up to 210 cm. Our results thus support previous findings that Skylarks avoid high vegetation when selecting nest sites (Donald et al. 2001a, Toepfer & Stubbe 2001). However, we found that Skylarks can successfully finish nesting even under the rapidly growing vegetation of maize fields, probably due to the low density/coverage of this crop. Skylarks have been reported to avoid dense vegetation possibly because of impaired orientation (Pätzold 1983) and hindered ground locomotion (Jenny 1990, Odderskaer et al. 1997), yet explicit tests of this idea are lacking.

Our data on Skylark clutch size and length of the nesting cycle fall within the range of variation reported from other case studies (Delius 1965, Donald 2004, Hegemann 2012). As is common for multibrooded species (Crick et al. 1993), Skylark clutch sizes have increased towards the middle part of the breeding season (Tab. 1, Fig. 4a), when the most chicks can be reared, and then have declined again as the optimal time for nesting passed. Clutches were, on average, marginally larger in maize fields compared to other crops, but this was because the latter sample comprised small clutches from the beginning of the nesting season; for any given date the mean clutch size was almost equal in both crops. The hatchability of individual eggs (86% in all crops pooled) was lower than the average values found in Western Europe (about 95%; Weibel 1999, Donald et al. 2002). In spite of similar clutch sizes, the mean number of chicks fledged per successful nest was markedly lower in maize fields compared to other crops, especially after controlling for date (Table 1). The difference between crops and the more pronounced seasonal pattern in brood size (Fig. 4b) compared to clutch size (Fig. 4a) was likely a consequence of the lower hatchability and higher partial nestling mortality in maize fields and in the early/late nests. Indeed, the hatchability of individual eggs was marginally lower in maize compared to other crops . Clutches and nests placed in sparsely vegetated fields should be more exposed to fluctuating microclimates, which might reduce embryonic and nestling growth efficiency (Olson et al. 2006, Tieleman et al. 2008).

The overall Skylark nest success ("Mayfield" estimates) ranges from 22% to 40% (Weibel 1999, Donald et al. 2002, Jeromin 2002, Kragten et al. 2008) across West European farmland. In this study we observed very low nest success ranging from 8% (raw estimate) to 12% (model estimate), while the difference between crops was less than 1%. Given this low nest success and only a moderate size of fledged broods, which was just below the published values (about 2.8 to 3.5 chicks: (Delius 1965, Schläpfer 1988, Wilson et al. 1997, Weibel 1999), the resulting nest productivity was also very low – less than 0.4 chicks produced per nesting attempt in both crops. So far the lowest nest productivity has been reported from grassland fields in southern England (0.63, Donald et al. 2002). In any case, the observed nest productivity may not be sustainable, regardless the renesting potential of Skylarks (Donald 2004).

At least 84% (maize) and 65% (other crops) of primary nest losses were caused by predation. These values are in accordance with data from Skylark populations breeding on farmland (generally >70%; Weibel 1999, Donald et al. 2002). The incidence of nest desertion in our study (13% of all nests) was also similar to values reported elsewhere (10–13%; Weibel 1999, Donald et al. 2002). Most nest desertions (18 of 20) took place during periods of unfavorable rainy and cold weather, especially in April. Frequent soil and water erosion in wide row fields (maize, sugar beet, early stage opium poppy) during rainfall (Bazzoffi et al. 1998) increases the risk of nest flooding. Indeed, flooding of Skylark nests has been reported as the major cause of nest failure in the low and sparsely vegetated meadows close to the airport's runways (Griesser & Hegelbach 1999).

The prevalence of predation in this study implies that the patterns in nest survival rate (Fig. 4c,d) largely reflect the variability in predation rates. As expected, daily nest survival during the egg stage increased with vegetation height above the nest (Table 3), suggesting better protection from visually searching avian predators with vegetation growth. After controlling for an effect of vegetation height, there was little difference in nest survival between crops, suggesting that comparatively low vegetation during the egg stage was accessible to all predators, regardless of crop type. However, the positive effect of vegetation height was not detectable during the nestling stage (Table 3), i.e. in that part of nesting season when vegetation was on average taller (Fig. 2), and mammals took a large share of predation (own unpublished data). Accordingly, after controlling for vegetation height, the nest survival during the nestling stage was marginally lower in maize compared to other crops (Table 3, Fig. 4d), suggesting that tall, yet relatively sparse, maize is more accessible to mammalian predators than denser vegetation of other crops. Altogether, the results suggest that nests in bare fields and low vegetation of all crops were under a high pressure from locally dominant avian predators (53 of 84 predation events) and that whilst the high vegetation was generally safer for nesting, the high-grown maize fields late in the season were well accessible for mammalian predators.

Our results on use of nesting habitat and nesting success are unlikely to be influenced by biased nest sampling with regard to increasing vegetation height/density in the course of the breeding season. In fact, the age of nests at discovery marginally decreased throughout the season, and about half (55%) of all nests were already found before/during egg laying. Most importantly, these patterns did not differ between maize fields and the other crops. Nest predation rates are sometimes thought to be potentially affected by video monitoring (Richardson et al. 2009). However, we are reasonably confident that neither the presence of a camera near the nest, nor the repeated visits associated with the video recording, increased the nest predation rate at our sites (Praus & Weidinger 2010), which is in line with the current opinion that nest cameras generally do not increase nest predation (Ribic *et al.* 2012). Finally, the low age of sampled nests throughout the entire breeding season, together with high numbers of nest found already destroyed (presumably depredated early in the nesting cycle; not included in the analysis), suggest that our estimates of nest survival/predation rate were not seriously affected by our nest searching method. Hence we believe that the very low nest success was real and might realistically characterize Skylark breeding performance in crop fields in the study area.

Wide row spring crop fields, represented mainly by maize, sugar beet and opium poppy have become an important breeding habitat for Skylarks in the second half of nesting season. Their frequent use for nesting (Schläpfer 1988, Toepfer & Stubbe 2001, Eraud & Boutin 2002), together with the very low nest success as found in this study, suggest that these crops offer an attractive, yet risky, nesting habitat for Skylarks, especially late in the season when autumn-sown crops are too dense. The projected future increase and spatial aggregation of maize for use in energy cropping might therefore contribute to the continuing decline of Skylark populations. We propose that the main factors responsible for the low nesting success in spring wide crop fields are the high risk of nest predation. Comparative data on Skylarks from other areas as well as data on other species are needed to validate and extend our conclusions to farmland birds in general (Brandt & Glemnitz 2014).

ACKNOWLEDGEMENTS

The work was supported by funding from Palacky University (IGA PrF_2012_021 and IGA PrF_2013_007). Comments by Paul F. Donald and T. Mazgajski greatly improved the earlier draft of this paper.

REFERENCES

Bazzoffi P., Pellegrini S., Rocchini A., Morandi M., Grasselli O. 1998. The effect of urban refuse compost and different tractors tyres on soil physical properties, soil erosion and maize yield. Soil. Till. Res. 48: 275–286.

Berzsenyi Z., Lap Q. 2004. Studies on the effect of plant density on maize growth using Richards function. Proceeding for the 4th International Crop Science Congress: 513–516.

Brambilla M., Falco R., Negri I. 2012. A spatially explicit assessment of within-season changes in environmental suitability for farmland birds along an altitudinal gradient. Anim. Conserv. 15: 638–647.

Brandt K., Glemnitz M. 2014. Assessing the regional impacts of increased energy maize cultivation on farmland birds. Environ. Monit. Assess. 186: 679–697.

Busche G. 1994. Zum Niedergang von „Wiesenvögeln" in Schleswig-Holstein 1950 bis 1992. J. Ornithol. 135: 167–177.

Crick H. Q. P., Gibbons D. W. & Magrath R. D. 1993. Seasonal changes in clutch size in British birds. J. Anim. Ecol. 62: 263–273.

Czech statistical office 2012. [Crop area and first harvest estimates in the Czech Republic in 2012]. Available at: http://www.czso.cz/csu/csu.nsf/1e01747a199f30f4c1256bd50038ab23/94912c113edf4287c1257a460031d437/$FILE/skl072612analyza.pdf (Accessed December 17, 2014)

Čandová D. 2011. [Utilization of maize crop to biogas production]. PhD thesis. Czech University of Life Science, Prague.

Davis S. K. 2005. Nest-Site Selection Patterns and the Influence of Vegetation on Nest Survival of Mixed-Grass Prairie Passerines. Condor 107: 605–616.

de Carli E., Fornasari L., Bani L., Bottoni L. 1998. Trend in distribution, abundance and habitat features of Skylark *Alauda arvensis* in northern Italy. Game and Wildlife 15: 387–396.

Delius J. D. 1965. A population study of Skylarks *Alauda arvensis*. Ibis 107: 466–492.

Donald P. F. 2004. The Skylark. T & AD Poyser, London.

Donald P. F., Vickery J. A. (eds) 2001. The ecology and conservation of Skylarks *Alauda arvensis*. RSPB, Sandy.

Donald P. F., Buckingham D. L., Muirhead L. B., Evans A. D., Kirby W. B., Schmitt S. I. A. 2001a. Factors affecting clutch size, hatching rates and partial brood losses in Skylark *Alauda arvensis* nests on lowland farmland. In: Donald P. F., Vickery J. A. (eds). The ecology and conservation of Skylarks *Alauda arvensis*: 63–77. RSPB, Sandy.

Donald P. F., Evans A. D., Buckingham D. L., Muirhead L. B., Wilson J. D. 2001b. Factors affecting the territory distribution of Skylarks *Alauda arvensis* breeding on lowland farmland. Bird Study 48: 271–278.

Donald P. F., Evans A. D., Muirhead L. B., Buckingham D. L., Kirby W. B., Schmitt S. I. A. 2002. Survival rates, causes of failure and productivity of Skylark *Alauda arvensis* nests on lowland farmland. Ibis 144: 652–664.

Engel J., Huth A., Frank K. 2012. Bioenergy production and Skylark (*Alauda arvensis*) population abundance—a modelling approach for the analysis of land-use change impacts and conservation options. GCB Bioenergy 4: 713–727.

Eraud C., Boutin J. M. 2002. Density and productivity of breeding Skylarks *Alauda arvensis* in relation to crop type on agricultural lands in western France. Bird Study 49: 287–296.

Flohre A., Fischer C., Aavik T., Bengtsson J., Berendse F., Bommarco R., Ceryngier P., Clement L. W., Dennis C., Eggers S., Emmerson M., Geiger F., Guerrero I., Hawro V., Inchausti P., Liira J., Morales M. B., Oñate J. J., Pärt T., Weisser W. W., Winqvist C., Thies C., Tscharntke T. 2011. Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids and birds. J. Appl. Ecol. 21: 1772–1781.

Fuller R. J. (ed). 2012. Birds and habitat: Relationships in Changing Landscapes. Cambridge University Press.

Gevers J., Høye T. T., Topping C. J., Glemnitz M., Schröder B. 2011. Biodiversity and the mitigation of climate change through bioenergy: impacts of increased maize cultivation on farmland wildlife. GCB Bioenergy 3: 472–482.

Gilroy J. J., Anderson G. Q. A., Grice P. V., Vickery V. A., Sutherland W. J. 2010. Mid-season shifts in the habitat associations of Yellow Wagtails *Motacilla flava* breeding in arable farmland. Ibis 152: 90–104.

Griesser M., Hegelbach J. 1999. Territorialität und Brutbiologie der Feldlerche *Alauda arvensis* in extensiv bewirtschafteten Wiesen des Flughafens Zürich-Kloten. Ornithol. Beob. 96: 73–82.

Hagemeijer W. J. M., Blair M. J. (eds). 1997. The EBCC Atlas of European Breeding Birds: Their distribution and abundance. T & AD Poyser, London.

Hart J. D., Milsom T. P., Fisher G., Wilkins V., Moreby S. J., Murray A. W. A., Robertson P. A. 2006. The relationship between Yellowhammer breeding performance, arthropod abundance and insecticide applications on arable farmland. J. Appl. Ecol. 43: 81–91.

Hegemann A. 2012. Strive to survive: The Skylark's ecology and physiology in an annual-cycle perspective. PhD Thesis. University Groningen, Groningen.

Hole D. G., Whittingham M. J., Bradbury R. B., Anderson G. Q. A., Lee P. L. M., Wilson J. D., Krebs J. R. 2002: Widespread local House-sparrow extinctions – Agricultural intensification is blamed for the plummeting populations of these birds. Nature 148: 931–932.

Jenny M. 1990: Territorialität und brutbiologie der Feldlerche *Alauda arvensis* in einer intensiv genutzten agrarlandschaft. J. Ornithol. 131: 241–265.

Jeromin K. 2002. Zur Ernährungsökologie der Feldlerche (*Alauda arvensis* L. 1758) in der Reproduktionsphase. PhD Thesis. Christian-Albrechts-Universität, Kiel.

Kragten S., Trimbos K. B., de Snoo G. R. 2008. Breeding Skylarks *Alauda arvensis* on organic and conventional arable farms in the Netherlands. Agr. Ecosyst. Environ. 126: 163–167.

Nagy S., Nagy K., Szép T. 2009. Potential impact of EU accession on common farmland bird populations in Hungary. Acta Ornithol. 44: 37–44.

Odderskaer P., Prang A., Poulsen J. G., Andersen P. N., Elmegaard N. 1997. Skylark (*Alauda arvensis*) utilisation of micro-habitats in spring barley fields. Agr. Ecosyst. Environ. 62: 21–29.

Olson C. R., Vleck, C. M., Vleck D. 2006. Periodic Cooling of Bird Eggs Reduces Embryonic Growth Efficiency. Physiol. Biochem. Zool. 79: 927–936.

Pätzold R. 1983. Die Feldlerche. Die Neue Brehm-Bücherei 323. A. Ziemsen Verlag, Wittenberg-Lutherstadt.

Praus L., Weidinger K. 2010. Predators and nest success of Sky Larks *Alauda arvensis* in large arable fields in the Czech Republic. Bird Study 57: 525–530.

Reif J., Voříšek P., Šťastný K., Bejček V., Petr J. 2008. Agricultural intensification and farmland birds: new insights from a central European country. Ibis 150: 569–605.

Rheinwald G. 1993. Atlas der Verbbreitung und Hänfigkeit der Brutvögel Deutschlands. Dachverband Deutscher Avifaunisten, Germany.

Ribic C. A., Thompson F. R., Pietz P. J. 2012. Video Surveillance of Nesting Birds. University of California press.

Richardson T. W., Gardali T., Jenkins S. H. 2009. Review and meta-analysis of camera effects on avian nest success. J. Wildlife Manage. 73: 287–293.

Robertson J., Berg Å. 1992. Status and population changes of farmland birds in southern Sweden. Ornis Svecica 2: 119–130.

Saurbrei R., Ekschmitt K., Volters W., Gottschalk T. K. 2014. Increased energy maize production reduces farmland bird diversity. GCB Bioenergy 6: 265–274.

Schläpfer A. 1988. Populationsökologie der Feldlerche *Alauda arvensis* in der intensiv genutzen Agrarlandschaft. Ornithol. Beob. 85: 309–371.

Schümann K., Engel J., Frank K., Huth A., Luick R., Wagner F. 2010. Naturschutzstandards für den Biomasseanbau. Ergebnisse des gleichnamigen F & E-Vorhabens. Bonn–Bad Godesberg: Bundesamt für Naturschutz.

Siriwardena G. M., Baillie S. R., Buckland S. T., Fewster R. M., Marchant J. H., Wilson J. D. 1998. Trends in the abundance of farmland birds: a quantitative comparison of smoothed Common Bird Census indices. J. Appl. Ecol. 35: 24–43.

Tieleman B. I., van Noordwijk H. J., Williams J. B. 2008. Nest site selection in a hot desert: Trade off between microclimate and predation risk? Condor 110: 116–124.

Toepfer S., Stubbe M. 2001. Territory density of the Skylark (*Alauda arvensis*) in relation to field vegetation in central Germany. J. Ornithol. 142: 184–194.

Tryjanowski P. 2000. Changes in breeding populations of some farmland birds in W Poland in relation to changes in crop structure, weather conditions and number of predators. Folia Zool. 49: 305–315.

Weibel U. M. 1999. Effects of wildflower strips in an intensively used arable area on Skylarks (Alauda arvensis). PhD thesis. Swiss Federal Institute of Technology, Zurich.

Wilson J. D. 2001. Foraging habitat selection by Skylarks *Alauda arvensis* on lowland farmland during the nestling period. In: Donald P.F., Vickery J.A. (eds). The Ecology and Conservation of Skylarks *Alauda arvensis*. 91–101. Sandy, RSPB.

Wilson J. D., Evans J., Browne S. J., King J. R. 1997. Distribution and breeding success of Skylarks *Alauda arvensis* on organic and intensive farmland in southern England. J. Appl. Ecol. 34: 1462–1478.

Wilson J. D., Evans, A. D., Grice P. V. 2009. Bird Conservation and Agriculture. Cambridge University Press.

Winter M., Douglas H. J., Shaffer J. A. 2005. Variability in vegetation effects on density and nesting success of grassland birds. J. Wildl. Manage. 69: 185–197.

Table 1. Linear mixed models showing effects of predictor variables on clutch and brood size in the Skylark. Shown are estimates from the full model where all predictors were kept regardless of their formal significance ($p < 0.05$ indicated by bold face). Effect of crop is shown for maize vs. other crops (= reference category). Vegetation height (m) and date (linear and squared term) were continuous predictors; all dates were centred by the annual median prior analysis. For random effect of year, the variance component (±SE) is shown where estimable; however, conclusions remained qualitatively the same when year was modeled as a fixed effect. Sample size was 128 (clutch size) and 33 (brood size) nests. Predictions of the models are plotted in Fig. 4 a,b.

	Response = Clutch size		Response = Brood size	
Predictor	Estimate	SE	Estimate	SE
Intercept	2.6151	0.2945	0.6918	0.6888
Crop	0.0009	0.1434	**-1.3138**	**0.5755**
Height	0.6193	0.3425	1.1864	0.6650
Date	**0.0368**	**0.0118**	**0.1192**	**0.0338**
Date^2	**-0.0003**	**0.0001**	**-0.0014**	**0.0004**
Year (random)	0.0000	0.0000	0.3228	0.4756

Table 2. Daily survival rates (DSR) of Skylark nests in maize and other crop fields in the Czech Republic during the breeding seasons 2009–2011. Shown are raw estimates calculated as a ratio of survived to exposed nest-days and estimates yielded by the models (Table 3) where covariates (height, date) were set at crop-specific mean values found in the data set.

Crop	Total	Nest-	Failed	Raw estimate		Model estimate	
Nesting stage	nests	days	nests	DSR	95% CI	DSR	95% CI
Maize							
Eggs	71	436	49	0.888	0.854–0.916	0.906	0.865–0.936
Nestlings	34	205	19	0.907	0.859–0.943	0.911	0.850–0.949
Other crops							
Eggs	85	448	61	0.864	0.829–0.894	0.890	0.840–0.925
Nestlings	28	184	10	0.946	0.902–0.974	0.951	0.875–0.982

Table 3. Logistic mixed models showing effects of predictor variables on daily survival rates of nests during the egg and nestling stages. For sample size (number of nest-days) see Table 2, for other explanation see Table 1. Predictions of the models are plotted in Fig. 4 c,d.

	Response = DSR (egg stage)		Response = DSR (nestling stage)	
Predictor	Estimate	SE	Estimate	SE
Intercept	0.4381	0.6871	2.1949	0.9316
Crop	0.0221	0.2568	-1.0094	0.6900
Height	**1.2058**	**0.5178**	-0.8186	0.7399
Date	**0.0514**	**0.0238**	0.0177[a]	0.0458[a]
Date^2	**-0.0005**	**0.0002**	0.0002	0.0005
Year (random)	0.0444	0.0778	0.0784	0.2736

Figures

Fig. 1. Number of nest initiations (observed or back-calculated first egg laying dates; columns) and the number of monitored active Skylark nests (i.e. exposure nest-days as shown in Table 2; solid line) over the course of the nesting season.

Fig. 2. Mean (±SE) vegetation height (cm) at Skylark nests on the day of first egg laying: solid line, black circles; chick hatching: dashed line, open squares and fledging: dotted line, black triangles, over the course of the nesting season.

Fig. 3. Mean (±SE) number of eggs in complete clutch (white columns), number of hatchlings (grey columns) and number of fledglings (black columns) in Skylark nests over the course of the nesting season (n = number of nests). The values are raw means calculated from the pooled data; for model outputs see Fig. 4 a,b.

Fig. 4. Seasonal variation in clutch size (number of eggs, a), brood size (number of fledglings, b) and daily survival rate of nests with eggs (c) and nestlings (d) in Skylark. Shown are values predicted by the respective models (a and b: Table 1; c and d: Table 3) for "other crops" (thin solid line; dashed lines represent 95% confidence limits) and maize (bold solid line; confidence limits not shown). Predicted values are plotted over the observed range of dates in the respective crop type; all dates were centred by annual median prior analysis. Predicted values are for crop height set to a typical value common to both crop types (a: 0.2 m; b: 0.6 m; c and d: 0.4 m).

Fig. 1.

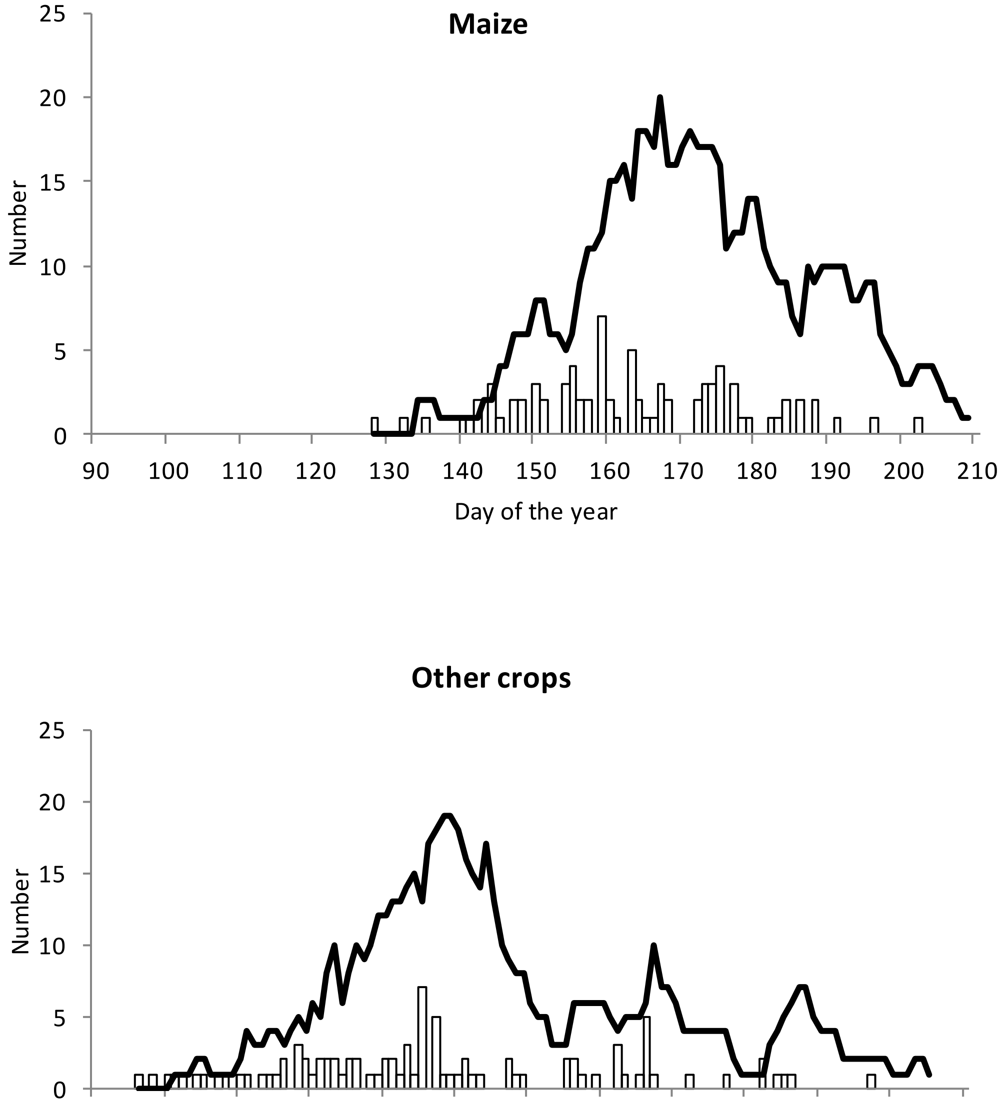

Maize
25
20
15
10
5
0
Number
90
100
110
120
130
140
150
160
170
180
190
200
210
Day of the year
Other crops
25
20
15
10
5
0
Number
90
100
110
120
130
140
150
160
170
180
190
200
210
Day of the year

Fig. 2.

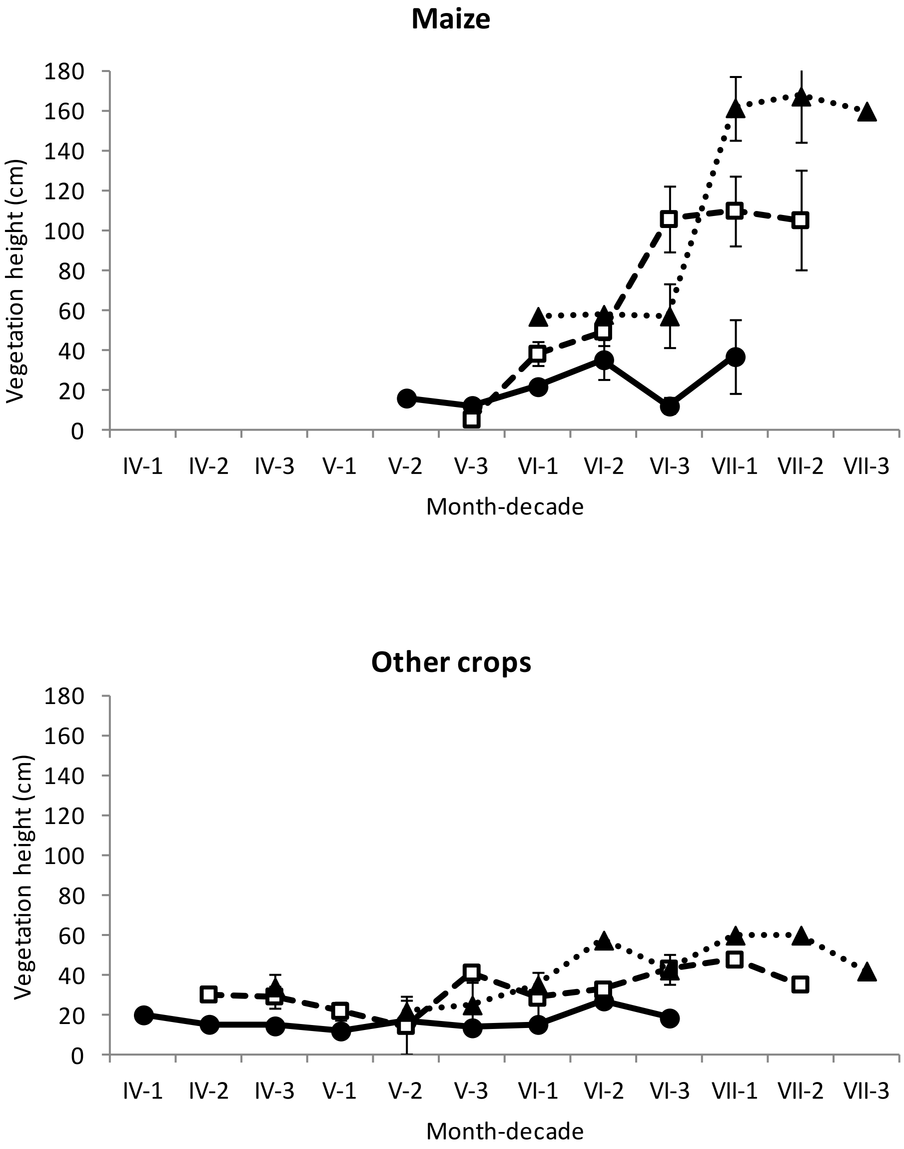

Maize
Vegetation height (cm)
0
20
40
60
80
100
120
140
160
180
IV-1
IV-2
IV-3
V-1
V-2
V-3
VI-1
VI-2
VI-3
VII-1
VII-2
VII-3
Month-decade
Other crops
Vegetation height (cm)
0
20
40
60
80
100
120
140
160
180
IV-1
IV-2
IV-3
V-1
V-2
V-3
VI-1
VI-2
VI-3
VII-1
VII-2
VII-3
Month-decade

Fig. 3.

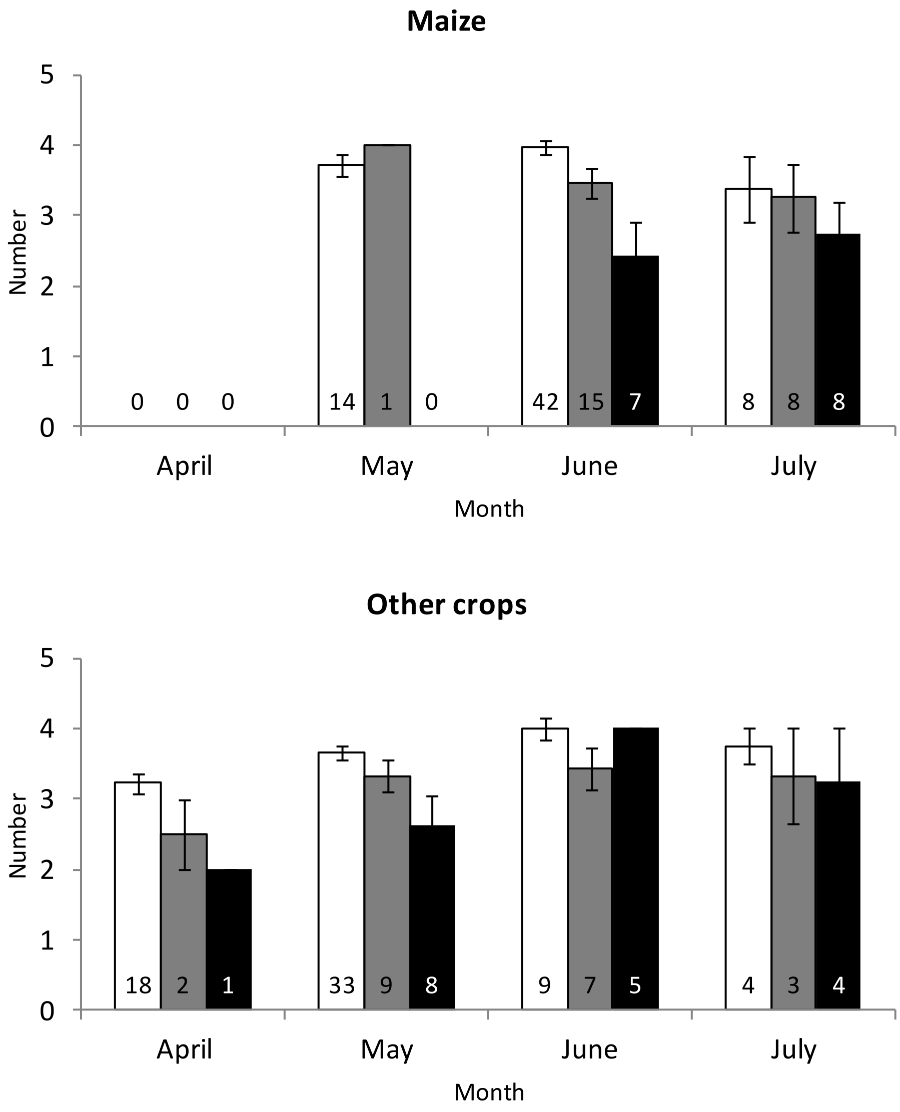
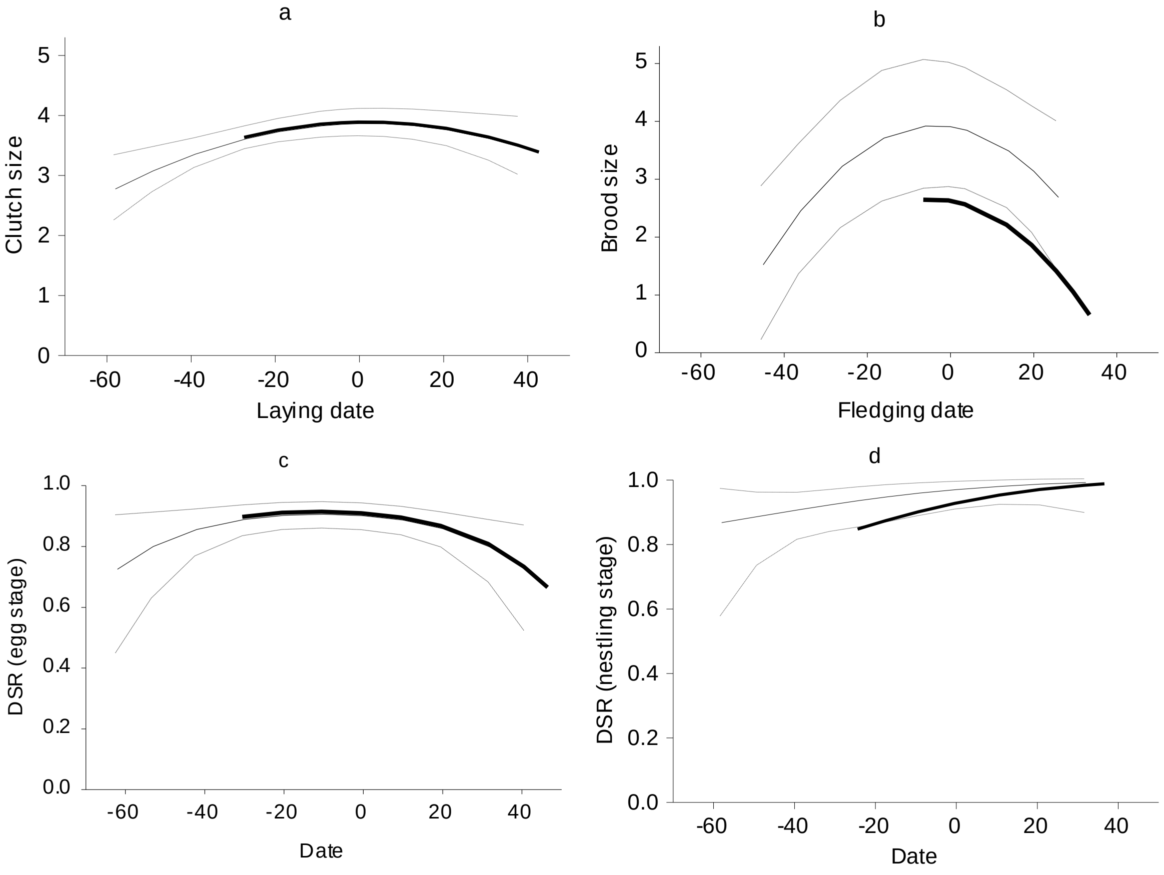

Maize
Number
5
4
3
2
1
0
0 0 0
14 1 0
42 15 7
8 8 8
April
May
June
July
Month
Other crops
Number
5
4
3
2
1
0
18 2 1
33 9 8
9 7 5
4 3 4
April
May
June
July
Month

Fig. 4.


a
Clutch size
0
1
2
3
4
5
-60
-40
-20
0
20
40
Laying date
b
Brood size
0
1
2
3
4
5
-60
-40
-20
0
20
40
Fledging date
c
DSR (egg stage)
0.0
0.2
0.4
0.6
0.8
1.0
-60
-40
-20
0
20
40
Date
d
DSR (nestling stage)
0.0
0.2
0.4
0.6
0.8
1.0
-60
-40
-20
0
20
40
Date

CONTRIBUTION V.

Praus, L. & Weidinger, K. Complex patterns of incubation behaviour in the Skylark (*Alauda arvensis*) breeding in arable fields. (*manuscript*)

Complex patterns of incubation behaviour in the Skylark (*Alauda arvensis*) breeding in arable fields

LIBOR PRAUS[1]* & KAREL WEIDINGER[1]

[1]Department of Zoology and Laboratory of Ornithology, Faculty of Science, Palacky University, 17. listopadu 50, 771 46 Olomouc, Czech Republic
*Corresponding author, e-mail: libor.praus@gmail.com

ABSTRACT

Incubation behaviour is largely determined by inherent physiological demands of parents and embryos, and consequently, there might be only a narrow window for behavioral adjustments. We asked what factors affect incubation behaviour in Skylarks breeding in crop fields. This rather uniform habitat permitted us to control for habitat heterogeneity while focusing on the targer explanatory variables. By means of continuous video recording we obtained 75 full-day samples of incubation behaviour from 55 nests. We evaluated incubation patterns in relation to ambient temperature and vegetation characteristics, while controlling for incubation progress and clutch size. Novel finding of this study is that within-day variation (time-specific attentiveness and length of individual bouts) was not independent of the variation found on a daily basis (daily mean values of respective variable), as these two data levels interacted in a complex manner. Attentiveness was on average higher in less favourable conditions, i.e. on cold days and in nests under tall vegetation (wet nest sites); however, attentiveness was disproportionally higher in morning and evening hours, when microclimatic effects were accentuated. In contrast, better nest concealment (protection from predators rather than proxy of nest microclimate) releaved females from incubation duties on average, yet disproportionally so during mid-day in contrast to morning and evening hours. We showed that the most remarkable patterns in incubation behaviour emerged only after the interactions between daytime and other predictors were taken into account. These findings suggest that the way time is allotted may be equally as important as the total amount of time spent incubating.

Key words: Incubation, Skylark, *Alauda arvensis*, nest attentiveness, agricultural intensification, nest concealment

INTRODUCTION

Avian incubation behaviour is very conservative with almost all species relying on contact with the adult to raise egg temperature to a level suitable for embryonic development (Haftorn 1988, Deeming 2002a). Incubating parent must balance thermal needs of the developing embryos with their own energetic needs by leaving the nest to forage (Conway & Martin 2000a, Tinbergen & Williams 2002).

The principal characteristic of incubation behaviour is incubation attentiveness defined as the proportion of time the eggs are incubated by a parent. Total nest attentiveness is strongly limited by available time and energy (Matysioková & Remeš 2014). In gyneparental systems, where only the female incubates, daytime incubation is usually intermittent, i.e. bouts of attentiveness (on-bouts) are interspersed with frequent foraging bouts (off-bouts). Total attentiveness is then given by the ratio of average (or sum) on-bout to off-bout lengths. It follows that incubating parent can keep same attentiveness through proportionally increasing/decreasing lenght of individual on- and off-bouts, thus decreasing/increasing frequency of incubation rhythm. Conversely, any disproportional change in lengths of on- and off-bouts results in change in total attentiveness, regardless of incubation rhythm. Incubation behaviour is thus potentially plastic trait that allows incubating birds to cope with changing environmental conditions and their own needs.

Indeed, incubation behaviour was shown to vary with ambient temperature and insolation (Hötker 1990, Kovařík et al. 2009, Tieleman et al. 2008), food supply (Zimmerling & Akney 2005, Barnett & Briskie 2010, Boulton et al. 2010, Lothery et al. 2014) including allofeeding rate (Pearse et al. 2004), predation risk (Ghalambor & Martin 2002, Massaro et al. 2008, Cervencl et al. 2011) and success of previous nesting attempt (Chalfoun & Martin 2010). Specifically, birds incubating at low ambient temperature take shorter off-bouts, which prevents eggs from cooling to temperatures below the physiological zero temperature (Zerba & Morton 1983, Conway & Martin 2000a, Carey 2002, Kovařík et al. 2008, MacDonald et al. 2014). At the other extreme, as ambient temperature rises above 40.5°C, females are forced to take shorter off-bouts to prevent eggs from overheating to lethal temperatures during their absence (Conway & Martin 2000a, Tieleman et al. 2008). Food suplemented parents spend less time off the nest than hunger parents (Chalfoun & Martin 2007, Barnett & Briskie 2010, Lothery et al. 2014). In environments with high nest predation by visualy guided predators, natural selection favors infrequent nest trips opposite to short off-bout duration (Conway & Martin 2000b, Massaro et al. 2008). Small birds mostly could not assess and respond beforehand to territory level nest-predation risk, but parents whose nests were depredated reduced clutch sizes and activity at nests attempted later in the season by increasing the length of bouts and decreasing the number of trips to feed nestlings (Chalfoun & Martin 2010).

Effective resolution of the trade-off between embryos and parent is particularly complicated in species with unasisted single-sex incubation. Moreover, in small ground-nesting steppe passerines which usually build rudimentary nests at open sites, the unattended eggs are exposed to high temperature variation and to predators (Deeming 2002a). Vegetation cover and height have been shown to be the critical factors for nest-site selection in ground-nesting birds (Helzer & Jelinski 1999), because they can counteract predation and overheating simultaneously (Wells & Fuhlendorf 2005, Tieleman et al. 2008, Gillis et al. 2012).

Nowadays the steppe habitat is represented mostly by unnatural arable land in Europe (Stoate et al. 2009). Agricultural systems alter biotic interactions and behavioural patterns of many organisms and can have serious environmental consequences (Matson et al. 1997). Arable fields are characterized by rapid and unpredictable (from the bird perspective) changes of vegetation cover and height during the breeding season as well as by interannual changes of complete habitat features (Feddes et al. 1978). Moreover, crop monocultures reduce availability of safe nesting and foraging sites (Donald 2004, Atkinson et al. 2005). Accordingly farmland ground-nesting birds might have little opportunity to assess habitat characteristics for adequate nest site choice to the demands of the clutch and their own needs. Plastic adjustements of incubation behaviour might be critical for successful reproduction under such conditions. However, as far as we know, there have been no studies of incubation behaviour in this particular study system.

The goal of this study was to to find out what factors affect nest attentiveness and bouts duration in the the Skylark (*Alauda arvensis*), a typical ground nesting passerine abundantly breeding in crop fields across Europe (Donald 2004, Šťastný et al. 2006). The nesting season of Skylark lasts from beginning of April to late July in lowland arable fields in the Czech Republic (Šťastný & Hudec 2011). During this period the lenght of daylight changes by about 3.5 h and mean daily temperature raises by more than 10°C. Unlike many previous studies we used continuous videorecording to analyse 24-hour samples of incubation behaviour. Moreover, Skylark nest sites in arable fields vary from bare ground to tall vegetation throughout the whole breeding season. The uniform habitat of large arable fields permitted us to control for habitat heterogeneity while focusing on the targer explanatory variables. We evaluated variation in Skylark incubation patterns in relation to ambient temperature and vegetation characteristics, while controlling for incubation progress and clutch size.

MATERIALS AND METHODS

Study area

The data were collected during the breeding season 2009-2011 in the East Bohemia Region, the Czech Republic (49° 55.39' N, 15° 59.33' E, altitude 240-500 m). The study area of c 60 km² is characterized by predominance of conventionally managed farmland (>80% of total area, mean parcel size about 50 ha) interspersed with remnants of deciduous woodland (<5% of total area) and villages. Main crop types were: winter wheat *Triticum aestivum* (45%); maize *Zea mays* (15%); winter rape *Brassica napus subsp. napus* (15%), spring barley *Hordeum vulgare* (10%); sugar beet *Beta vulgaris* (5%); lucerne *Medicago sativa*,opium poppy *Papaver somniferum*, oilseed caraway *Carum carvi*, pea *Pisum sativum* and brown bean *Vicia faba* (each ≤2%).

Weather data (Appendix 1) were obtained from measuring stations in Hrochův Týnec (5 km NW of the study area; daily precipitation) and Pardubice (17 km NW of the study area;. mean daily temperature). Although these data might not correspond exactly to conditions in the study area in terms of absolute values, we assumed they provide reasonable indices for the purpose of our analysis.

Nest searching and monitoring

Nest searching was undertaken from the beginning of the breeding season in the middle of April and continued until nesting activity had ceased in late July. Roughly, 100 days per year were devoted to nest searching in the whole study area. We located nests by systematically searching in suitable plots (≤60% mean vegetation coverage) of arable field parcel, 35% of sample nests was found by the accidental flushing of incubating females. Of the 55 nests included into the analysis, 9 nests were found during nest building, 25 during egg laying and 21 during incubation.

Nests were monitored using continuous video surveillance to record parental behaviour and to determine nest fates. The video monitoring systems consisted of a video camera (40 × 35 mm) with infrared-emitting diodes, a portable security digital video recorder (DVR; Yoko RYK-9107), and a 12V/40-65Ah deep cycle battery. The DVR was housed in a weatherproof plastic box (125 × 95 × 50 mm) and connected to the camera by a 5-m cable and to the battery by a 1-m cable. All outer parts of the system were camouflaged by brown-green spotted painting. The camera was mounted on a piece of wire that was inserted in the ground and allowed the adjustment of camera position. Cameras were placed 0.7–2.0 m from nests (depending on nest visibility) and 2–20 cm above the ground, never exceeding the height of surrounding vegetation. We used local natural material (dry vegetation, stones) to mask the camera; all other parts (box, battery, cables) were buried under ground. We set the DVR to record continually with a frequency of 10 fps at 640 × 480 pixel resolution. These settings allowed for 4.5 days of recording on a 16 GB memory card. There was usually no response from the birds to the installed recording equipment, and incubation typically resumed within <15 minutes after the camera had been installed. We visited the nests usually (70% cases) every fourth day to check nest content and to change the battery and memory card, the rest of the nest visits were at 3-day intervals.

Two vegetation characteristics were recorded (by L.P.) on each nest visit. Vegetation height was measured directly above the nest (cm). Nest cover scored visibility of the eggs from direct view of an observer standing above the nest into three categories: well visible from above, intermediately covered, and completely covered.

Data analysis

Continuous video monitoring of nests provided a large amount of video footage. To analyze incubation behaviour we have to subsample from the available data. The sampling unit was a 24 h period starting at midnight, taken from continuous recordings of the entire nesting cycle. We considered video records from days without heavy rain, without disturbance by agricultural operations, and midway between observer visits. We purposely sampled recordings to cover the whole breeding season (late April-late July) and all stages of incubation (1-11 day). The day of incubation (day 1 = the 1st day after clutch completion) was determined from a combination of egg floatation and known laying dates. The length of incubation in the study population was 11.15 ±0.90 SD days (n = 62 nests). We also paid care to sample nests over the full range of crop heights and concealment categories (Appendix 2). Included into the analysis were values of vegetation height and cover recorded on the last nest visit before the sampling day.

Sampled 24-hour videorecordings were reviewed in the lab by L.P. to determine the length of working day (*sensu* Shaw & Creswell 2014), i.e. the period from the first morning departure from the nest to the last evening arrival to nest prior overnight incubation, and the legths of all consecutive on- and off-bouts. Our data represent three hierarchical data units (Table 1). In all, 55 nest were sampled. Although Skylark females were not individually marked, we assume that these nests represented different females due to their wide spatial distribution over the study area during three years. Twenty of these 55 nests were sampled twice, resulting in 75 daily damples. The lowest data unit was an individual on/off bout. We conducted analyses on two data levels.

In the analysis of incubation behaviour on a daily basis we modeled mean daylong values of incubation attentiveness and on- and off-bout length. Attentiveness in this case was calculated as a proportion of the total time spent incubating during the working day. Similarly, length of all recorded on- and off-bouts were averaged over the working day. The explanatory variables (Appendix 2) were clutch size, day of incubation, mean daily temperature, vegetation height and nest cover (three categories). To account for double sampling of some nests we entered nest identity as the random effect in the models.

In the within-day analysis we modeled lengths of individual on- and off-bouts. Attentiveness ("time-specific attentiveness") in this case was calculated from the lengths of individual subsequent on- and off-bouts. The explanatory variables were the same as in the analysis on a daily basis. To analyse daily variation in behaviour we entered the relative time of day as an additional explanatory variable. We used relative timing instead of absolute timing to account for variation in the length of daylight period. We divided the period from sunrise to sunset (= 100%) into five periods each encompasing 20% of the daylight period. Timing of each bout was then classified into these five periods yielding categorical explanatory variable with 5 levels. The bouts starting just after sunset (c 2.5% of all bout) were classified into the last period of daylight. Division of daylight into five periods was sufficent to capture the daily pattern of incubation behaviour (Fig. 1). To account for natural data clustering we entered identity of the daily sample as the random effect in the models.

In both analyses we fitted general mixed models implemented in PROC MIXED (SAS Institute, Inc. 2013) with the variables indicated above. We applied Box-Cox transformation to all three response variables (Table 1) to conform with normality assumptions. However, even an analysis of raw data yielded qualitatively similar results. We focused on detecting patterns in the data rather than on formal hypothesis testing. In the between-day analysis we kept the main effects of all explanatory variables in the models regardless of their statistical significance. Next we converted parameter estimates into standardized effect sizes (Nakagawa & Cuthill 2007) to assess relative importance of individual explanatory variables. Our goal in the within-day analysis was to assess incremental effects of daytime and interaction of daytime with the other explanatory variables in explaining the daily pattern of incubation. Hence we fitted set of seven models containing: main effects of all five explanatory variables (as in between-day analysis), the same as in preceding model with added main effect of daytime, the same as in preceding model with added interaction of daytime with one of the five other explanatory variable. We adopted model selection approach to rank these models according to AICc criterion (Burnham & Anderson 2002). We avoided fitting models with all interaction effects of interest entered simultaneously due their complexity and risk of getting spurious results. To visualize the above interaction effects, we plotted model predictions against daytime for selected levels of the explanatory variable involved in the particular interaction, while keeping the other explanatory variables fixed at the modal value.

Finally, we repeated all the above analyses with a subset of data restricted to the nests located in maize fields (Appendicces 2, 3, 4, 5, 6, 7). By this we hoped to minimize uncontroled environmental variation that might have influenced our conclusions based on the pooled sample of nests from different crops. We adopted this approach instead of entering crop type as an additional explanatory variable because the distribution of nests among crops was very uneven. Nevertheless, because the restricted data set yielded very similar results we present here only the results based on the complete data set.

RESULTS

Overall characteristics of incubation behaviour

We analysed 75 complete daily samples of incubation behaviour (2009: n=14; 2010: n=24; 2011: n=37) from 55 nests (2009: n=11; 2010: n=18; 2011: n=26). In total we checked 1114.38 h of active daylight period and 2150/2075 individual off/on bouts (Table 1). The length of working day lasted on average 14.87± 0.14 (SE) h (range 11.87 – 17.07 h). Total incubation attentiveness was 0.69 per working day (Table 1) or 0.81 per 24 h. Females took on average 28.67 ± 1.02 off-bouts and the time spent off the nest totalled 272.85 ± 7.34 min per 24 h. Females did not leave the nest during the hours of darkness. Incubating feeding by males was not recorded.

Variation on a daily basis

Our models explained only a small part of the variation among mean daily values of incubation attentiveness and bout length (Table 2). Standardized effect sizes for all explanatory variables were small to moderate (r < 0.3) and their confidence intervals mostly contained zero (Fig. 2). The notable exception were the effects of ambient temperature and vegetation height. Attentiveness decreased with increasing temperature, which effect resulted from shortening of on-bouts and lenghtening of off-bouts. Attentiveness increased with the height of vegetation above the nest, which effect was mostly attributable to lenghtened on-bouts, while the legth of off-bouts was little affected. Attentivenes tended to decrease with increasing vegetation cover of the nest, which effect was due to shortening of on-bouts. Attentiveness was only little affected by the day of incubation and by the clutch size. Nevertheless, on- and off-bout lenghts increased with increasing clucth size, thus indicating lower frequency of incubation bouts.

Within-day variation

All measured characteristics of incubation behaviour varied markedly during the day (Fig. 1, Appendix 5). Attentiveness was highest in the morning and evening hours corresponding to the first and the last 20% of the daylight period. This pattern resulted from disproportional variation of on- and off-bout lengths. On-bouts were longest in the morning and evening, except the period just prior the end of activity, while off-bouts shortened gradually during the evening hours.

The models of time-specific attentiveness and individual bout lengths suggest that daytime alone, as well as in interaction with other factors, is an important predictor of incubation behaviour (Table 3). Models containing interaction of daytime with other predictors ranked better than models containing only the main effect of daytime (except for model of off-bout length), which in turn ranked better than models not including daytime. Visualized predictions from the above models revealed distinctive patterns suggesting interactive effects – attentiveness and on-bout length varied throughout the day according to the level of other predictors (Fig. 3).

DISCUSSION

Overall incubation pattern

Skylark females breeding in arable fields face wide variation of environmental conditions during the incubation period. Continuous videorecording provided detailed insight into the correlates of incubation rhytm in this specific habitat. The overall incubation attentiveness was about 0.70 per working day and it varied markedly with time of day. Females spent more time attending clutches in the early morning and in the evening, with lower and stable attentiveness during the rest of the day. This is in accordance with patterns found in most temperate passerines with uniparental incubation (Skutch 1962, Conway & Martin 2000b, Chalfoun & Martin 2007, Davis & Holmes 2012). Similar values of total attentiveness were found in other species of larks breeding across a range of habitats (Tieleman et al. 2008, MacDonald 2014). Not only the attentiveness, but also the mean length of on- and off-bouts and the number of daily departures, were very similar to what is known about incubation rhytm in other small open nesting passerines (Norment 1995, Rauter & Rayer 1997, Joyce et al. 2001, Kovařík et al. 2009). Total absence of incubation feeding conforms to an expectation from the high nest predation pressure in this study system (Praus & Weidinger 2010, 2015), because benefits of incubation feeding can be offset by the cost of increased nest predation rate (Ghalambor & Martin 2002, Matysioková et al. 2011).

Variation on a daily basis

Incubation behaviour varied considerably on a daily basis. Specifically, mean daily attentiveness ranged from 0.5 to 0.8, on-bout length from 10 to 57 min and off-bout length from 4 to 21 min (Table 1). Nest sites and sampling days in our data set represented a wide range of vegetation characteristics and weather conditions, respectively. However, models with vegetation characteristics, mean daily temperature, clutch size and incubation stage as predictors of incubation behaviour revealed only small to moderate (r < 0.3) effects with wide confidence intervals (Fig. 2). Nevertheless, all estimated effects were in the expected directions.

Not surprisingly, attentiveness decreased with rising ambient temperature, which is general pattern found in temperate passerines (Conway & Martin 2000a, Deeming 2002). Also the size of this effect fall within the range of univariate correlations reported from comparative analyses for North American passerines (Conway & Martin 2000b). The effect of rising ambient temperature on attentiveness resulted from the opposing effects on off-bout (lenghtening) and on-bout (shortening) length. This indicates that longer foraging bouts taken at high ambient temperature were not associated with lenghtened on-bouts due to rewarming cost.

The opposing effects of vegetation height and vegetation cover reflect the different meaning of these two nest site characteristics as defined in this study. Given the homogeneity and uniform height of crop monocultures, vegetation height was a proxy of the total amount of vegetation around the nest. Water vapor pressure interacts in a complex manner with temperature to define local microclimate under vegetation cover (Tuller & Chilton 1973, McArthur 1990). Hence, attentiveness and on-bout length increasing with vegetation height could be explained as a nest protection against soil and vegetation moisture formed under shadow of tall vegetation.

In contrast, nest cover was only weakly related to nest height (r = 0.18) as it measured concelament of the nest itself from the observer/predator view, independently of the amount of vegetation around the nest. Hence we interpret nest cover as a proxy of nest concealment from visually oriented predators rather than a measure of nest site microclimate. Birds facing high nest predation risk adopt an incubation strategy that minimizes time of absence from conspicious nest that could attract predator (Conway & Martin 2000b). Accordingly, we found that attentiveness and on-bout length decreased with nest vegetation cover, thus suggesting lower predation risk perceived by females with well concealed nests.

We were not primarily interested in effects of clutch size and stage of incubation, yet we included these variables into the models as potential predictors of incubation behaviour.

The positive relationship between clutch size and nest attentiveness found in some species of birds (Jones 1987, Larsen et al. 2003) was not detectable in this study. Nevertheless, clutch size was the only predictor with similar effect, in terms of size and direction, on both on- and off-bouts; females with larger clutches took longer off-bouts followed by longer on-bouts.

Within-day variation

Incubation behaviour varied not only on a daily basis, but it showed distinct variation within a day. Daily course of nest attentiveness mostly reflected changes in on-bout lenght. High attentiveness and on-bout lenght at the begining and at the end of daily activity might represent response to low ambient temperature at dawn and dusk. Lower and comparatively stable attentiveness and on-bout lenght during mid-day (from c. 0.2 to 0.8 of daylight period) may not be fully explained by the daily course of ambient temperature, which would predict steady decrease in attentiveness until late afternoon. Obviously, other factors are involved in addition to temperature. For instance, foraging might be more efficient during mid-day because of higher arthropod activity (Holmes et al. 1978). Intermittent incubators set their incubation investment at levels dictated by energetic constraints on parents, not maximizing developmental conditions of offspring (Ardia et al. 2009)**.** Depletion of nutrient reserves as incubation proceed could cause decrease in total attentiveness through shortening of on-bout duration in mid-day in later stages of incubation (Afton 1980, Coates & Delehanty 2008; Fig. 3).

Off-bouts showed less variation (on absolute scale) during a day than on-bouts. Longer off-bouts at morning hours could be brought on by high hunger level of females after fasting overnight (Reid et al. 1999). Relatively stable lenght of off-bouts during a day is in agreement with the hypothesis that incubating females modify their behaviour (i.e. foraging bouts) so as to minimize the cost of rewarming eggs and the risk of cooling the eggs through by varying the frequency rather than length of off-bouts (Camfield & Martin 2009, MacDonald 2014). The observed drop of off-bout lenght at the end of daily activity might reflect prior sufficient food supplementation for overnight incubation (Moreno 1989, Smith et al. 1989, Chalfoun & Martin 2007, Lothery et al. 2014).

Interactive effects

Novel finding of this study is that variation in incubation behaviour within and between days was not independent but interacted in a complex manner. Specifically, the pattern of within-day variation depended on daily mean value of given behavioural trait, which in turn depended on the value of other predictors.

Ambient temperature and vegetation height were the best predictors of incubation attentiveness on a daily basis. Not only the mean daily attentiveness decreased on warmer days (Fig. 2), but also the pattern of daily variation changed from U-shaped to flat profile (Fig. 3). The interaction between daytime and vegetation height was of opposite direction; mean daily attentiveness increased with vegetation height and the daily pattern changed from flat to U-shaped profile. In fact, there is no contradiction between these two findings as they refer to the same phenomenon. Cold days and nests under tall vegetation (i.e. wet nest sites; Tuller & Chilton 1973) represented less favourable conditions for incubation, where attentiveness was on average higher, but it was disproportionally higher in morning and evening hours, when microclimatic effects were accentuated.

Different pattern emerged from interaction between daytime and vegetation cover, which is a measure of nest concealment rather than proxy of nest microclimate. Better nest concealment releaved females from incubation duties during mid-day, but not in morning and evening hours; hence the change from flat to U-shaped profile of daily variation in attentiveness with increasing nest cover.

Conclusions

Incubation behaviour is largely determined by inherent physiological demands of parents and embryos, and consequently, there might be only a narrow window for behavioral adjustments (Deeming 2002a). In spite of this we found considerable variation in incubation behaviour of Skylarks nesting in seemingly uniform habitat of arable fields. The most remarkable patterns emerged only after the interactions between daytime and other predictors were taken into account. These findings suggest that the way time is allotted may be equally as important as the total amount of time spent incubating. Obtaining these results would not be possible without continuous videorecording, which we promote as an essential tool for studies of long and uninterrupted samples of incubation behaviour. We have also showed that analyses of daily patterns based on relative daytime might be more revealing than those based on absolute daytime, particularly in species with prolonged nesting season. One potential weakness of this study is the correlative nature of all conclusions. Nevertheless, the habitat of crop fields represents a kind of natural experiment where part of environmental variation is filtered out by agricultural operations.

The Skylark is one of the few passeriness nesting exclusively on the ground in natural, as well as human-altered open habitats. Here we showed that temperature and vegetation surrounding the nest are important predictors of incubation patterns, through their effects on nest microclimate (Ar & Sidis 2002, Wells & Fuhlendorf 2005). The amount of unexplained variation in our models may have been due to other uncontrolled factors, especially risk of nest predation and varying food availability (Conway & Martin 2000b, Zimmerling & Akney 2005). Although the overall nest predation rate did not show a clear daily pattern and was independent of vegetation progress throughout the breeding season (Praus & Weidinger 2010, 2015), the question of predator-specific effects on nest predation and possible interaction with microclimate of nest site is open to further study.

REFERENCES

Ar, A. & Sidis, Y. (2002). Nest microclimate during incubation. In: D. C. Deeming, D. C. (ed.): *Avian incubation: Behaviour, environment, and evolution*. Oxford University Press, Oxford: 143–160.

Ardia, D. R., Pérez, H. J., Chad, E. K., Voss, M. A. & Clotfelter, E. D. (2009). Temperature and life history: experimental heating leads female tree swallows to modulate egg temperature and incubation behaviour. *J. Anim. Ecol.* **78:** 4–13.

Atkinson, P. W., Fuller, R. J., Vickery, J .A., Conway, G. J., Tallowin, J. R. B., Smith, R. E. N., Haysom, K. A., Ings, T. C., Asteraki, E. J. & Brown, V. K. (2005): Influence of agricultural management, sward structure and food resources on grassland field use by birds in lowland England. *J. Appl. Ecol.* **42:** 932–942.

Barnett, C. A. & Briskie, J. V. (2010). Silvereyes *Zosterops lateralis* increase incubation attentiveness in response to increased food availability. *Ibis* **159:** 169–172.

Boulton, R. L., Richard, Y., Armstrong, D. P. (2010). The effect of male incubation feeding, food and temperature on the incubation behaviour of New Zealand Robins. *Ethology* **116:** 490–497.

Burhans, D. E. & Thompson, F. R. (2001). Relationship of songbird nest concealment to nest fate and flushing behaviour of adults. *Auk* **118:** 237–242.

Burnham, K. P. & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. Springer-Verlag, Berlin.

Camfield, A. F. & Martin, K. (2009). The influence of ambient temperature on Horned Lark incubation behaviour in an alpine environment. *Behaviour* **146:** 1615–1633.

Carrey, C. (2002). Incubation in extreme environments. In: Deeming, D. C. (ed): *Avian incubation: Behaviour, Environment and Evolution*. Oxford University Press, Oxford: 238–253.

Chalfoun, A. D. & Martin, T. E. (2007). Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis. *Anim. Behav.* **73:** 579–585.

Chalfoun, A. D. & Martin, T. E. (2010). Parental investment decisions in response to ambient nest-predation risk versus actual predation on the prior nest. *Condor* **112:** 701–710.

Coates, P. S. & Delehanty, D. J. (2008). Efects of environmental factors on incubation patterns of Greater Sage-grouse. *Condor* **110:** 627–638.

Cody, M. L. (ed.) (1985). *Habitat selection in birds*. Academic Press, Orlando, Florida.

Conway, C. J. & Martin, T. E. (2000a): Effects of ambient temperature on avian incubation behavior. *Behav. Ecol.* **11:** 178–188.

Conway, C. J. & Martin, T. E. (2000b). Evolution of passerine incubation behavior: Influence of food, temperature, and nest predation. *Evolution* **54:** 670–685.

Davis, K. S. & Holmes, T. G. (2012). Sprague's Pipit incubation behavior. *Studies in Avian Biology* **43:** 67–75.

Deeming, D. C. (ed) (2002a). *Avian incubation: Behaviour, Environment and Evolution*. Oxford University Press, Oxford.

Donald, P. F. (2004). *The Skylark*. T & AD Poyser, London.

Donald, P. F., Sanderson, F.J., Burfield, I.J., van Bommel, F.P.J. (2006). Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990-2000. *Agr. Ecosyst. & Environ*.**116:** 189–196.

Feddes, R. A., Kowalik, P. J. & Zaradny, H. (1978). *Simulation of field water use and crop yield*. Pudoc-DLO, Wageningen, The Netherlands.

Ghalambor, C. K. & Martin, T. E. (2002). Comparative manipulation of predation risk during incubation reveals variability in the plasticity of parental responses. *Behav. Ecol*. **13:** 101–108.

Gillis, H., Gauffre, B., Huot, R. & Bretagnolle, B. (2012). Vegetation height and egg coloration differentially affect predation rate and overheating risk: an experimental test mimicking a ground-nesting bird. *Can. J. Zool*. **90:** 694–703.

Guerrero, I., Morales, M. B., Onate, J. J., Geiger, F., Berendse, F., de Snoo, G., Eggers, S., Pärt, T., Bengtsson, J., Clement, L. W., Weisser, W. W., Olszewski, A., Ceryngier, P., Hawro, V., Liira, J., Aavik, T., Fischer, CH., Flohre, A., Thies, C. & Tscharntke, T. (2012). Response of ground-nesting farmland birds to agricultural intensification across Europe: Landscape and field level management factors. *Biol. Conserv*. **152:** 74–80.

Haftorn, S. (1988). Incubating female passerines do not let the egg temperature fall below the "physiological zero temperature" during their absences from the nest. *Ornis Scand.* **19:** 97–110.

Helzer, C. & Jelinski, D. (1999). The relative importance of patch area and perimeter-area ratio to grassland breeding birds. *Ecol. Appl.* **9:** 1448–1458.

Hartman, C. A., & Oring, L. W. (2003). Orientation and microclimate of Horned Lark nests: The importance of shade. *Condor* **105:** 158–163.

Holmes, R. T., Sherry, T. W. & Bennett, S. E. (1978). Diurnal and individual variability in the foraging behavior of American Redstarts (*Setophaga ruticilla*). *Oecologia* **36:** 141–149.

Hötker, H. (1990). *Der Wiesenpieper: ANTHUS PRATENSIS*. Die neue Brehm-Bücherei , Ziemsen, Wittenberg Lutherstadt.

Jones, G. (1987). Time and energy constraints during incubation in free-living Swallows (*Hirundo rustica*): An experimental study using precision electronic balances. *J. Anim. Ecol.* **56:** 229–245.

Joyce, E. M., Sillet, T. S. & Holmes, R. T. (2001). An inexpensive method for quantifying incubation patterns of open-cup nesting birds, with data for Black-throated Blue Warblers. *J. Field Ornithol*. **72:** 369–379.

Kovařík, P., Pavel, V. & Chutný, B. (2009). Incubation behaviour of the Meadow Pipit (*Anthus pratensis*) in an alpine ecosystem of Central Europe. *J. Ornithol.* **150:** 549–556.

Larsen, V. A., Lislevand, T. & Byrkjedal, I. (2003). Is clutch size limited by incubation ability in northern lapwings? *J. Anim. Ecol.* **72:** 784–792.

Lothery, C. J., Thompson, C. F., Lawler, M. L. & Sakaluk, S. K. (2014). Food supplementation fails to reveal a trade-off between incubation and self-maintenance in female House Wrens. *Plos One* **9:** e106260.

MacDonald, E.C., Camfield, A. F., Jankowski, J. E. & Martin, K. (2014). An alpine-breeding songbird can adjust dawn incubation rhythms to annual thermal regimes. *Auk* **131:** 495–506.

Martin, T. E. (1993). Nest predation and nest sites. New perspectives on old patterns. *BioScience* **43:** 523–532.

Massaro, M., Starling-Windhof, A., Briskie, J. V. & Martin, T. E. (2008). Introduced mammalian predators induce behavioural changes in parental care in an endemic New Zealand bird. *Plos One* **3:** e2331.

Matson, P. A., Parton, W. J., Power, A. G. & Swift, M. J. (1997). Agricultural intensification and ecosystem properties. *Science* **277:** 504–509.

Matysioková, B., Cockburn, A. & Remeš, V. (2011). Male incubation feeding in songbirds responds differently to nest predation risk across hemispheres. *Anim. Behav*. **82:** 1347–1356.

Matysioková, B. & Remeš, V. (2014). The importance of having a partner: male help releases females from time limitation during incubation in birds. *Frontiers in Zoology* **11:** 24. (*in press*).

McArthur, A. J. (1990). Thermal interaction between animal and microclimate: Specification of a standard environmental temperature for animals outdoors. *J. Theor. Biol*. **148:** 331–343.

Moreno, J. (1989). Energetic constraints on uniparental incubation in the wheatear *Oenanthe oenanthe* (L.). *Ardea* **77:** 107–115.

Nakagawa, S. & Cuthill, I. C. (2007). Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol. Rev*. **82:** 591–605.

Norment, Ch. J. (1995). Incubation patterns in Harris`s Sparrow and White-crowned Sparrows in the Northwest territories, Canada. *J. Field Ornithol.* **66:** 553–563.

Pearse, A. T., Cavitt, J. F. & Cully, J. F. (2004). Effects of food supplementation on female nest attentiveness and incubation mate feeding in two sympatric wren species. *Wilson Bull*. **116:** 23–30.

PECBMS (2011). *Trends of common birds in Europe, 2011 update*. European Bird Census Council, Prague. (*http://www.ebcc.info/index.php?ID=457*)

Praus, L. & Weidinger, K. (2010). Predators and nest success of Sky Larks *Alauda arvensis* in large arable fields. *Bird Study* **57:** 525–530.

Praus, L. & Weidinger, K. (2015). Breeding biology of the Skylark *Alauda arvensis* in maize and other crop fields. *Acta Ornithologica* **50:** 1 (*in press*)

Rauter, C. & Reyer, H. U. (1997). Incubating pattern and foraging effort in the female Water Pipit *Anthus spinoletta*. *Ibis* **139:** 441–446.

Reid, J. M, Monaghan, P. & Ruxton, G. D. (1999). The effect of clutch cooling rate on Starling, *Sturnus vulgaris* incubation strategy. *Anim. Behav*. **58:** 1161–1167.

Skutch, A. F. (1962). The constancy of incubation. *Willson Bull*. **74:** 115–152.

Smith, H. G., Kallander, H., Hultman, J. & Sanzen, B. (1989). Female nutritional state affects the rate of male incubation feeding in the Pied Flycatcher *Ficedula hypoleuca*. *Behav. Ecol. Sociobiol.* **24:** 417–420.

Stoate, C., Báldi, A., Beja, P., Boatman, N. D., Herzon, I., van Doorn, A., de Snoo, G. R., Rakosy, L. & Ramwell, C. (2009). Ecological impacts of early 21 st century agricultural change in Europe – A review. *J. Environ. Manage.* **91:** 22–46.

Šťastný, K., Bejček, V. & Hudec, K. (eds.) (2006). *Atlas hnízdního rozšíření ptáků v České republice*. Aventium, Prague, Czech Republic.

Šťastný, K. & Hudec, K. (eds.) (2011). *Fauna ČR, Ptáci 3/I*. Academia, Prague, Czech Republic.

Tieleman, I. B., van Noordwijk, H. J. & Williams, J. B. (2008). Nest site selection in a hot desert: Trade-off between microclimate and predation risk? *Condor* **110:** 116–124.

Tinbergen, J. M. & Williams, J. B. (2002). Energetics of incubation. In: Deeming, D. C. (ed): *Avian incubation: Behaviour, Environment and Evolution*. Oxford University Press, Oxford: 298–313.

Tuller, S. E. & Chilton, R. (1973). The role of dew in the seasonal moisture balance of a summer-dry climate. *Agr. Meteorol*. **11:** 135–142.

Wells, K. & Fuhlendorf, S. (2005). Comparison of microclimate at grassland bird nests with different substrates. *Prairie Nat*. **37:** 21–28.

With, K. A. & Webb, D. R. (1993). Microclimate of ground nests. The relative importance of radiative cover and wind breaks for three grasland species. *Condor* **95:** 401–413.

Zerba, E. & Morton, M. L. (1983). Dynamics of incubation in Mountain White-crowned Sparrows. *Condor* **85:** 1–11.

Zimmerling, J. R. & Akney, C. D. (2005). Variation in incubation patterns of Red-winged Blackbirds nesting at lagoons and ponds in Eastern Ontario. *Wilson Bull*. **117:** 280–290.

Table 1. Descriptive characteristics of incubation behaviour (response variables) calculated for three hierarchical data units.

Response variable	n	Mean ±SD	Min, Max	Median	Box-Cox
Data unit = nest					
Mean attentiveness	55	0.70 ±0.06	0.56, 0.82	0.70	-
Mean on-bout (min)	55	24.12 ±8.42	10.37, 48.87	21.97	-
Mean off-bout (min)	55	9.85 ±2.95	4.52, 19.98	9.58	-
Data unit = daily sample					
Attentiveness	75	0.69 ±0.07	0.51, 0.85	0.70	1.70
Mean on-bout (min)	75	24.62 ±9.05	10.37, 57.45	22.75	-0.66
Mean off-bout (min)	75	10.22 ±3.33	4.03, 21.17	9.65	-0.21
Data unit = individual bout					
Attentiveness	2075	0.67 ±0.15	0.02, 0.99	0.68	1.69
On-bout (min)	2075	22.37 ±16.93	0.05, 18.37	18.37	0.14
Off-bout (min)	2150	9.52 ±9.00	0.17, 234.80	8.43	0.17

[a] Exponents of the Box-Cox transformation applied to the response variables before fitting models.

Table 2. Parameter estimates for predictors of daily mean values of attentiveness, on-bout length and off-bout length (n=75 daily samples, 55 nests). Random effect of nest identity was forced into all models. All response variables were Box-Cox transformed prior analysis (see Table 1); for details of explanatory variables see Appendix 2.

Response/Explanatory variable	Estimate	Lower CL	Upper CL
Response: Attentiveness [a]			
Intercept	0.7330	0.6235	0.8425
Clutch size	0.0037	-0.0163	0.0237
Day of incubation	-0.0025	-0.0082	0.0032
Mean daily temperature (º C)	**-0.0048**	**-0.0089**	**-0.0008**
Vegetation height (m)	**0.0581**	**0.0035**	**0.1126**
Vegetation cover (medium)	-0.0137	-0.0621	0.0348
Vegetation cover (high)	-0.0385	-0.0803	0.0034
Response: mean On-bout [b]			
Intercept	0.0134	0.0034	0.0234
Clutch size	0.0015	-0.0003	0.0033
Day of incubation	-0.0004	-0.0009	0.0002
Mean daily temperature (º C)	-0.0002	-0.0006	0.0002
Vegetation height	**0.0055**	**0.0006**	**0.0105**
Vegetation cover (medium)	-0.0028	-0.0073	0.0016
Vegetation cover (high)	-0.0029	-0.0067	0.0009
Response: mean Off-bout [c]			
Intercept	0.0038	-0.0001	0.0076
Clutch size	0.0005	-0.0002	0.0012
Day of incubation	-0.0001	-0.0002	0.0002
Mean daily temperature (º C)	0.0001	-0.0001	0.0002
Vegetation height	-0.0005	-0.0024	0.0014
Vegetation cover (medium)	-0.0001	-0.0018	0.0016
Vegetation cover (high)	0.0002	-0.0013	0.0017

[a] Δ AICc (vs intercept model) = 3.28; $R^2 = 0.14$

[b] Δ AICc (vs intercept model) = 2.28; $R^2 = 0.14$

[c] Δ AICc (vs intercept model) = 8.97; $R^2 = 0.06$

Table 3. Models explaining within-day variation in attentiveness and individual bout lengths (n= 2075/2150 on/off bouts from 75 daily samples). Random effect of daily sample was forced into all models. All response variables were Box-Cox transformed prior analysis (see Table 1). X indicates the main effects of clutch size, day of incubation, mean daily temperature, vegetation height and vegetation cover – the same predictors as in the models of between-day variation (Table 2). Time is a 5-level categorical predictor indicating relative timing within the period from sunrise to sunset (see Methods). Shown for each model is the number of parameters (K), value of log-likelihood, ∆ AICc relative to the best model and the approximate proportion of explained variance (R^2).

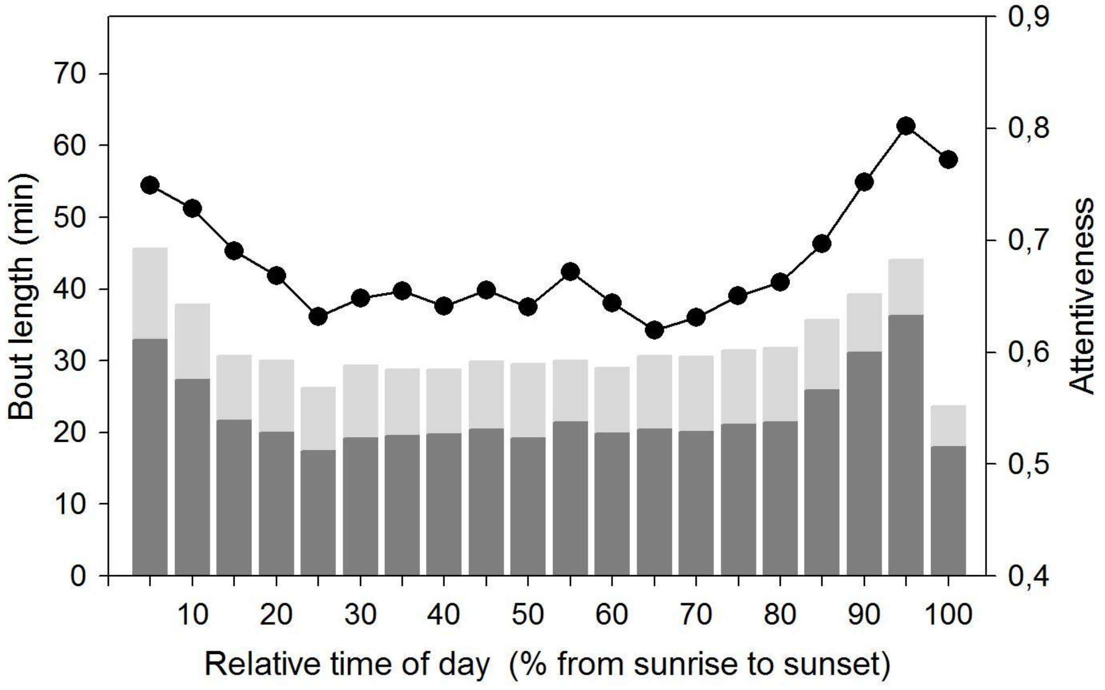
Model	K	-2logL	∆ AICc	R^2
Response: Attentiveness				
X + time + time*cover	20	-2460.0	0.0	0.120
X + time + time*clutch	16	-2422.3	29.5	0.095
X + time + time*temperature	16	-2422.3	29.6	0.095
X + time + time*height	16	-2420.6	31.3	0.094
X + time + time*day	16	-2414.2	37.6	0.090
X + time	**12**	**-2404.6**	**39.1**	0.083
X	8	-2304.1	131.5	0.013
Intercept	2	-2286.2	137.3	
Response: On-bout				
X+time+time*cover	20	-12977.5	0.0	0.083
X+time+time*temperature	16	-12954.2	15.2	0.072
X+time+time*clutch	16	-12942.3	27.1	0.067
X+time+time*height	16	-12938.4	31.0	0.065
X+time+time*day	16	-12937.5	31.9	0.065
X+time	**12**	**-12927.5**	**33.8**	0.060
Intercept	2	-12798.7	142.4	
X	8	-12810.2	143.0	0.006
Response: Off-bout				
X+time+time*temperature	16	-16202.6	0.0	0.028
X+time	**12**	**-16184.9**	**9.5**	0.019
X+time+time*day	16	-16193	9.6	0.023
X+time+time*cover	20	-16198.6	12.1	0.026
X+time+time*clutch	16	-16187.8	14.8	0.021
X+time+time*height	16	-16186.9	15.7	0.020
Intercept	2	-16144.3	30.0	
X	8	-16150.5	35.9	0.003

Fig. 1. The daily pattern of incubation plotted on relative vs. absolute time scale. Shown is the mean length of on-bouts (dark part of columns), off-bouts (light part of columns) and nest attentiveness (points conected by a line). Based on 1114.38 h of active daylight period. Absolute times are given in CEST (GMT+3 h).

Fig. 2. Effect size (with 0.95 CI) of individual explanatory variables included in the models of between-day variation in mean on-bout length (black circle), off-bout length (white circle) and nest attentiveness (black square). For parameter estimates on the original scale see Table 2. Vegetation cover was a 3-level categorical predictor where the least covered nests represented the reference category.

Fig. 3. Interactive effects between the time of day and other predictors of incubation behaviour. Plotted values are predictions (±CI) for nest attentiveness (left panels, black square), on-bout (right panel, black circle) and off-bout (right panel, white circle) length from respective models shown in Table 3. Explanatory variables not involved in the particular interaction were kept at their modal values.

Fig. 1.


Bout length (min)
0
10
20
30
40
50
60
70
Attentiveness
0,4
0,5
0,6
0,7
0,8
0,9
10
20
30
40
50
60
70
80
90
100
Relative time of day (% from sunrise to sunset)

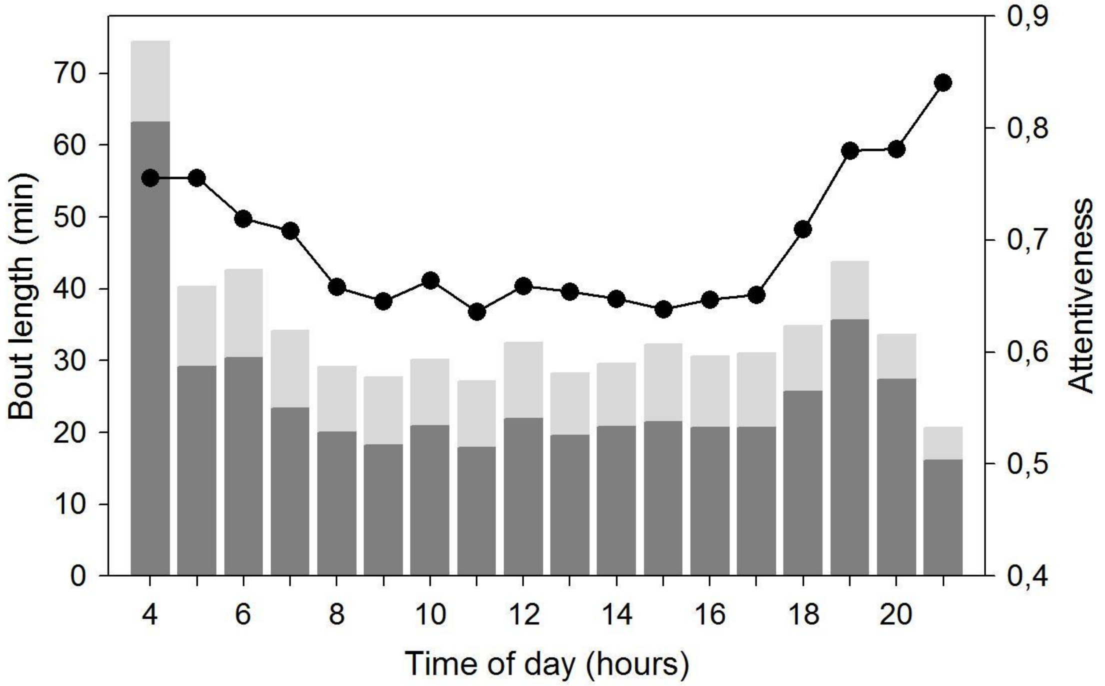

Bout length (min)
0
10
20
30
40
50
60
70
Attentiveness
0,4
0,5
0,6
0,7
0,8
0,9
4
6
8
10
12
14
16
18
20
Time of day (hours)

Fig. 2.

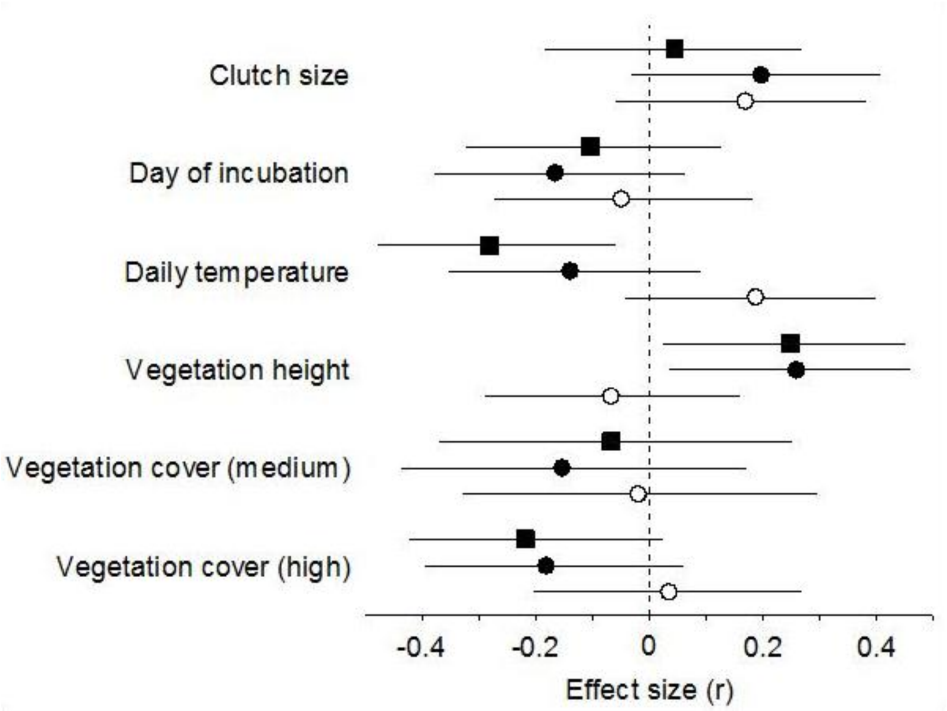

Clutch size
Day of incubation
Daily temperature
Vegetation height
Vegetation cover (medium)
Vegetation cover (high)
-0.4
-0.2
0
0.2
0.4
Effect size (r)

Fig. 3.

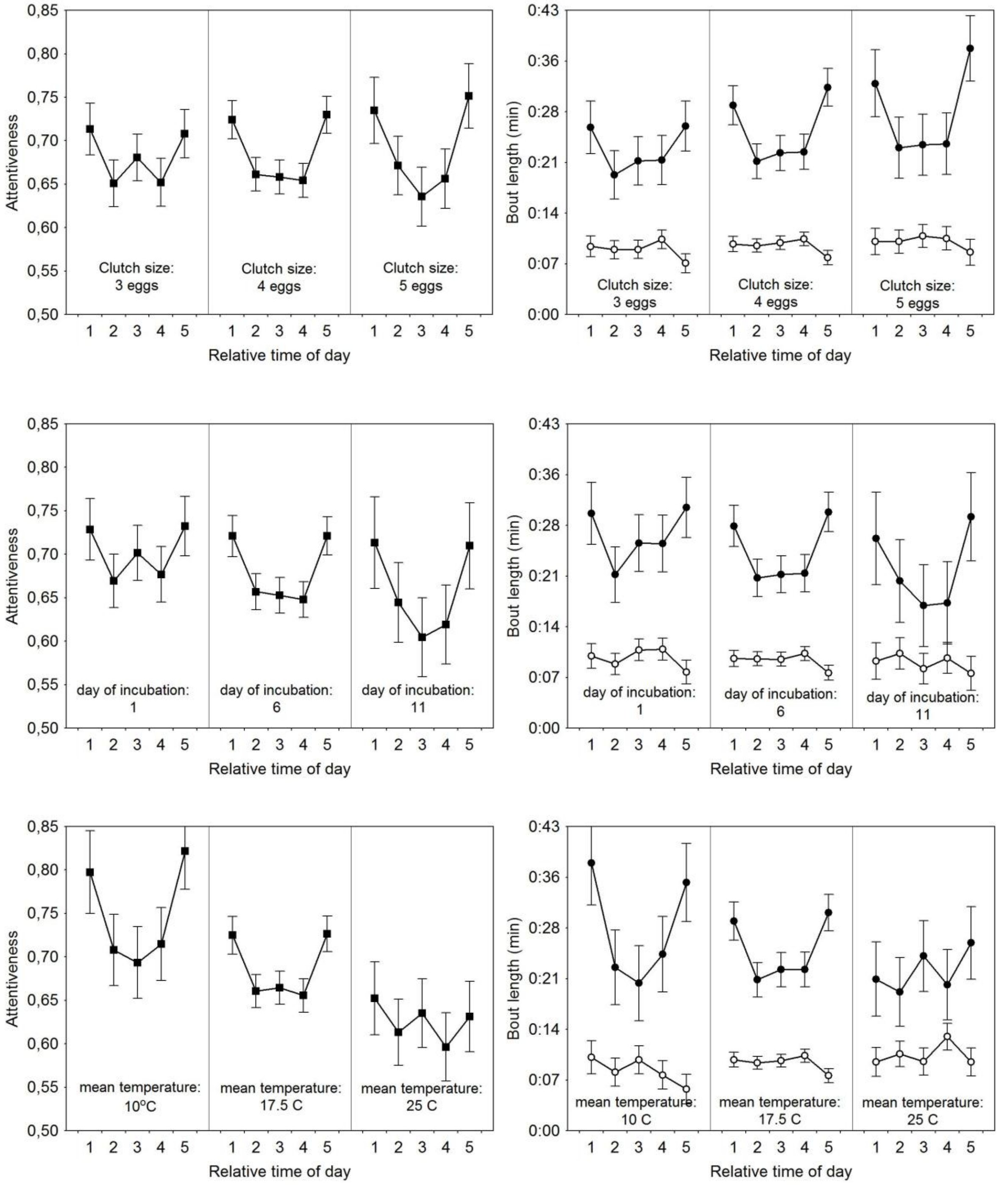
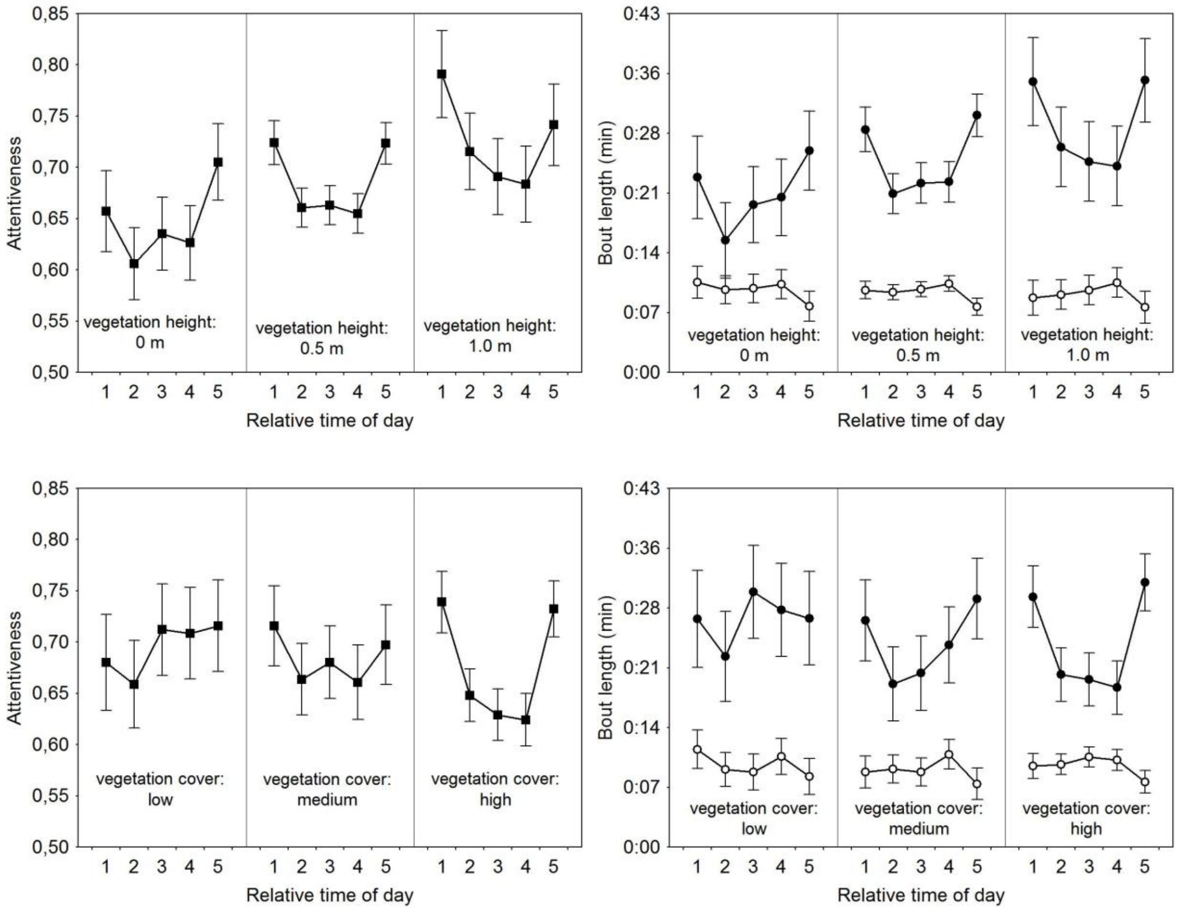

Attentiveness
0,85
0,80
0,75
0,70
0,65
0,60
0,55
0,50
Bout length (min)
0:43
0:36
0:28
0:21
0:14
0:07
0:00
Clutch size: 3 eggs
Clutch size: 4 eggs
Clutch size: 5 eggs
day of incubation: 1
day of incubation: 6
day of incubation: 11
mean temperature: 10°C
mean temperature: 17.5 C
mean temperature: 25 C
mean temperature: 10 C
1 2 3 4 5
Relative time of day

Fig. 3. (continued)



Appendix 1.

Monthly precipitation (mm) and mean daily temperature (°C) in the study area during the observation period.

Year/Month	April	May	June	July
		Monthly sum of precipitation (mm)		
2009	15.4	63.1	97.0	106.4
2010	59.7	108.2	42.1	156.4
2011	18.9	67.5	78.5	134.4
		Mean daily temperature (°C; ±SE)		
2009	13.2 ±0.4	14.7 ±0.6	16.2 ±0.6	19.6 ±0.5
2010	9.5 ±0.6	13.1 ±0.5	18.4 ±0.7	21.7 ±0.7
2011	11.8 ±0.6	14.5 ±0.8	18.7 ±0.5	18.2 ±0.6

Appendix 2.

Characteristics of explanatory variables used in the analyses. The total dataset included 75 daily samples from 55 nests; a subset of nests from maize fields included 46 daily samples from 30 nest).

	n	Mean ±SD	Min, Max	Median
Data unit = nest (all nests)				
Ordinal date	55	157.6 ±23.8	108.0, 202.0	161.5
Clutch size	55	3.8 ±0.8	2.0, 5.0	4.0
Day of incubation	55	4.6 ±2.0	1.0, 8.5	5.0
Mean daily temperature (°C)	55	17.4 ±4.0	5.0, 25.1	17.4
Vegetation height (m)	55	0.5 ±0.3	0.0, 1.4	0.4
Nest cover (scale 1-3)	55	2.3 ±0.8	1.0, 3.0	2.5
Data unit = daily sample (all nests)				
Ordinal date	75	160.2 ±22.4	108.0, 202.0	164.0
Clutch size	75	3.9 ±0.8	2.0, 5.0	4.0
Day of incubation	75	4.9 ±2.9	1.0, 11.0	4.0
Mean daily temperature (°C)	75	17.7 ±4.2	5.0, 25.1	17.7
Vegetation height (m)	75	0.5 ±0.4	0.0, 1.5	0.4
Nest cover (scale 1-3)	75	2.3 ±0.8	1.0, 3.0	3.0
Data unit = daily sample (nests in Maize fields)				
Ordinal date	46	171.4 ±13.3	137.0, 202.0	169.5
Clutch size	46	4.0 ±0.8	2.0, 5.0	4.0
Day of incubation	46	5.0 ±3.1	1.0, 10.0	4.0
Mean daily temperature (°C)	46	18.7 ±3.7	11.2, 25.1	18.7
Vegetation height (m)	46	0.7 ±0.4	0.0, 1.5	0.6
Nest cover (scale 1-3)	46	2.3 ±0.8	1.0, 3.0	2.0

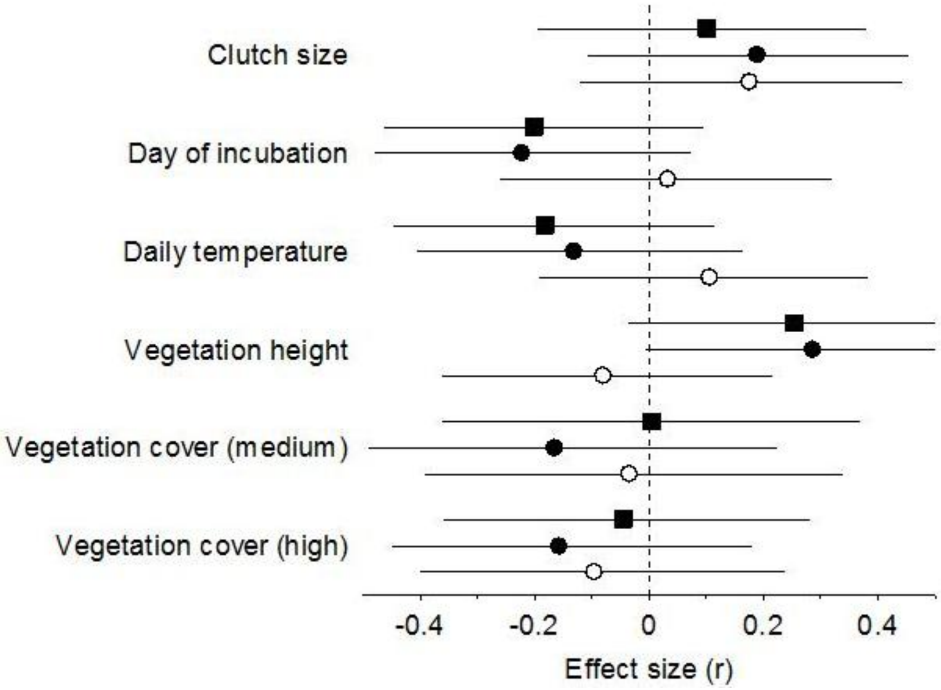
Appendix 3.

Pearson correlations among ordinal date and the explanatory variables in the total data set (above diagonal, n = 75 daily samples) and in the subset of nests from maize fields (below diagonal, n = 46 daily samples). See Appendix 2 for descriptive statistics.

Variable	1	2	3	4	5	6
Ordinal date (1)		0.26	0.09	0.59	0.66	0.02
Clutch size (2)	-0.15		0.08	0.00	0.25	0.12
Day of incubation (3)	0.28	0.04		-0.04	0.31	0.26
Mean daily temperature (4)	0.34	-0.23	-0.09		0.39	-0.12
Vegetation height (5)	0.72	0.13	0.37	0.28		0.18
Nest cover (6)	0.21	0.26	0.37	-0.20	0.26	

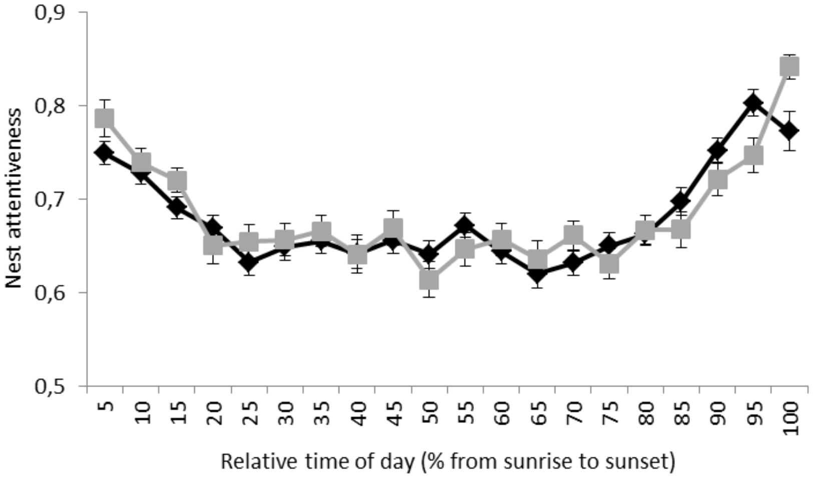
Appendix 4.

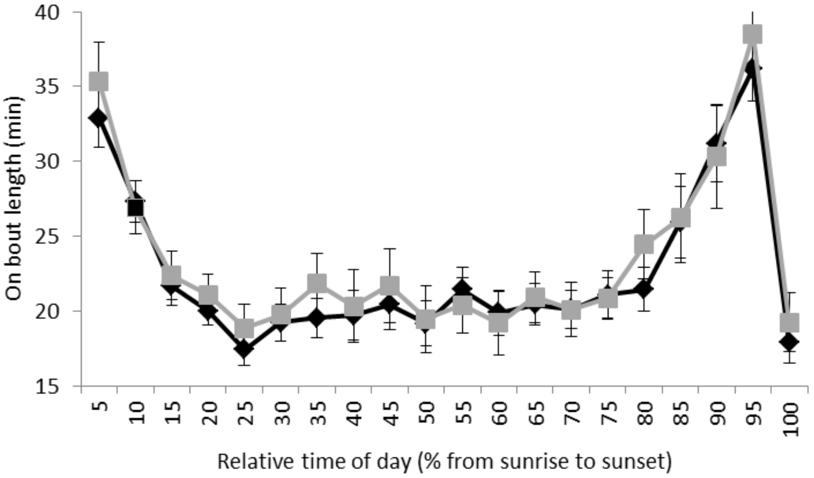
Effect size (with 0.95 CI) of individual explanatory variables included in the models of between-day variation in mean on-bout length (black circle), off-bout length (white circle) and nest attentiveness (black square). Based on the subset of data from Maize fields (n = 46 daily samples from 30 nests). Compare with results based on the total data set of nests from all crops (Fig. 2).

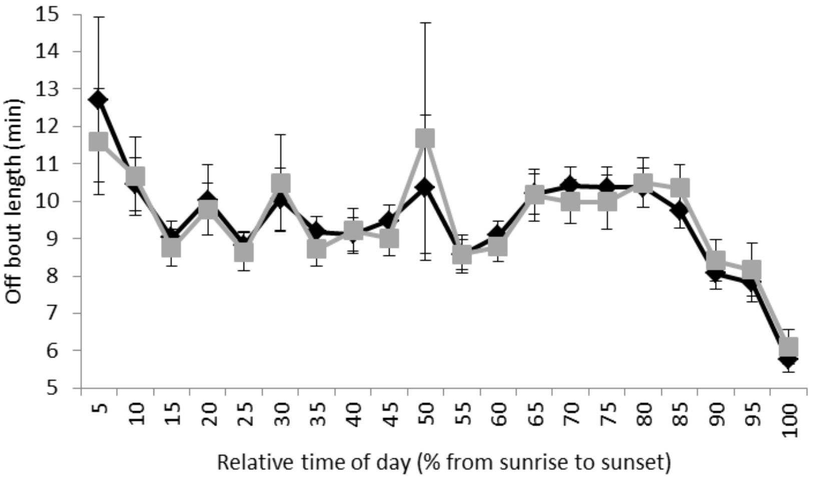


Appendix 5.

Comparison of daily pattern of incubation behaviour between subset of nests from maize fields (grey line; n = 46 daily samples from 30 nests) and the total data set of nests from all crops (black line; n = 75 daily samples from 55 nests). Shown are raw means (±SE).







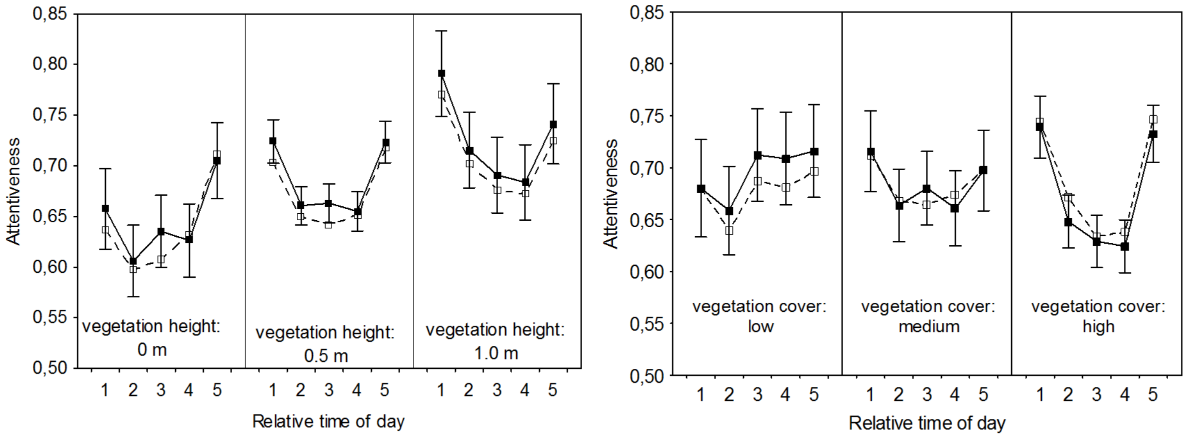
Appendix 6.

Descriptive characteristics of incubation behaviour calculated for three hierarchical data units. Based on the subset of data from Maize fields (n = 46 daily samples from 30 nests). Compare with results based on the total data set of nests from all crops (Table 1).

	n	Mean ±SD	Min, Max	Median
Data unit = nest				
Mean attentiveness	30	0.700 ±0.052	0.572, 0.816	0.699
Mean on-bout	30	25.417 ±9.133	10.367, 48.867	22.783
Mean off-bout	30	10.117 ±2.817	4.517, 19.983	10.117
Data unit = daily sample				
Attentiveness	46	0.700 ±0.063	0.564, 0.852	0.706
Mean on-bout	46	25.750 ±9.750	10.367, 57.500	23.000
Mean off-bout	46	10.183 ±2.883	4.083, 19.983	10.050
Data unit = individual bouts				
Attentiveness	1254	0.673 ±0.147	0.038, 0.992	0.684
On-bout	1254	23.133 ±17.900	1.167, 158.550	19.167
Off-bout	1300	9.550 ±8.483	0.167, 227.250	8.600

Appendix 7.

Comparison of interactive efects in daily patterns of nest attentiveness between the subset of nests from maize fields (dashed line; n = 46 daily samples from 30 nests) and the total data set of nests from all crops (solid line; n = 75 daily samples from 55 nests). See Figure 3 for further explanation.



CURRICULUM VITAE

Libor Praus, M.Sc.

Date and place of birth:	July 3, 1982, Hradec Králové, Czech Republic
E-mail:	libor.praus@gmail.com
Education:	
2008 – till now	Ph.D. study of Zoology, Faculty of Science, Palacký University in Olomouc. Topic: Effects of nest predators on ground nesting birds in intensively used arable fields. Supervisor: doc. Mgr. Karel Weidinger, Dr.
2005 – 2008	Pedagogical minimum of Biology for Secondary schools, Faculty of Science, Palacký University in Olomouc
2002 – 2007	M.Sc. study of Systematic biology and Ecology, Faculty of Science, Palacký University in Olomouc. Master thesis: Postfledging movements and survival of juvenile flycatchers (genus *Ficedula*). Supervisor: Prof. Ing. Stanislav Bureš, CSc.
Research stay:	April – July 2012, University of Groningen, Animal Ecology Group
IF publications:	**Praus, L.** & Weidinger, K. (2015). Breeding biology of the Skylark *Alauda arvensis* in maize and other crop fields. *Acta Ornithologica* **50: 1.** (*in press*) **Praus, L.**, Hegemann, A., Tieleman, B. I. & Weidinger, K. (2014). Predators and predation rates of Skylark *Alauda arvensis* and Woodlark *Lullula arborea* nests in a semi-natural area in the Netherlands. *Ardea* **102:** 87–94. (DOI: 10.5253/078.102.0112) **Praus, L.** & Weidinger, K. (2010). Predators and nest success of Sky Larks *Alauda arvensis* in large arable fields. *Bird Study* **57:** 525–530. (DOI: 10.1080/00063657.2010.506208)
Czech reviewed publications:	**Praus, L.** (2014). Hnízdní výskyt havranů polních (*Corvus frugilegus*) v Opavě v roce 2014. *Zprávy MOS* **72:** 66–71. **Praus, L.** (2013). Současné rozšíření chocholoušů obecných (*Galerida cristata*) ve východních Čechách. *Panurus* **22:** 1–18. **Praus, L.** (2013). Aktuální výskyt chocholoušů obecných (*Galerida cristata*) na střední Moravě. *Zprávy MOS* **71:** 38–44.

Praus, L. & Weidinger, K. (2011). Střevlíci (*Carabidae*) jako potenciální nebezpečí pro mláďata skřivanů polních (*Alauda arvensis*) na hnízdech. *Sylvia* **47:** 91–94.

Koleček, J., Paclík, M., **Praus, L**., Vymazal, M., Tyller, Z., Turčoková, L., Sedláček, J. & Figura, R. (2011). Hnízdní a zimní početnost ptáků dvou středomoravských lužních lesů. *Zprávy MOS* **69:** 4–17.

Praus, L. (2009). Neobvykle umístěné hnízdo ťuhýka šedého (*Lanius excubitor*) na Chrudimsku. *Panurus* **18:** 63–67.

Popularization articles:

Praus, L. (2014). Vymizí chocholouš obecný z Českých zemí?
Živa **2:** 83–85.

Praus, L. (2014). Strnad zahradní – nenápadná vzácnost Hlučínska.
Vlastivědné listy **2:** 37–38.

Praus, L. (2012). Skřivan polní – nepřítel stísněných prostorů.
Naše příroda **1:** 8–13.

Book chapters:

Praus, L. (2014). Zoologická podsbírka Slezského zemského muzea. In: Vlk, P. (ed.). *Museum Silesiae*. SZM Opava, 110–117.

Praus, L. (2014). Dermoplastické preparáty ptáků z Opavského gymnazijního muzea. In: Šíl, J. (ed.). *Země a její muzeum*. SZM Opava, 57–61, 264–266.

Participation in conferences:

Praus L. & Weidinger K. (2013). Teplota a vegetační kryt ovlivňují inkubační chování skřivana polního (*Alauda arvensis*). Sborník abstraktů z konference Zoologické dny Brno 7. – 8. února 2013: 186–187 (*poster*).

Praus L. & Weidinger K. (2011). Nest success and predators of Sky Lark (*Alauda arvensis*) and Lapwing (*Vanellus vanellus*) nests in arable fields in the Czech Republic. In: Book of abstracts: 8th Conference of the European Ornithologist Union, Riga August 27-30, 2011 (*poster*).

Praus L. & Weidinger K. (2011). Inkubační chování skřivanů polních (*Alauda arvensis*) v intenzivních polních kulturách. Sborník abstraktů z konference Zoologické dny Brno 17. – 18. února 2011: 182–183 (*presentation*).

Praus, L. & Weidinger, K. (2011). Hnízdní úspěšnost a predátoři skřivana polního (*Alauda arvensis*) a čejky chocholaté (*Vanellus vanellus*) v intenzivních polních kulturách. Sborník abstraktů z konference ČSO Ornitologie – Věda pro každého. Mikulov na Moravě 7. – 9. 10. 2011: 61–62 (*poster*).

Praus L. & Weidinger K. (2010). Hnízdní biologie skřivana polního (*Alauda arvensis*) v intenzívních polních kulturách. Metody a výsledky výzkumu ptačích populací V. Sborník abstraktů z celostátní ornitologické konference k 35. výročí založení Východočeské pobočky České společnosti ornitologické 22. – 24. 10. 2010: 40. (*presentation*)

Praus L. & Weidinger K. (2010). Predátoři hnízd skřivana polního (*Alauda arvensis*) a čejky chocholaté (*Vanellus vanellus*) v intenzivních polních kulturách. Metody a výsledky výzkumu ptačích populací V. Sborník abstraktů z celostátní ornitologické konference k 35. výročí založení Východočeské pobočky České společnosti ornitologické 22. – 24. 10. 2010: 41. (*presentation*)

Kutal, M. & **Praus, L.** (2009). The neighbour wolf: Conservation of large carnivores in the Beskysy Mts., Czech Republic. In: Book of abstracts: 2nd European Congress of Conservation Biology. Czech University of Life Sciences, Prague. (*poster*)

Professional experience:

2013 – till now	Silesian museum Opava, Curator of Zoological collections
2006 – 2009	Friends of the Earth Czech Republic – Olomouc local group. Projects in conservation of large carnivores in Beskydy mountains, educational programs, editor of bulletin Ekologické listy

Voluntary activities:

Active member of The Czech Society for Ornitology (Birdlife CZ) and its regional brands; organizing projects in conservation and monitoring of farmland birds and swifts, public education.

Editor in chief of Panurus, Ornithological journal of the East Bohemian Branch of the Czech Society for Ornithology at the Museum of East Bohemia, Pardubice

Holder of Bird-ringing license for the Czech Republic

PALACKÝ UNIVERSITY OLOMOUC

FACULTY OF SCIENCE

DEPARTMENT OF ZOOLOGY AND LABORATORY OF ORNITHOLOGY

Effects of nest predators on ground nesting birds in intensively used arable fields

P1527 – Biology
Zoology

Summary of the Ph.D. Thesis

Libor Praus

OLOMOUC 2015

Palacký University Olomouc
Faculty of Science

Summary of the Ph.D. Thesis
Ph.D. Candidate: M.Sc. Libor Praus

Study programme: P1527 Biology
Study field: Zoology

Title of Ph.D. Thesis:

Effects of nest predators on ground nesting birds in intensively used arable fields

Supervisor: doc. Mgr. Karel Weidinger, Dr.

Reviewers:

prof. MVDr. Emil Tkadlec, CSc.
Department of Ecology & Environmental Sciences
Faculty of Science
Palacký University Olomouc

prof. Mgr. Miroslav Šálek, Dr.
Department of Ecology
Faculty of Environmental Sciences
Czech University of Life Sciences

The oral defence will take place on June 24, 2015 in front the Commission for the Ph.D. thesis of Study field Zoology at the Department of Zoology, Faculty of Science, Palacký University, room S2, 17. listopadu 50, Olomouc.

The Ph.D. Thesis is available in Department of Science and Research, Palacký University, 17. listopadu 12, Olomouc.

ABSTRACT

Agricultural intensification may increase an impacts of predators on the reproductive performance of declining populations of farmland birds. Still, there is little definitive evidence of nest success and predator identity in intensive arable fields. In order to clarify whether nest predators really contribute to declines in farmland ground nesting birds, I used video monitoring to identify nest predators and quantify nest success in the Skylark (*Alauda arvensis*) and Lapwing (*Vanellus vanellus*). Both species share common nesting habitats in sparsely vegetated arable fields, but their life histories suggest different vulnerabilities to nest predation. Results showed very low nest success in the Skylark, but relatively high success in the Lapwing. Skylark nests were vulnerable to all local predators, while it seems that Lapwings can avoid avian predators. The species composition of predators and patterns in nest predation rates mostly differed from those reported from Western Europe.

Because of expected differences in predator identity and nest survival among nesting habitats and regions, I further quantified nest success and identified nest predators for a high-density population of Skylarks as well as Woodlarks (*Lulllula arborea*) breeding in more natural heath and grassland habitats in the Netherlands. Populations of both species co-occur in this area and their nests are similar targets for local predators; even so their nest predators might differ, because these larks differ in the selection of their nest sites. My results suggest that Skylark nests located in open sites were preyed upon mainly by red foxes (*Vulpes vulpes*), while the main predators of Woodlark nests, located generally closer to trees, were Carrion Crows (*Corvus corone*).

Changes in agricultural practices, especially shifts from spring-sown to autumn-sown crops, can limit the number of breeding attempts of Skylarks. Under these circumstances, Skylarks are forced to shift to different breeding sites or habitats. In spite of the seasonal shift in nest sites in my study, nest predation rates did not show a clear seasonal trend; however, the proportion of predation attributed to birds decreased along with vegetation growth. My results suggest that the recently increasing area of maize fields in particular provide an attractive, yet risky, nesting habitat for Skylarks, especially late in the season when autumn-sown crops are too dense.

Nest proximity to field edges may also have a negative influence on breeding productivity, with nests placed closer to edges experiencing higher rates of nest predation. I found that Skylarks seem to avoid areas close to field edges in spite of the comparatively low predation cost associated with nesting there.

Variation in nest predation risk during the breeding period may be an important source of natural selection on parental behaviour. Skylark females spent more time attending clutches in the early morning and evening, with more frequent recesses during the afternoon. Moreover, this diurnal variation was dependent on (i.e. interacted with) ambient temperature and vegetation characteristics at the nest site (height and concealment). This suggests that the way incubation time is allotted during the day may be equally as important as the total amount of time spent incubating.

Keywords: nest success, nest predation, video-monitoring, *Alauda arvensis*, *Vanellus vanellus, Lullula arborea*, agricultural intensification, edge effect, incubation behaviour

ABSTRAKT

Krajinné změny spojené s intenzifikací zemědělství mohou zvyšovat negativní vliv predace na hnízdní produktivitu ubývajících ptačích druhů zemědělské krajiny. Přesto dodnes chybí přesnější odhady hnízdní úspěšnosti a identity predátorů pozemních hnízd v intenzivních polních kulturách. V předkládané práci jsem si položil otázku, zda mohou predátoři ptačích hnízd přispívat k poklesu ubývajících druhů polních ptáků. Hnízdní úspěšnost a identitu predátorů jsem sledoval pomocí kontinuálního video-monitoringu. Za svůj hlavní modelový druh jsem si zvolil skřivana polního (*Alauda arvensis*) a doplňkově čejku chocholatou (*Vanellus vanellus*). Oba druhy sdílejí společné hnízdní prostředí v řídce porostlých polích, nicméně jejich odlišné životní styly naznačují rozdílnou zranitelnost hnízdní predací. U skřivaních hnízd jsem zaznamenal vysokou denní míru predace, naopak hnízdní úspěšnost čejek byla relativně vysoká. Skřivani byli zranitelní všemi přítomnými predátory, zatímco čejky svá hnízda dokázaly aktivně ubránit proti ptačím predátorům. Druhové složení predátorů a vzorce hnízdní predace se lišily od studií ze západní Evropy.

Z důvodu očekávaných rozdílů v identitě predátorů a hnízdní úspěšnosti mezi odlišnými hnízdními prostředími a geografickými regiony jsem dále kvantifikoval hnízdní úspěšnost a identitu predátorů také u populace skřivanů polních a skřivanů lesních (*Lullula arborea*) hnízdících ve více přirozeném prostředí atlantských vřesovišť v severním Nizozemsku. Populace obou druhů skřivanů se zde vyskytují na stejném území a jejich hnízda představují podobný typ kořisti pro predátory, nicméně se tyto dva druhy liší výběrem hnízdních stanovišť. Zatímco skřivani polní se vyhýbají okrajům lesa i jednotlivým stromům, skřivani lesní svá hnízda často umísťují pod vzrostlé dřeviny. Mé výsledky naznačují, že hlavní hnízdní predátoři se mohou mezi těmito dvěma blízce příbuznými druhy lišit. Hnízda skřivanů polních umísťovaná v otevřeném prostoru byla častěji predována liškou obecnou (*Vulpes vulpes*), zatímco hlavním predátorem hnízd skřivanů lesních byla vrána černá (*Corvus corone*).

Dnešní převaha ozimých plodin limituje počet hnízdních pokusů skřivanů polních na jednom stanovišti z důvodu jejich přílišné hustoty v druhé polovině sezóny. Přesto jsem nepozoroval jasný sezónní trend v přežívání hnízd. Nicméně proporce ptačích predátorů klesala ve prospěch savců se zvětšující se výškou vegetace. V druhé polovině května nabývala na významu zejména pole osetá kukuřicí, která představují pro skřivany atraktivní, ale rizikové hnízdní prostředí.

Produktivita skřivaních hnízd může být negativně ovlivněna i blízkostí polních okrajů, kde je očekáván větší pohyb predátorů. Mé výsledky naznačují, že skřivani skutečně preferují umísťování hnízd spíše ve středu polí, přesto jsem nezaznamenal výrazně zvýšené predační riziko v blízkosti polních okrajů.

Rozdílné predační riziko může být významným zdrojem selekce vzorců inkubačního chování. Přítomnost samic skřivanů na hnízdě byla silně ovlivněna denním průběhem. Skřivani trávili více času na snůšce ráno a večer, frekvence odletů byla nejvyšší okolo poledne. Denní variabilita inkubačního chování byla ovlivněna a interagovala s teplotou a rozvojem vegetace. To naznačuje, že správné rozvržení inkubačních směn v rámci dne je stejně důležité jako celková intenzita inkubace.

Klíčová slova: hnízdní úspěšnost, predace ptačích hnízd, video-monitoring, *Alauda arvensis*, *Vanellus vanellus*, *Lullula arborea*, intenzifikace zemědělství, okrajový efekt, inkubační chování

Content

INTRODUCTION

Nest predation is one of the major selective agents shaping avian life histories (Martin 1995). Nest predation rates are influenced by features of the habitat, the nesting birds themselves, as well as by the numbers and behaviour of predators present, so rates in the same species vary greatly among different areas and times (Newton 2013).

Human-induced habitat alterations often result in the loss or degradation of suitable breeding habitats for bird specialists (Fuller 2012). Loss of suitable nesting habitat can result in higher nest densities and subsequently higher density-dependent predation rates (Schmidt & Whelan 1999, Misenhelter & Rotenberry 2000, Pescador & Peris 2001), and habitat changes may also force birds to nest in more dangerous habitat types (Donald 2004, Evans 2004, Morris & Gilroy 2008). Moreover, habitat changes can lead to shortened breeding seasons and thus less opportunity for renesting (Chamberlain et al. 1999, Schmidt & Whelan 1999, Donovan & Thompson 2001).

Populations of many farmland bird species have declined throughout Western and Central Europe since the advent of agricultural intensification in the 1950s (van Beusekom 2004, Donald et al. 2006, Voříšek et al. 2009, Hayhow et al. 2014), which has resulted in depressed food availability (Fuller et al. 1995, Hart et al. 2006) and loss of suitable breeding habitats for farmland birds (Hole et al. 2002, Benton et al. 2003, Donald 2004, Flohre et al. 2011). It has been demonstrated that habitat loss does not fully explain the observed population declines of farmland birds (Evans 2004). It is plausible that nest predation interacts with farmland habitat change and contributes to declines of ground nesting passerines in impoverished agricultural landscapes (Donald 2004, Morris & Gilroy 2008, Gilroy et al. 2011).

The numbers of some avian (Baillie et al. 2006, Šťastný et al. 2006) and mammalian (Harris et al. 1995, Anděra & Gaisler 2012) predators have increased over the last decades. All these predators are generalists (Hanski et al. 1991, Newton 2013), and thus predation rates on any particular prey species are likely to be independent of its density. Bird nests are only a supplementary type of prey for almost all predators, but even so nest predation can cause prey population declines. Thus, the combination of habitat loss and invading predator species may act in concert, causing further negative effects on farmland birds. As such, nest predation may be an issue worthy of consideration in the design of measures to aid the recovery of farmland bird species.

Although previous studies often implied predator-specific effects on nest survival, there is still little definitive evidence of nest success and predator identity for ground nesting birds of open habitats in different regions or habitats, or between species with different life histories (MacDonald & Bolton 2008, Morris & Gilroy 2008, Teunissen et al. 2008).

In order to clarify whether generalist predators really contribute to population declines in farmland birds, one must first investigate sources of nesting mortality and the relative importance of different nest predators in habitats of conventionally managed arable fields. In the past it was difficult to be certain of nest fates and the identity of predators, but recently identification of nest predators has become more reliable using camouflaged nest video cameras (Ribic et al. 2012), which provide precise nest survival times and nest fates. Therefore I used video monitoring to quantify nest success, the identity of nest predators and the behaviour of nest-attending adults in ground nesting birds in intensive arable fields and in semi-natural habitats. The results of my research should help elucidate the causal relationships between farmland habitat change and nest predation, which is essential for developing appropriate management options to reverse the population declines of farmland birds.

AIMS OF THE THESIS

A prerequisite for sensible interpretations of nest predation rates is knowledge of nest predators. Hence I first quantified nest fates and nest predator identity in two species breeding in intensively managed arable fields, the Skylark *Alauda arvensis* and the Lapwing *Vanellus vanellus*. Both these species share common nesting habitat; however the Skylark, a small passerine that relies solely on nest crypsis for defence against nest predators, is expected to experience higher predation by possibly different predators in comparison to the Lapwing, a wader who relies on early detection and active nest defence against bird predators. The majority of observed nests were monitored using continuous video surveillance.

Because of expected differences in predator identity and nest survival among nesting habitats and regions, I also further quantified nest success and identified nest predators for a high-density population of Skylarks as well as Woodlarks *Lulllula arborea* breeding in more natural heath and grassland habitats in the Netherlands. Populations of both lark species co-occur in this area and their nests are similar targets for local predators. Yet, the two species differ in the selection of their microhabitats; while Skylarks avoid forest edges and even the proximity of single trees, Woodlarks usually nest close to trees and/or forest edges (Donald 2004). Hence I explored whether this different nest site selection within a semi-natural area relates to species-specific vulnerability to nest predation.

Disturbances associated with placing video cameras and nest visits may introduce bias to estimations of nest survival rates and predator identification (Richardson et al. 2009, Ribic et al. 2012). I therefore evaluated the possible effects of the presence of a camera on predation through an artificial nest experiment with dummy cameras in same area where real Skylark nests were studied.

Agricultural intensification has resulted in a reduction of landscape heterogeneity due to the increasing size of individual arable fields and changes in the structure of crop monocultures. I compared characteristics of Skylark breeding biology and daily survival rates in the "extreme" habitat of maize fields, where vegetation may grow about 150 cm during a single nesting cycle, and other crops with more modest vegetation growth rates. I posed the question whether nesting success can be affected by rapid changes in vegetation growth throughout the breeding season.

Not only the selection of particular crops as breeding habitat but also the spatial distribution of nests within arable fields is expected to influence nest predation rates and predator identities, therefore I asked if nest predation rates are affected by the edge effect, when predation rates are expected to decline with increasing distance from field edges.

Apart from selecting safe nesting habitats, birds can minimize nest predation risk through adequate parental behaviour (Ghalambor & Martin 2002, Massaro et al. 2008, Cervencl et al. 2011), e.g. parental activity may respond to variation in nest concealment (Burhans & Thompson 2001, Lima 2009). The uniform habitat of arable fields facilitates studies of parental behaviour by minimizing habitat heterogeneity within individual crop types. Therefore I evaluated variation in Skylark incubation patterns and its plasticity in relation to vegetation characteristics, season, ambient temperature, incubation progress and clutch size.

SURVEY OF RESULTS

Chapter 1: Predators and nest success of the Skylark and Lapwing in arable fields in the Czech Republic

Using continuous video recording, we monitored 161 of 186 found Skylark nests and 18 Lapwing nests during three breeding seasons from 2009-2011. The number of monitored Skylark nest days during the breeding season showed a unimodal distribution with a peak in late May and early June.

Skylark nests experienced a higher overall mortality rate than Lapwing nests; the major cause of mortality in both species was predation. Daily predation rate was higher in Skylarks (0.084) than in Lapwings (0.011).

The 104 documented predation events at Skylark nests were caused by: Marsh Harrier (*Circus aeroginosus*) (32), Montagu's Harrier (*Circus pygargus*) (18), stone marten (*Martes foina*) (14), Hooded Crow (*Corvus cornix*) (13), wild boar (*Sus scrofa*) (9), red fox (*Vulpes vulpes*) (8), Common Raven (*Corvus corax*) (2), domestic cat (*Felis silvestris f. catus*) (2), hedgehog (*Erinaceus sp.*) (2), european polecat (*Mustela putorius*) (1), European Magpie (*Pica pica*) (1), Eurasian Jackdaw (*Corvus monedula*) (1) and an unidentified bird of prey (1). Two Lapwing nests were depredated by red fox, and one by wild boar and by stone marten.

The spatial distribution of predation events suggests that results are not based on repeated sampling of the same individual predators, and that the data may successfully be used for further analysis of spatial relationships. Skylark nests were vulnerable to a full range of local predators across different locations (crops, vegetation height, distance) and seasonal timing. Nests were under risk of predation also at any time of day; mammalian predators were responsible for all nocturnal predation events, while bird predators predominate during daylight.

Chapter 2: Predators and predation rates of Skylark and Woodlark nests in a semi-natural area in the Netherlands

We quantified nest success and identified nest predators in a high-density population of Skylarks and Woodlarks breeding in a semi-natural heath- and grassland area in the Netherlands characterized by permanently low and sparse vegetation in 2012.

A total of 58 Skylark and 40 Woodlark nests were found. The overall nest success of Skylarks was 33%, Woodlarks had a slightly lower nest success (22%) than Skylarks. On video we documented 11 predation events by four species of predators. Predators of Skylark nests were red fox (5), Carrion Crow (*Corvus corone*) (1) and european adder (*Vipera berus*) (1). Woodlark nests were depredated by Carrion Crow (2), Eurasian Jay (*Garrulus glandarius*) (1) and red fox (1).

One possible drawback of this study is the small study area, which has a similar size as the home ranges of the main predators (Bijlsma 2013). This could account for multiple predation events by a particular predator species/individuals, and the possibly pseudo-replicated data may not be representative of predation patterns at larger spatial scales. Even so, our results suggest that the main nest predators might differ between the two co-occurring lark species. Skylark nests located in more open sites were preyed upon mainly by red foxes, while the main predators of Woodlark nests, located generally closer to trees, were corvids.

Chapter 3: Research disturbances and the risk of nest predation

Placing video cameras near active bird nests and the disturbances associated with nest visits may introduce bias to estimations of nest survival rates and predator identification (Richardson et al. 2009, Ribic et al. 2012). Therefore, we conducted an experiment to evaluate potential bias in our data in arable fields. We compared daily predation rates (DPR) between the first and the subsequent days that followed after a nest visit by means of logistic regression; to evaluate the effect of the presence of a camera on predation rates we conducted an artificial nest experiment with dummy cameras in 2011. This experiment was run in same area where real Skylark nests were studied. Artificial nests were arranged in pairs. We placed a dummy camera (a realistic model of the cameras used for video monitoring) and simulated the process of camera deployment with all associated disturbances to the nest surroundings at one of the paired nests. The other paired nest served as a control without a camera.

Daily predation rates were not higher on the first day after an observer visit (0.062) compared with subsequent days (0.081). Of the 100 artificial nest pairs, at least one nest was depredated in 65 cases. Of these, a nest with a dummy camera was predated first in 29 cases, whereas a control nest without a camera was predated first in 36 cases.

The marginally lower DPR on the day just after a nest visit as well as at artificial nests with dummy cameras indicate that there are no detectable negative effects of research activities on predation rates. This also supports the suitability of our field protocol, minimising the visible parts of video equipment and limiting the time spent at nests. The absence of a temporal relationship between the timing of nest visits and the timing of depredation events indicates that overall nest survival in this study was not seriously influenced through altered depredation risk.

Chapter 4: Habitat characteristics of arable fields and their effects on Skylark breeding biology and nest predation rates.

Skylarks placed nests in a wide variety of habitats. Of a total 186 Skylark nests in arable fields, 92 nests were found in maize fields, while the rest were found in nine other crops: sugar beet (*Beta vulgaris*) (31), opium poppy (*Opium somniferum*) (20), winter wheat (*Triticum aestivum*) (11), alfalfa (*Medicago sativa*) (10), spring barley (*Hordeum vulgare*) (8), pea (*Pisum sativum*) (4), oilseed caraway (*Carum carvi*) (3), brown bean (*Vicia faba*) (3), potatoes (*Solanum tuberosum*) (2). The number of nests found in individual crops was not proportional to the proportion of those crops in the study area.

The overall nest predation rate of Skylarks did not show a clear trend over the course of the nesting season. However, the proportion of bird (vs mammal) predation decreased over the course of season, along with vegetation growth. This marked seasonal trend in predator composition probably results from the seasonal development of vegetation in the fields selected for nesting. The sparse but high vegetation of maize fields might provide suitable hiding and foraging sites for mammalian predators in late June and July (Panek & Bresinski 2002, Schley & Roper 2003), thus increasing their predation upon late Skylark nests located in such fields. The comparatively low vegetation height of all crops early in the season makes early nests more visible for bird predators and more accessible for their aerial attacks. The very low nest success found in this study suggests that none of the various crops provides safe nesting habitat. Both sparsely vegetated fields early in the season and wide row crops late in the season offer an attractive, yet risky, nesting habitat for Skylarks, especially late in the season when autumn-sown crops are too dense (Donald 2004).

Despite the fact that these results might not be representative of the whole landscape, we believe they are valid for the crops well represented in our data (maize, sugar beet).

Chapter 5: Spatial distribution of Skylark nests within arable fields: Edge effects and predation

Skylarks were found to avoid areas close to field edges (<20 m) for nest placement. In contrast, field interior areas more than 200 m from field edges were preferred for nest placement. This pattern cannot be accounted for by the spatial distribution of the nest searching effort. Nevertheless, nest predation rates were only slightly and non-significantly higher along field edges. The proportion of bird/mammal predation did not vary systematically with the distance from a field edge.

This pattern can be tentatively explained by the composition of local nest predators (Chapter 1). The dominant bird predators probably use the entire area of fields as a foraging zone approximately uniformly, irrespective of field edges (Underhill-Day 1985, Vogrin 1998, Hudec & Šťastný 2005). Contrary to expectations (e.g. Šálek et al. 2009) we found mammalian predators in the interior of large fields, which suggests extensive home ranges and high mobility (Harris et al. 1995, Genovesi et al. 1997, Anděra & Geisler 2012).

Chapter 6: Incubation and feeding behaviour of Skylarks with nests in arable fields

In total, 75 complete daily samples of incubation behaviour were analysed from 55 nests, with 1114.38 h during the active daylight period and 2150/2075 individual on/off bouts. Nest attentiveness was 0.81 (per 24 hour) or 0.69 (per working day). The length of the working day lasted on average 14.87 h (range 11.87 – 17.07 h). Daily activity began mostly after sunrise (on average 1.0 h after sunrise) and ended around sunset (on average 0.05 h before sunset). Number of on/off bouts during one day distinctively varied between individual females. The average on-bout duration was 22.3min (n = 2075) and average off-bout duration was 9.5 min (n = 2150).

Females spent more time attending clutches in the early morning and evening, with more frequent recesses during the afternoon. Moreover, this diurnal variation was dependent on (i.e. interacted with) ambient temperature and vegetation characteristics at the nest site (crop height and nest concealment). This suggests that the way incubation time is allotted during the day may be equally as important as the total amount of time spent incubating.

Female nest attentiveness decreased markedly from the incubation to nestling stage and further with the increasing age of nestlings. Feeding rates increased with nestling age.

CONCLUSIONS

- Video monitoring of active nests was an important method to reveal nest fates and predator identities.

- Nest success in intensive arable fields was very low in Skylarks, but relatively high in Lapwings. Skylark nests were vulnerable to all local predators, while it seems that Lapwings can avoid avian predation. Species composition of predators of Skylark nests and patterns in nest predation rates mostly differed from those reported from Western Europe, where the majority of depredation has been attributed to mammals. Our data show that Harriers account for almost half of total depredation events on Skylark nests in the Czech Republic.

- A distinctly different composition of nest predators was found in a semi-natural area in the Netherlands, where the main nest predators differed between co-occurring Skylarks and Woodlarks, possibly because differences in nest site selection.

- The high predation rates on Skylark nests were a consequence of sampling nests from risky plots (crops), not a consequence of disturbances associated with the research.

- Nest predation rates in Skylarks did not show a clear trend over the course of nesting season. The proportion of predation by birds decreased over the course of season, along with vegetation growth. The very low nest success found in arable fields suggests that none of the various crops provide safe nesting habitat. Wide row crops late in the season offer an attractive, yet risky, nesting habitat for Skylarks, especially late in the season when autumn-sown crops are too dense.

- Skylarks seem to avoid areas close to field edges in spite of the comparatively low predation cost associated with nesting there. This avoidance of field edges or preference for field interiors might reflect past selection pressures not detected in the present-day arable field habitats.

- The incubation behaviour of Skylarks nesting in arable fields was basically similar to what is known about passerine species with comparable life histories. Incubation behaviour was rather stable on a daily basis, yet it markedly varied within the day. This suggests the way incubation time is allotted during the day may be equally as important as the total amount of time spent incubating.

- Farmland ground nesting birds could be made less vulnerable to nest predation by managing habitats to ensure nests will be better hidden from predators or located in locations less favoured by predators.

REFERENCES

Anděra, M. & Gaisler, J. (2012). *Savci České republiky*. Academia, Praha.

Baillie, S. R., Marchant, J. H., Crick, H. Q. P., Noble, D. G., Balmer, D. E., Coombes, R. H., Downie, I. S., Freeman, S. N., Joys, A. C., Leech, D. I., Raven, M. J., Robinson, R. A. & Thewlis, R. M. (2006). *Breeding birds in the wider countryside: Their conservation status 2005*. BTO, Thetford.

Benton, T. G., Vickery, J. A. & Wilson, J. D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol*. **18:** 182–188.

Bijlsma, R.G. (2013). Trends en broedresultaten van roofvogels in Nederland in 2012. *De Takkeling* **21:** 5–48.

Burhans, D. E. & Thompson, F. R. (2001). Relationship of songbird nest concealment to nest fate and flushing behavior of adults. *Auk* **118:** 237–242.

Cervencl, A., Esser, W., Meier, M., Oberdiek, N., Thyen, S., Wellbrock, A. & Exo, K. M. (2011). Can differences in incubation patterns of Common Redshanks *Tringa totanus* be explained by variations in predation risk? *J. Ornithol.* **152:** 1033–1043.

Chamberlain, D. E. & Crick, H. Q. P. (1999). Population declines and reproductive performance in Skylarks *Alauda arvensis* in different regions and habitats of the United Kingdom. *Ibis* **141:** 38–51.

Donald, P. F. (2004). *The Skylark*. T & AD Poyser, London.

Donald, P. F., Sanderson, F. J, Burfield, I. J., van Bommel, F. P. J. (2006). Further evidence of continent-wide impacts of agricultural intensification on European farmland birds 1990-2000. *Agr. Ecosyst. Environ*. **116:** 189–196.

Donovan, T. M. & Thompson, F. R. (2001). Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. *Ecol. Appl.* **11:** 871–882.

Evans, K. L. (2004). The potential for interactions between predation and habitat change to cause population declines of farmland birds. *Ibis* **146:** 1–13.

Flohre, A., Fischer, C., Aavik, T., Bengtsson, J., Berendse, F., Bommarco, R., Ceryngier, P., Clement, L. W., Dennis, C., Eggers, S., Emmerson, M., Geiger, F., Guerrero, I., Hawro, V., Inchausti, P., Liira, J., Morales, M. B., Oñate, J. J., Pärt, T., Weisser, W. W., Winqvist, C., Thies, C. & Tscharntke, T. (2011). Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids and birds. *J. Appl. Ecol.* **21:** 1772–1781.

Fuller, R. J., Gregory, R. D., Gibbons, D. W., Marchant, J. H., Wilson, J. D., Baillie, S. R. & Carter, N. (1995). Population declines and range contractions among lowland farmland birds in Britain. *Conserv. Biol.* **9:** 1425–1441.

Fuller, R. J. (2012). *Birds and habitats: relationships in changing landscapes*. Cambridge University press.

Genovesi, P., Sinibaldi, I. & Boitani, L. (1997). Spacing patterns and territoriality of the stone marten. *Canad. J. Zool.* **75:** 1966–1971.

Ghalambor, C. K. & Martin, T. E. (2002). Comparative manipulation of predation risk during incubation reveals variability in the plasticity of parental responses. *Behav. Ecol.* **13:** 101–108.

Gilroy, J. J., Anderson, G. Q. A., Vickery, J. A., Grice, P. V. & Sutherland, W. J. (2011). Identifying mismatches between habitat selection and habitat quality in a ground-nesting farmland bird. *Anim. Conserv.* **14:** 620–629.

Hanski, I., Hansson, L. & Henttonen, H. (1991). Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.* **60:** 353–367.

Harris, S., Morris, P., Wray, S. & Yalden, D. (1995). *A review of British mammals: population estimates and conservation status of British mammals other than cetaceans*. JNCC, UK.

Hart, J. D., Milsom, T. P., Fisher, G., Wilkins, V., Moreby, S. J., Murray, A. W. A. & Robertson, P. A. (2006). The relationship between Yellowhammer breeding performance, arthropod abundance and insecticide applications on arable farmland. *J. Appl. Ecol.* **43:** 81–91.

Hayhow, D. B., Conway, G., Eaton, M. A., Grice, P. V., Hall, C., Holt, C. A., Kuepfer, A., Noble, D. G., Oppel , S., Risely, K., Stringer, C., Stroud, D. A., Wilkinson, N. & Wotton, S. (2014). *The state of the UK's birds 2014*. RSPB, BTO, WWT, JNCC, NE, NIEA, NRW & SNH, Sandy, Bedfordshire.

Hole, D. G., Whittingham, M. J., Bradbury, R. B., Anderson, G. Q. A., Lee, P. L. M., Wilson, J. D. & Krebs, J. R. (2002). Widespread local House Sparrow extinctions – Agricultural intensification is blamed for the plummeting populations of these birds. *Nature* **148:** 931–932.

Hudec, K. & Šťastný, K. (2005). *Fauna ČR Ptáci 2/I*. Academia, Praha.

Lima, S. L. (2009). Predators and the breeding birds: behavioral and reproductive flexibility under the risk of predation. *Biol. Rev.* **84:** 485–513.

MacDonald, M. A., Bolton, M. (2008). Predation on wader nests in Europe. *Ibis* **150:** 54–73.

Martin, T. E. (1995). Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.* **65:** 101–127.

Massaro, M., Starling-Windhof, A., Briskie, J. V. & Martin, T. E. (2008). Introduced mammalian predators induce behavioural changes in parental care in an endemic New Zealand bird. *Plos One* **3:** e2331.

Misenhelter, M. D. & Rotenberry, J. T. (2000). Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. *Ecology* **81:** 2892–2901.

Morris, A. J. & Gilroy, J. J. (2008). Close to the edge: predation risks for two declining farmland passerines. *Ibis* **150:** 168–177.

Newton, I. (2013). *Bird populations*. W. Collins, London.

Panek, M. & Bresinski, W. (2002). Red fox *Vulpes vulpes* density and habitat use in a rural area of western Poland in the end of 1990s, compared with the turn of 1970s. *Acta Theriol*. **47:** 433–442.

Pescador, M. & Peris, S. (2001). Effects of land use on nest predation: an experimental study in Spanish croplands. *Folia Zool*. **50:** 127–136.

Ribic, C. A., Thompson, F. R. & Pietz, P. J. (2012). *Video surveillance of nesting birds*. University of California Press, London.

Richardson, T. W., Gardali, T. & Jenkins, S. H. (2009). Review and meta-analysis of camera effects on avian nest success. *J. Wildl. Manage*. **73:** 287–293.

Schley, L. & Roper, T. J. (2003). Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. *Mammal. Rev*. **33:** 43–56.

Schmidt, K. A. & Whelan, C. J. (1999). Seasonal fecundity in songbirds: can abandonment, renesting, and double brooding ameliorate high nest predation and brood parasitism? *Conserv. Biol*. **13:** 46–57.

Šálek, M., Kreisinger, J., Sedláček, F. & Albrecht, T. (2009). Corridor vs. hayfield matrix use by mammalian predators in an agricultural landscape. *Agric. Ecosyst. Environ.* **134:** 8–13.

Šťastný, K., Bejček, V. & Hudec, K. (2006). *Atlas hnízdního rozšíření ptáků v České republice.* Aventinum, Praha.

Teunissen, W., Schekkerman, H., Willems, F. & Majoor, F. (2008). Identifying predators of eggs and chicks of Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa* in the Netherlands and the importance of predation on wader reproductive output. *Ibis* **150:** 74–85.

Underhill-Day, J. C. (1985). The food of breeding Marsh Harriers *Circus aeruginosus* in East Anglia. *Bird Study* **32:** 199–206.

van Beusekom, R., Huigen, P., Hustings, F., de Pater, K. & Thissen, J. (2004). *Rode Lijst van de Nederlandse broedvogels*. Tirion Uitgevers B. V., Baarn.

Vogrin, M. (1998). Abundance and habitat selection of breeding *Corvus corone cornix* on agricultural land in Central Slovenia. *Acta Zool. Lituan*. **8:** 127-130.

Voříšek, P., Klvaňová, A., Brinke, T., Cepák, J., Flousek, J., Hora, J., Reif, J., Šťastný, K. & Vermouzek Z. (2009). Stav ptactva České republiky 2009. *Sylvia* **45:** 1–38.

LIST OF CONTRIBUTIONS

I. Praus, L. & Weidinger, K. (2010). Predators and nest success of Sky Larks *Alauda arvensis* in large arable fields. *Bird Study* **57:** 525–530. (DOI: 10.1080/00063657.2010.506208)

II. Praus, L. & Weidinger, K. (2011). Střevlíci (Carabidae) jako potenciální nebezpečí pro mláďata skřivanů polních (*Alauda arvensis*) na hnízdech. [Ground Beetles (Carabidae) as potential predators of Skylark (*Alauda arvensis*) fledglings]. *Sylvia* **47:** 91–94. (*Czech*)

III. Praus, L., Hegemann, A., Tieleman, B. I. & Weidinger, K. (2014). Predators and predation rates of Skylark *Alauda arvensis* and Woodlark *Lullula arborea* nests in a semi-natural area in the Netherlands. *Ardea* **102:** 87–94. (DOI: 10.5253/078.102.0112)

IV. Praus, L. & Weidinger, K. (2015). Breeding biology of the Skylark *Alauda arvensis* in maize and other crop fields. *Acta Ornithologica* **50:** 1. (*in press*)

V. Praus, L. & Weidinger, K. Complex patterns of incubation behaviour in the Skylark (*Alauda arvensis*) breeding in arable fields. (*Manuscript*)

CURRICULUM VITAE

Libor Praus, M.Sc.

Date and place of birth: July 3, 1982, Hradec Králové, Czech Republic

E-mail: libor.praus@gmail.com

Education:

2008 – till now	Ph.D. study of Zoology, Faculty of Science, Palacký University in Olomouc. Topic: Effects of nest predators on ground nesting birds in intensively used arable fields. Supervisor: doc. Mgr. Karel Weidinger, Dr.
2005 – 2008	Pedagogical minimum of Biology for Secondary schools, Faculty of Science, Palacký University in Olomouc
2002 – 2007	M.Sc. study of Systematic biology and Ecology, Faculty of Science, Palacký University in Olomouc. Master thesis: Postfledging movements and survival of juvenile flycatchers (genus *Ficedula*). Supervisor: prof. Ing. Stanislav Bureš, CSc.

Research stay: April – July 2012, University of Groningen, Animal Ecology Group

IF publications:

Praus, L. & Weidinger, K. (2015). Breeding biology of the Skylark *Alauda arvensis* in maize and other crop fields. *Acta Ornithologica* **50: 1.** (*in press*)

Praus, L., Hegemann, A., Tieleman, B. I. & Weidinger, K. (2014). Predators and predation rates of Skylark *Alauda arvensis* and Woodlark *Lullula arborea* nests in a semi-natural area in the Netherlands. *Ardea* **102:** 87–94. (DOI: 10.5253/078.102.0112)

Praus, L. & Weidinger, K. (2010). Predators and nest success of Sky Larks *Alauda arvensis* in large arable fields. *Bird Study* **57:** 525–530. (DOI: 10.1080/00063657.2010.506208)

Czech reviewed publications:

Praus, L. (2014). Hnízdní výskyt havranů polních (*Corvus frugilegus*) v Opavě v roce 2014. *Zprávy MOS* **72:** 66–71.

Praus, L. (2013). Současné rozšíření chocholoušů obecných (*Galerida cristata*) ve východních Čechách. *Panurus* **22:** 1–18.

Praus, L. (2013). Aktuální výskyt chocholoušů obecných (*Galerida cristata*) na střední Moravě. *Zprávy MOS* **71:** 38–44.

Praus, L. & Weidinger, K. (2011). Střevlíci (*Carabidae*) jako potenciální nebezpečí pro mláďata skřivanů polních (*Alauda arvensis*) na hnízdech. *Sylvia* **47:** 91–94.

Koleček, J., Paclík, M., **Praus, L**., Vymazal, M., Tyller, Z., Turčoková, L., Sedláček, J. & Figura, R. (2011). Hnízdní a zimní početnost ptáků dvou středomoravských lužních lesů. *Zprávy MOS* **69:** 4–17.

Praus, L. (2009). Neobvykle umístěné hnízdo ťuhýka šedého (*Lanius excubitor*) na Chrudimsku. *Panurus* **18:** 63–67.

Popularization articles:

Praus, L. (2014). Vymizí chocholouš obecný z Českých zemí? *Živa* **2:** 83–85.

Praus, L. (2014). Strnad zahradní – nenápadná vzácnost Hlučínska. *Vlastivědné listy* **2:** 37–38.

Praus, L. (2012). Skřivan polní – nepřítel stísněných prostorů. *Naše příroda* **1:** 8–13.

Book chapters:

Praus, L. (2014). Zoologická podsbírka Slezského zemského muzea. In: Vlk, P. (ed.). *Museum Silesiae*. SZM Opava, 110–117.

Praus, L. (2014). Dermoplastické preparáty ptáků z Opavského gymnazijního muzea. In: Šíl, J. (ed.). *Země a její muzeum*. SZM Opava, 57–61, 264–266.

Participation in conferences:

Praus L. & Weidinger K. (2013). Teplota a vegetační kryt ovlivňují inkubační chování skřivana polního (*Alauda arvensis*). Sborník abstraktů z konference Zoologické dny Brno 7. – 8. února 2013: 186–187 (*poster*).

Praus L. & Weidinger K. (2011). Nest success and predators of Sky Lark (*Alauda arvensis*) and Lapwing (*Vanellus vanellus*) nests in arable fields in the Czech Republic. In: Book of abstracts: 8th Conference of the European Ornithologist Union, Riga August 27-30, 2011 (*poster*).

Praus L. & Weidinger K. (2011). Inkubační chování skřivanů polních (*Alauda arvensis*) v intenzivních polních kulturách. Sborník abstraktů z konference Zoologické dny Brno 17. – 18. února 2011: 182–183 (*presentation*).

Praus, L. & Weidinger, K. (2011). Hnízdní úspěšnost a predátoři skřivana polního (*Alauda arvensis*) a čejky chocholaté (*Vanellus vanellus*) v intenzivních polních kulturách. Sborník abstraktů z konference ČSO Ornitologie – Věda pro každého. Mikulov na Moravě 7. – 9. 10. 2011: 61–62 (*poster*).

Praus L. & Weidinger K. (2010). Hnízdní biologie skřivana polního (*Alauda arvensis*) v intenzívních polních kulturách. Metody a výsledky výzkumu ptačích populací V. Sborník abstraktů z celostátní ornitologické konference k 35. výročí založení Východočeské pobočky České společnosti ornitologické 22. – 24. 10. 2010: 40. (*presentation*)

Praus L. & Weidinger K. (2010). Predátoři hnízd skřivana polního (*Alauda arvensis*) a čejky chocholaté (*Vanellus vanellus*) v intenzivních polních kulturách. Metody a výsledky výzkumu ptačích populací V. Sborník abstraktů z celostátní ornitologické konference k 35. výročí založení Východočeské pobočky České společnosti ornitologické 22. – 24. 10. 2010: 41. (*presentation*)

Kutal, M. & **Praus, L.** (2009). The neighbour wolf: Conservation of large carnivores in the Beskysy Mts., Czech Republic. In: Book of abstracts: 2nd European Congress of Conservation Biology. Czech University of Life Sciences, Prague. (*poster*)

Professional experience:

2013 – till now	Silesian museum Opava, Curator of Zoological collections
2006 – 2009	Friends of the Earth Czech Republic – Olomouc local group. Projects in conservation of large carnivores in Beskydy mountains, educational programs, editor of bulletin Ekologické listy

Voluntary activities:	Active member of The Czech Society for Ornitology (Birdlife CZ) and its regional brands; organizing projects in conservation and monitoring of farmland birds and swifts, public education.
	Editor in chief of Panurus, Ornithological journal of the East Bohemian Branch of the Czech Society for Ornithology at the Museum of East Bohemia, Pardubice
	Holder of Bird-ringing license for the Czech Republic