Predators and Predation Rates of Skylark Alauda arvensis and Woodlark Lullula arborea Nests in a Semi-Natural Area in the Netherlands

Authors: Praus, Libor, Hegemann, Arne, Tieleman, B. Irene, and Weidinger, Karel

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]

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 incuba-

tion) 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-moni-

tored 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.

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)