**Seasonal habitat use and breeding performance of the Eurasian Skylark (*Alauda arvensis*) in Central European farmland**


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*To all living beings that share the joy of life*

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## Summary

The Common Agricultural Policy (CAP) of the European Union has often been identified as a driver of recent agricultural intensification and thus of biodiversity loss. All major taxa, including vascular plants, arthropods, mammals, and birds, have undergone dramatic population declines on farmland during the second half of the 20th century. In that context, I started my PhD project on the seasonal habitat use and breeding performance of the Eurasian Skylark (*Alauda arvensis*), one of the current CAP's greatest "loser" species. During the spring and summer of 2017 to 2019, I collected comprehensive data on the breeding biology of the Skylark population in the heterogeneous farmland south of Göttingen, Lower Saxony, in Germany. The new insights gained as a result of the project are presented in this dissertation.

**Chapter 1** gives an overview of the crisis facing European farmland birds, the interference of agricultural intensification with the breeding biology of Skylarks, and my thesis objectives. Intensified land use is associated with many processes, such as an increased application of pesticides and fertilizers or landscape homogenization. However, the widespread cultivation of dense-growing crops likely poses the most significant challenge to breeding Skylarks, as they strongly depend on accessible vegetation for both nest building and foraging. Crop growth during the breeding season is thought to induce an increasing paucity of suitable nesting and foraging habitats. Therefore, this PhD project aimed to investigate the seasonal changes in habitat use and breeding performance due to the growing crop vegetation. All findings are interpreted to provide recommendations for improved Skylark conservation.

**Chapter 2** deals with the decreasing suitability of winter cereals as nesting habitat, which is expected to be the primary driver behind the decline of Skylarks by curtailing the potential time for breeding of this multi-brooded species. My co-authors and I investigated: (i) the extent to which Skylarks in our study area prematurely cease nesting activity, switch nesting habitats, or breed on high-risk linear structures, like tramlines, when winter cereals have become impenetrable. Moreover, we explored: (ii) if nest success decreases throughout the breeding season, and (iii) how often Skylarks make a successful breeding attempt per year. To answer our research questions, we radio-tagged 28 adult Skylarks in April of 2018 and 2019 and documented the habitat use and breeding success for half of them during a full breeding season. Additionally, we searched for Skylark nests of untagged pairs, resulting in 96 total monitored nests. All, except one radio-tagged Skylark, showed breeding activity beyond July 1st. A mixed-effect logistic regression model (GLMM) revealed that the probability of starting a breeding attempt did not decrease seasonally. Therefore, our study could not observe a premature termination of breeding. As indicated by an analysis of centroid shifts of Skylark home ranges, three-quarters of tagged Skylarks kept their home range throughout a breeding season. All home ranges were composed of winter cereals and at least one other

habitat type, with only two exceptions. Skylarks switched nesting habitats away from winter cereals to crops like sugar beet or set-aside from late May onwards. According to a Mayfield logistic regression, corn and linear structures were high-risk nesting sites but only played a minor role in breeding. A further Mayfield logistic regression revealed that nest success did not decrease over time and was exceptionally high, with a nest survival of ca. 54%. Taken together, we could not detect a curtailment of the breeding season, and Skylarks had time to make 1.5 to 1.8 breeding attempts, of which 0.8 were successful. We conclude that crop diversity in our study area guaranteed individuals a chance for successful nests throughout the breeding season.

**Chapter 3** investigates the assumption that the growing crop vegetation gradually hampers Skylarks' access to food and thus decreases food availability in modern farmland. We analyzed (i) habitat selection concerning prey biomass/diversity, vegetation cover, and distance to foraging sites, (ii) the general and seasonal habitat use, and (iii) seasonal development of foraging parameters (e.g., the feeding frequency) as indicators of food availability. During the breeding seasons of 2018 and 2019, we documented the foraging flights of chick-raising pairs at 51 nests. Furthermore, we collected data on vegetation cover, arthropod abundance, and distance to the foraging sites within the surroundings of 42 of these nests. As revealed by a generalized additive mixed model and an analysis of relative variable importance, Skylarks selected foraging habitats mainly based on the distance to the nest, with a clear preference for habitats closer than 112 m. The most frequent habitat types within Skylark home ranges (winter wheat, sugar beet, corn, annual flower strips, and field paths) could not be ranked according to their overall relevance as foraging habitat in a compositional analysis. GLMM models showed a seasonally decreasing use of sugar beet and annual flower strips and increasing use of winter wheat relative to their availability in home ranges. According to linear mixed-effect models and a linear regression model, none of the analyzed foraging parameters worsened over time. Instead, the feeding frequency even increased with the ongoing breeding season. We suggest that the heterogeneous farmland in our study area allowed Skylarks to establish diverse home ranges, which enabled spatial synergetic effects with flexible adaptations of habitat use to changing conditions and prevented any deterioration of foraging parameters.

**Chapter 4** emphasizes seasonal changes of nest locations within winter cereals. In this study, my co-authors and I tested if Skylarks actively avoid high-risk linear structures, like tramlines and field edges, as nesting sites in the early breeding season. Between 2017 and 2019, we located 32 nests in winter cereals before the end of May and showed that Skylarks nested 2 m further away from linear structures than expected if nest location was random. Furthermore, we found a higher nest predation risk on linear structures and a shifting of nesting sites towards them later in the breeding season. Because we interpret the initial avoidance as the ability of

Skylarks to assess predation risk at fine spatial scales, we present the idea of additional tramline fragments as a modification of Skylark plots for conservation management.

**Chapter 5** identifies the heterogeneous composition of our study area as the probable reason we did not find a seasonal curtailment of the breeding season or a seasonal decrease in food availability. I relate our results to other research that pointed to the benefits of farmland heterogeneity. I also interpret it as the most significant advantage of our studies providing arguments for crop diversification on the individual level and not based on breeding pair densities. Additionally, I discuss potential shortcomings of my PhD project, like the impossibility of studying the influence of bad weather due to the extraordinarily hot and dry conditions during the fieldwork period. The chapter finishes with suggestions for future research on Skylarks.

# Chapter 1

# General introduction

## 1.1. Modern agriculture in the European Union and the farmland bird crisis

Covering about 40% of the area within the European Union (EU), farmland has immense importance as a habitat for a variety of plants and animals (European Commission 2017; Eurostat 2020). Half of all species in Europe depend to some extent on agriculture (Kristensen 2003). Taking birds as a concrete example, farmland is the primary habitat type for 30% of them (BirdLife International 2021). Due to this extraordinary relevance, recent population collapses of all major taxa in agricultural landscapes are alarming. Decreasing numbers were reported for arable plants (Richner et al. 2015), insects (Goulson 2019), and mammals (Macdonald et al. 2007) over the last decades.

Scientists put particular focus on the population dynamics of farmland birds in Europe because they are useful indicators of agrobiodiversity (Butler et al. 2010; Gregory et al. 2005). Birds are (i) easy to monitor, (ii) sensitive to land use, and (iii) popular among people (Tryjanowski et al. 2011). One of the most prominent monitoring indices is the *common farmland birds indicator* that summarizes European population trends of 39 farmland-associated species (PECBMS 2022b). The development of this index is worrying: 24 species are in decline with an overall index decrease of -59% since 1980 (PECBMS 2022b). BirdLife International (2013) translates the declines into 300 million fewer farmland birds to make the loss more illustrative. A highly regarded recent study by Burns et al. (2021) calculates a general loss of 520 to 620 million birds only in EU territory within the last 40 years, of which most individuals belong to species that are associated with agricultural land.

The principle mechanisms behind the farmland bird crisis in the EU are well-studied and primarily associated with an agricultural intensification within the second half of the 20th century (Donald et al. 2006; Donald et al. 2001b; Emmerson et al. 2016; Krebs et al. 1999; Robinson and Sutherland 2002). Pesticide use (Geiger et al. 2010; Gibbons et al. 2015; Hallmann et al. 2014; Rands 1985), landscape homogenization (Benton et al. 2003; Šálek et al. 2021), a decreasing area of set-aside with a simultaneous increase in the cultivation of corn (Busch et al. 2020; Tarjuelo et al. 2020; Traba and Morales 2019), and reduced food availability in fields during winter (Robinson et al. 2004; Siriwardena et al. 2008) have all been connected to declining populations of farmland birds.

Agricultural intensification has been driven by the Common Agricultural Policy (CAP) in the EU, impressively demonstrated by the EU accession of Eastern European countries that adopted the CAP and experienced farmland bird declines thereafter (Reif and Vermouzek 2019; Sanderson et al. 2013). Initially, the CAP connected higher crop yields directly with higher income for farmers while penalizing extensification (Donald 2004; Donald et al. 2002b). The EU acknowledged the problem, cut the link between subsidies and production, and developed strategies to halt biodiversity loss. These still include optional agri-environment-

climate measures (Batáry et al. 2015; Pe'er et al. 2017) and compulsory greening measures for farmers established during a CAP reform in 2013 (European Commission 2013, 2011). However, strategies have thus far failed to fulfill their purpose due to the integration of inefficient measures, low demands on crop diversification, and too many exemptions (Pe'er et al. 2017).

Consequently, the farmland bird crisis is still ongoing (European Environment Agency 2020; Keller et al. 2020). It remains unclear if the current CAP reform will stop the process (Hermoso et al. 2022). To achieve this goal and convince policy-makers, experience has shown the importance of both studies that analyze large-scale data sets and detailed studies on single species (Grice et al. 2004).

## 1.2. The Eurasian Skylark: A herald of spring falls silent

Among those farmland birds that greatly suffered from agricultural intensification is the Eurasian Skylark (*Alauda arvensis*). Since 1980, the European population has more than halved (PECBMS 2022a), corresponding to a loss of 68 million individuals only in the EU (Burns et al. 2021). Nevertheless, it is still a common and widespread farmland bird in Europe, with 44 to 79 million breeding pairs that make up about 30% of the world population (BirdLife International 2022; Hagist and Zellweger-Fischer 2020). Because of its popularity and its strong association with open landscapes, Skylarks became a flagship species of the farmland bird crisis (Copland et al. 2012; Donald 2004; Hiron et al. 2012). Numerous studies analyzed how intensified land use interferes with their habitat requirements (e.g., Chamberlain et al. 1999; Jenny 1990b; Kuiper et al. 2015; Praus and Weidinger 2015; Toepfer and Stubbe 2001). To understand this interaction, detailed knowledge on the ecology of Skylarks is necessary, which is reviewed in Donald (2004) and reproduced shortly in the following:

Skylarks occur across the Palearctic, only missing in most parts of the Arctic Circle. Within the Indomalayan realm, they are replaced by the closely related Oriental Skylark (*Alauda gulgula*). As birds of steppes and natural grassland, Skylarks avoid forests, wood, or other vertical structures. The clearance of forests in favor of farmland accelerated during the Bronze Age and created extensive open landscapes that Skylarks could inhabit. Today, it is a synanthropic species in Europe as most individuals live in agricultural land. From April to the beginning of August, Central European Skylarks usually make two to three breeding attempts with average clutch sizes between three to four eggs. Males fiercely defend territories that are marked with elaborated song flights. Vegetation that does not hamper mobility is essential for both nest building and the search for food on the ground. Actual plant species are less important so that Skylarks can breed in various crops and grassland. The nesting cycle is extremely short, with

an average of 11 days for incubation and only eight days of nestling stage. During that period, Skylarks mainly feed arthropods to their chicks, which is the preferred diet of adults as well. After leaving the nest by hopping, chicks are fed for roughly two more weeks when they also start to fly. As the breeding season ends, Skylarks switch to a more vegetable-based diet. Western European populations are often year-round residents, while Central and Eastern European Skylarks typically migrate to the Mediterranean region.

Independent of whether Skylarks are residents or migrants, they face serious problems in winter and/or on the way to their wintering grounds. Hirschfeld and Attard (2017) report ca. 900,000 Skylarks killed annually in four (Cyprus, France, Malta, Romania) of the six EU countries with legal Skylark hunting. The authors estimate that an additional 450,000 individuals were killed in Italy and had no access to reliable data for hunting bags from Greece. Therefore, more than 1.35 million Skylarks are legally killed each year in countries where many migrating Skylarks stay during winter. Against the background of their EU-wide decline, Skylark hunting is neither ethically nor politically justifiable any longer (Hirschfeld et al. 2019). Direct exploitation, to my knowledge, is the only significant negative impact on European Skylark populations that is not associated with land use, whereas a food shortage on farmland during winter is a result of modern farmland practices. The number of overwintering cereal stubble fields decreased due to the increased cultivation of autumn-sown cereals, which probably led to food depletion in a generally tough season (Evans et al. 2004; Geiger et al. 2014; Powolny et al. 2018).

A scarcity of food during the breeding season is also discussed as a consequence of the intensified use of pesticides (Boatman et al. 2004). Several studies relate it to reduced reproductive output and declining Skylark populations (Hallmann et al. 2014; Odderskær et al. 1997a). Poulsen et al. (1998) suggest that pesticide treatment reduced food availability in cereals and caused partial starvation of chicks at their study site. Although Donald et al. (2001c) believe that pesticide use affects the diet composition of chicks and possibly their condition, they expect it to be less important for the decline. Donald (2004) sees the main problem in a different concomitant of agricultural intensification: the cultivation of fast-growing crops impenetrable for Skylarks.

### 1.3. *Growing problems*: The seasonal challenge of breeding

The strong dependency of Skylarks on vegetation that is accessible enough to breed (Jenny 1990b; Jeromin 2002) and forage (Jenny 1990a; Pätzold 1983) on the ground likely interferes most with modern agricultural land use in manifold ways. Inorganic fertilizers increase the structural density of many current crops, resulting in crop vegetation that becomes too dense

for breeding and foraging later in the breeding season (Chamberlain et al. 2000; Donald 2004; Jenny 1990a; Weibel 1998). Especially the widespread switch from spring-sown cereals (called summer cereals) to autumn-sown cereals (called winter cereals) is thought to pose a challenge for breeding Skylarks (Chamberlain et al. 1999; Donald 2004; Donald and Vickery 2000). The crop vegetation of winter cereals becomes too dense from late May onwards, allowing only one instead of several breeding attempts (Chamberlain et al. 2000; Donald and Morris 2005; Wilson et al. 1997). Therefore, the only nesting sites within winter cereals that are still accessible are the bare tramlines with a high risk of nest predation (Donald et al. 2002a; Donald and Vickery 2000; Fischer et al. 2009). Furthermore, the densely growing sward structure reduces access to food and can induce a food shortage later in the breeding season (Donald and Morris 2005). As cereals cover about 40% of the arable land in the EU (Eurostat 2022), these past changes in cereal management are considered to be the shaping factors of Skylark population dynamics (Donald 2004; Donald and Morris 2005; Donald and Vickery 2000). According to models by Siriwardena et al. (2001), the decline of British Skylarks can be almost entirely explained by the increasing switch from summer to winter cereals.

Even though Skylarks are known for seasonal territory shifts to access more openly vegetated habitats (Eggers et al. 2011; Koleček et al. 2015; Schläpfer 1988), suitable alternatives to nest or forage are frequently lacking. Habitat heterogeneity in farmland strongly decreased due to larger fields with lower crop diversity and a reduced amount of fallow land (Benton et al. 2003; Tarjuelo et al. 2020; Traba and Morales 2019). Other common crops besides winter cereals are often challenging as well. The dense vegetation structure of winter rape is inaccessible during most of the breeding season (Koleček et al. 2015; Miguet et al. 2013). Corn is more openly vegetated, but breeding attempts suffer high predation rates (Praus and Weidinger 2015), and intensive pesticide applications reduce the availability of food (discussed in Koleček et al. 2015).

The need for open vegetation is also detrimental to breeding Skylarks in grassland-dominated landscapes. Although nests are mainly initiated after mowing, time intervals between two cutting events are too short on intensively used grassland to complete a full nesting cycle (Flade et al. 2003; Kuiper et al. 2015). Thus, the lowest nest survival rates within agricultural landscapes are typically found in these areas (Kuiper et al. 2015; Ottens et al. 2013; Poulsen et al. 1998). Skylarks that leave winter cereals after their first breeding attempt and settle down in grassland have almost no chance of nest success (Ottens et al. 2013).

Taken together, the negative impacts of modern agricultural land use on breeding Skylarks – either affecting nesting, foraging, or both - are thought to increase over time and accumulate later in the breeding season.

## 1.4. Thesis objectives and chapter outline

Despite comprehensive studies on the consequences of agricultural intensification for breeding Skylarks that provide a solid basis for scientists, several important uncertainties and knowledge gaps remain.

First, the increasing use of high-risk nesting sites like tramlines (Donald et al. 2002a), maize fields (Praus and Weidinger 2015), or grassland (Ottens et al. 2013) during the later breeding season implies a decreasing nest success. Other researchers suggest that many Skylarks give up breeding when winter cereals become impenetrable (Daunicht 1998; Donald 2004), so the average number of breeding attempts is reduced (Chamberlain et al. 2000; Wilson et al. 1997). Both a decreasing nest success and a decreasing motivation to start a breeding attempt would restrict the time for successful breeding to the early breeding season. To my knowledge, however, such a temporal restriction has not been directly proven thus far. A large amount of previous research based its conclusions on territory densities (e.g., Eggers et al. 2011; Koleček et al. 2015; Schmidt et al. 2022; Toepfer and Stubbe 2001), although high densities do not necessarily correspond to high-quality habitats with a high reproductive output. Instead, they can also be associated with ecological traps, site fidelity, or a lack of better habitats (Johnson 2007; Titeux et al. 2020; van Horne 1983). Many other studies analyzed how the choice of nesting sites influences Skylark nest success (e.g., Donald et al. 2002a; Kragten et al. 2008; Kuiper et al. 2015; Praus and Weidinger 2015; Wilson et al. 1997), but they could not connect their results with the annual reproductive output of individuals due to the difficulty of following Skylarks throughout a breeding season (Donald 2004). I am not aware of a study investigating a seasonal change of nest success or to which extent Skylark individuals react in a specific way (premature termination of breeding, switch to other crops, switch to linear structures like tramlines) to the growing vegetation of winter cereals. Related to this, data on the number of breeding attempts and of produced fledglings per pair and year are scarce (but, e.g., given in Jenny 1990b; Schläpfer 1988) despite the high relevance of breeding success for population dynamics (Godin et al. 2021; Roodbergen et al. 2012). Therefore, Donald (2004) called it the Holy Grail of today's Skylark research to report reliable estimates of the annual number of breeding attempts per pair in modern farmland.

Second, the growing vegetation of winter cereals and other fast-growing crops is expected to reduce the accessibility to prey (Donald and Morris 2005; Jenny 1990a; Weibel 1998) and thus the food availability for chick-raising Skylarks during the course of the breeding season. Despite being a plausible assumption, it remains untested. Seasonal changes in habitat use were rarely considered on a continuous time scale in spite of the essential role of time-scale dependencies on habitat selection (Miguet et al. 2013). Moreover, even though previous studies investigated the influence of arthropod abundance, vegetation density, and distance to

foraging sites on the foraging habitat selection of Skylarks (e.g., Jenny 1990a; Kuiper et al. 2013), they did not measure the relative importance of all influential parameters simultaneously which is crucial to prioritize conservation efforts.

Third, Skylark research on farmland and, in particular, studies that analyzed nest success or overall reproduction are not distributed equally across Europe. The majority of publications that I am aware of were conducted in Great Britain (e.g., Chamberlain et al. 1999; Donald et al. 2002a; Morris et al. 2004; Poulsen et al. 1998; Wilson et al. 1997) and, to a lesser extent, in the Netherlands (e.g., Hegemann et al. 2013; Kragten et al. 2008; Kuiper et al. 2015; Ottens et al. 2014). Extensive research on individual reproduction and habitat use, including foraging habitat selection, comes from Switzerland (e.g., Jenny 1990a, 1990b; Schläpfer 1988; Weibel 1999). According to Tryjanowski et al. (2011), the uneven distribution of farmland bird studies with a clear focus on Western Europe complicates a Pan-European halt of the farmland bird crisis, as insights gained in one region cannot be readily transferred to others. Regarding Skylarks, studies from Northern Europe demonstrate how important it is to be cautious with generalizations of causal relationships. Neither Fox (2004) in Denmark nor Wretenberg et al. (2006) in Sweden found a link between the cultivation of winter cereals and the population dynamics of farmland birds, including the Skylark. Therefore, each study contributing to a clearer view of the interaction between farmland birds and agricultural land use across Europe is highly relevant.

Fourth, detailed data on individual breeding success is not only scarce and geographically limited but mainly collected more than 30 years ago (e.g., Jenny 1990b; Schläpfer 1988). In the period since then, European farmland and the CAP have undergone significant changes, e.g., the abolition of set-aside (BirdLife International 2008) or the introduction of obligatory greening measures (European Commission 2013).

Based on the above, this PhD project aimed to analyze the habitat use and breeding performance of Skylarks during the breeding season, focusing on seasonal dynamics. I intended to improve our understanding of the present situation for Skylarks by addressing the knowledge gaps previously mentioned and by providing current data from a Central European population where winter cereals are the dominating crop. As a study site, I chose the farmland south of the city Göttingen in Lower Saxony, Germany, where I collected data within an area of ca. 8 km² between April and August from 2017 to 2019. The overall objective was the development of recommendations for the improved conservation of Skylarks. During the project, I wrote three scientific manuscripts representing the core of my dissertation, two of which are already published in peer-reviewed journals.

Chapter two investigates whether the time for successful breeding attempts is actually restricted to the early breeding season. In that study, my co-authors and I followed radio-

tagged Skylarks throughout the breeding season of 2018 and 2019 to describe how the individuals deal with the loss of winter cereals as suitable nesting habitats. We documented the nesting sites, the nest outcome, and the timing of all their breeding attempts to conclude how their habitat use is related to their reproductive output. Our findings were corroborated by nest data of untagged birds that also enabled us to model the influence of nest habitats and the ongoing breeding season on nest success with Mayfield logistic regressions. The work demonstrates on the individual level how crop diversity guarantees a chance for successful nests throughout the breeding season. It gives helpful input for decision-makers on how to prevent a further decline of Skylarks within conventionally managed farmland.

Chapter three analyzes whether Skylarks in 2018 and 2019 suffered a decreasing food availability later in the breeding season due to the growing crop vegetation. We documented the foraging flights of chick-raising pairs and collected data on vegetation cover, arthropod abundance, and distance to the foraging sites within the nest surroundings. Firstly, these three parameters were ranked according to their importance for the selection of foraging habitats using generalized additive models. Then, we modeled the seasonal use of habitat types with generalized linear mixed-effect models. Finally, linear mixed-effect models and a linear regression model revealed the development of important foraging parameters like the feeding frequency during the breeding season. Complementing our previous study on breeding success, this work underpins the essential role of heterogeneous farmland for chick-raising Skylarks.

Chapter four focuses on nesting sites within winter cereals as the primary habitat type for Skylarks in Europe. Based on Skylark nests found in winter cereals between 2017 and 2019, we compared the early nest site selection with a random nest distribution scenario in respect to high-risk linear structures like tramlines. Our results further inspired the idea of additional tramline fragments as a conservation measure for Skylarks. Thus, the study provides a specific example of the vital relationship between scientific insights and practical nature conservation work.

# Chapter 2

## Seasonal dynamics of nesting habitats and breeding success of Eurasian Skylarks

## 2.1. Abstract

A paucity of suitable nesting sites is one key driver behind the farmland bird crisis in Europe. Winter cereals become impenetrable for ground breeding birds like the Eurasian Skylark (*Alauda arvensis*), curtailing the potential time for breeding. As stable Skylark populations depend on multiple breeding attempts per year, the widespread cultivation of winter cereals is thought to be responsible for their tremendous decline. Nevertheless, data on the number of breeding attempts in modern farmland is scarce, and it is still unclear how individuals deal with the decreasing suitability of winter cereals. Therefore, we explored: (i) the extent to which Skylarks prematurely cease nesting activity, switch nesting habitats, or breed on linear structures like tramlines. Moreover, we analyzed: (ii) if the nest success decreases throughout the breeding season, and (iii) how often Skylarks make a successful breeding attempt per year. We radio-tagged 28 adults in a Central European population during April 2018 and 2019, tracked half of them for more than three months, and measured their breeding success. Additionally, we monitored nests of untagged pairs, resulting in 96 nests found. None, except one tagged individual, stopped breeding activity before July 1st. Home ranges were mainly stable, but Skylarks switched nesting habitats away from winter cereals to crops like sugar beet or set-aside. High-risk nesting sites like corn and linear structures only played a minor role in breeding. Overall, generalized linear models revealed no seasonal decrease in nest success, and tagged Skylarks had sufficient time to make 1.5 to 1.8 breeding attempts, of which 0.8 were successful. We suggest that heterogeneous farmland in our study area, which enabled diversely composed home ranges, prevented a curtailment of the breeding season. Thus, our study reinforces the need for crop diversification which gives Skylarks a chance to survive in modern farmland.

## 2.2. Introduction

Despite international agreement to halt biodiversity loss within the European Union (EU) (European Commission 2011), the tremendous declines of farmland birds as a consequence of agricultural intensification are still ongoing (European Environment Agency 2020; Keller et al. 2020). Greening measurements of the Common Agricultural Policy (CAP) have thus far failed to prevent further losses (Pe'er et al. 2017). Instead, policy-driven increases in corn cultivation and decreases in the area of fallow land further worsened the situation (Busch et al. 2020; Tarjuelo et al. 2020; Traba and Morales 2019). Butler et al. (2007) identified the loss of food and nesting habitats as key drivers underlying the biodiversity crisis in the cropped farmland areas. Among the bird species that greatly suffered from a paucity of nesting habitats caused by modern farmland practices is the Eurasian Skylark (*Alauda arvensis*) (Donald 2004; Hagist and Zellweger-Fischer 2020). Since 1980, the Skylark population of Europe has more than halved (PECBMS 2022a).

As ground-nesting birds with multiple breeding attempts per year, Skylarks depend on a vegetation structure that provides both sufficient nest cover and good accessibility throughout the breeding season (Donald 2004; Jenny 1990b; Jeromin 2002). In arable farmland, individual crops fulfill these conditions typically only within a certain period (Schläpfer 1988; Wilson et al. 1997). This crop-specific timeframe of suitability is of particular importance regarding cereals. More than 40% of arable land in the EU is cultivated with cereals (excluding corn and rice) (Eurostat 2022). Because of their prevalence as crops, a high proportion of European Skylarks inhabit these cereals, so previous changes in cereal management are thought to have strongly influenced the population dynamics (Donald 2004; Donald and Morris 2005; Donald and Vickery 2000). In particular, several studies suggest that the replacement of spring-sown cereals by autumn-sown cereals in many European regions heavily affected the breeding performance of Skylarks (Chamberlain et al. 1999; Donald and Vickery 2000; Jenny 1990b; Siriwardena et al. 2001). Unlike spring-sown cereals, autumn-sown cereals have a dense sward structure that allows only one breeding attempt in the early breeding season (Chamberlain et al. 2000; Donald and Morris 2005; Wilson et al. 1997). Therefore, Skylarks that initially nest in winter cereals have three different options to deal with this development.

First, individual breeding pairs can forgo further breeding attempts and prematurely cease nesting activity (Daunicht 1998; Donald 2004). Second, Skylarks can build their nests in habitats with more accessible vegetation, e.g., corn or grassland (Fischer et al. 2009; Ottens et al. 2013; Schläpfer 1988). However, these attempts frequently fail due to the high predation risk in corn (Praus and Weidinger 2015) or the regular mowing of grassland (Ottens et al. 2013). Furthermore, territory shifts are often necessary to access alternative nesting habitats in the first place (Schläpfer 2001), as agricultural intensification has homogenized farmland

(Benton et al. 2003). Shifts were documented directly for individual breeding pairs (Jenny 1990b; Schläpfer 1988) or concluded from seasonal shifts in habitat-specific territory density (Eggers et al. 2011; Koleček et al. 2015; Toepfer and Stubbe 2001). Third, breeding pairs can choose the unvegetated tramlines within cereal fields or the field edges as nesting sites later in the breeding season, even though these nests suffer high predation rates because linear structures are used as access routes by predators (Donald et al. 2002a; Fischer et al. 2009; Püttmanns et al. 2021). Both the switch to accessible yet dangerous nesting habitats and the choice of linear structures as nesting sites would reduce the *nest success* of Skylarks (i.e., the success of individual nests, Ottens et al. 2016) in the course of the breeding season. All three options have in common that the potential time for successful breeding attempts is restricted to the early breeding season. This actual curtailment may be the main reason for the European decline, as two to three breeding attempts per pair and year with a chance of success are probably essential for self-sustaining populations (Donald 2004; Wilson et al. 1997).

Notwithstanding the above, data on the individual number of breeding attempts of Skylarks in modern farmland is still scarce (but given in Ottens et al. 2013; Ottens et al. 2016) and was mainly collected over 30 years ago (Jenny 1990b; Schläpfer 1988). Related to this lack of data, we are not aware of a study that analyzed the extent to which Skylarks chose one of the three presented options after winter cereals became too dense for breeding. Moreover, Hiron et al. (2012) doubt the general inferiority of winter-sown crops compared to summer-sown crops and see a great need to track individual Skylarks for accurately estimating the quality of different breeding habitats.

Therefore, we aimed to investigate how individual Skylarks of a current Central European population handle the decreasing suitability of winter cereals as nesting habitat and if the time for successful breeding is restricted to the early breeding season. More precisely, we analyzed: (i) the extent to which Skylarks prematurely cease nesting activity, switch nesting habitats, or breed on linear structures of winter cereals when crop vegetation becomes impenetrable. Additionally, we analyzed: (ii) if nest success decreases throughout the breeding season, and (iii) how often Skylarks make a successful breeding attempt per year, here defined as *breeding success*. Thus, we tracked radio-tagged Skylarks throughout the breeding season, measured the breeding success, and corroborated our findings with nesting data of untagged pairs.

## 2.3. Methods
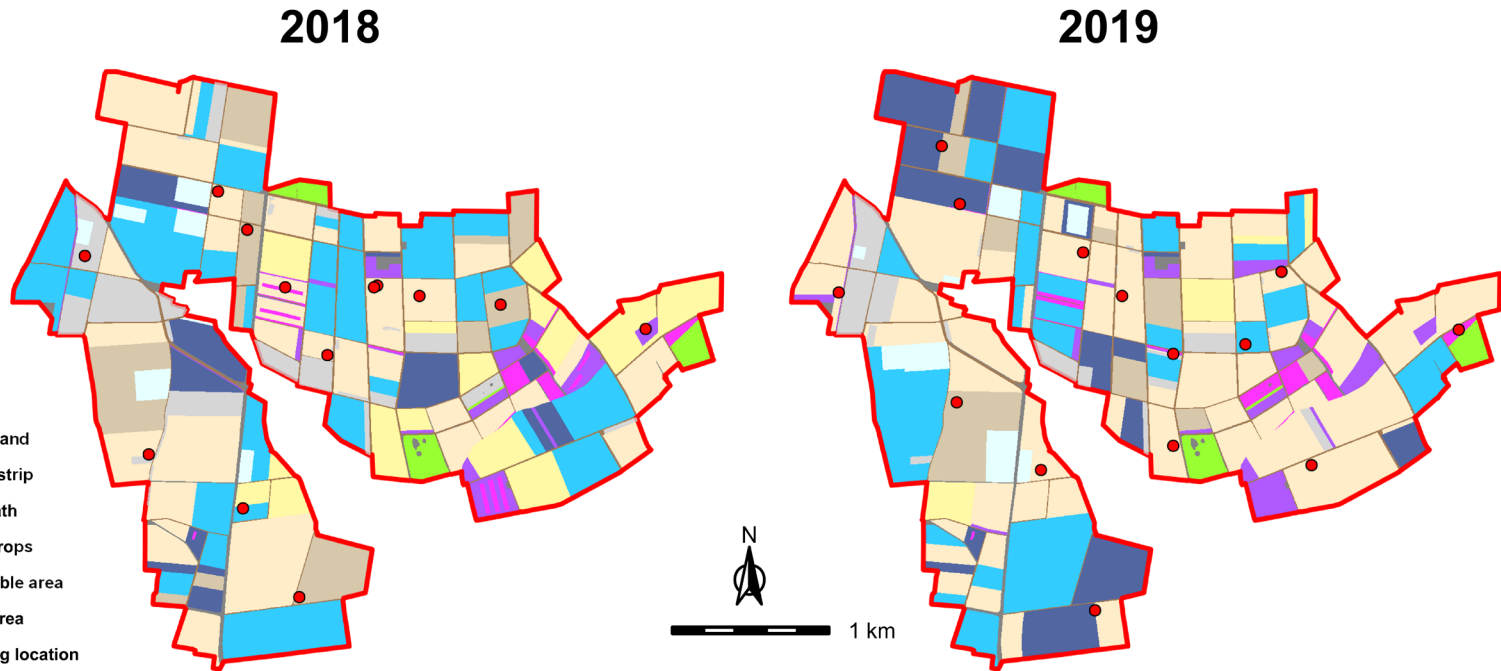
### 2.3.1. Study area

The study area (a total of 8.1 km²) is located in the south of Göttingen, Germany (N51° 29.631, E9° 56.595), and mostly identical to that of Püttmanns et al. (2021) and Püttmanns et al.

(2022). Skylark densities varied between three to four territories per 10 ha (estimations based on Langer 2017 and Meineke 2018, unpublished data). On a national scale, the regional climate is comparatively dry (mean annual temperature: 8.7°C, mean annual total precipitation: 644.9 mm; Vohl 2020). Farmland dominated the study site with 85.8% cropland and only 1.9% permanent grassland. Fields under organic farming made up 3.8%. The mean size of arable fields was 4.8 ha. Even though winter cereals were the most cultivated crops in 2018 and 2019 (winter wheat: 34.5% of the whole study area averaged over both years; winter barley: 8.2%), the study site lacked extensive areas of monocultures. Instead, sugar beet (21.2%), corn (9.6%), winter rape (6.9%), and other crops (e.g., asparagus, broad bean, clover, strawberry, and summer wheat: each ≤1.3%) were often cultivated next to winter cereals. Trial plots (2.4%) of the Faculty of Agricultural Sciences from the University of Göttingen and both sown flower strips (3.0%) and fallow land (1.3%), which were mainly established in the framework of the PARTRIDGE conservation project (PARTRIDGE 2021), further enriched the composition of habitats. The local network of field paths covered an area of 2.9% with a total length of approx. 30.2 km. Structures that Skylarks generally avoid, like buildings, hedgerows or woods, were rare (Figure 2.1).

## 2.3.2. Bird data

*Radio tracking*

At the beginning of the breeding season in April 2018 and 2019, we caught 14 Skylarks per year using mist nets. The netting took place at dawn or dusk within areas of high territorial activity across the study area (Figure 2.1). We used playback of the male song as a luring device. Caught birds were ringed and equipped with a radio tag (2018: standard pulse transmitter, 1.0 to 1.2 g, JDJC Corp., USA; 2019: PIP Ag392 for males, PIP Ag376 for females, 0.8 g to 1.2 g, Lotek, UK) that equaled 3 to 4% of the body weight. We glued the transmitter on a piece of cloth to the shortened back feathers. For sexing individuals, we used the wing length, as females have shorter wings, revealing a total of 23 tagged males and five females, including one pair. Later, field observations of sex-typical behavior (e.g., males in song flight) confirmed the sexing in all cases. Following their release, individuals were tracked twice a day for five days a week using a three-element folding Yagi antenna (F150-3FB, AF Antronics Inc., USA) and a telemetry receiver (R 1000, 148-174 MHz, Communications Specialists Inc., USA). In 37% of the localizations, we directly observed the tagged bird. All other positions were determined by triangulation.
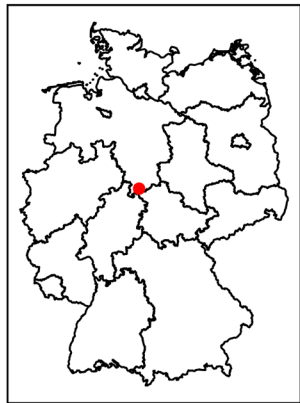
**Figure 2.1.** Location of the study area (red dot) within Germany (upper left corner) and its composition in 2018 and 2019. The same map design as in Püttmanns et al. (2022) was chosen to facilitate comparison. Other crops = asparagus, broad bean, clover, cup plant, potato, strawberry, summer barley, summer wheat, winter rye, and winter triticale; Unsuitable area = building, company site, highway, water body, and wood. Trapping locations are shown for sites where at least one Skylark was caught during April. Shapefiles of individual fields were provided by the *Servicezentrum Landentwicklung und Agrarförderung*, shapefiles of Germany and its federal states by DIVA-GIS (2021)

The mean time interval between two localizations of the same day was 3.6 h with a minimum of 1 h. Radio-tracking lasted until the tag fell off (21 cases), the signal was lost (five), or the bird was predated (two). On average, we tracked the Skylarks for 79 days, with 13 birds covering the whole Central European breeding season from mid-April to the end of July (Glutz von Blotzheim and Bauer 1985).

Besides this general approach, we caught an additional three Skylarks (two males, one female) in June 2018 to compensate for early tag losses. Two of these were partners of individuals that had recently lost their transmitter, so we could still make inferences on home range changes and the individual breeding success. Both were caught with mist nets erected above their nests following the explanations by Ottens et al. (2016). We tracked the additionally captured birds as described above until the loss of the transmitter (two) or predation (one).

*Nest monitoring*

To measure the breeding success of Skylarks, we had to document all successful breeding attempts of the radio-tagged individuals during a single breeding season. Thus, we systematically observed the behavioral events around the most recent localizations of every individual for several hours a week. The observations took place out of a hide like a car or a camouflaged tent. When we noticed clear indications of a nest (nest building, female returning to the nest for incubation, feeding of chicks), we searched for the nest in the focal area of breeding activity. Rope dragging to flush incubating females, a thermal binocular (Pulsar Accolade XQ 38), and the radio-tracking itself, in case of tagged females sitting on the nest, further assisted the nest search. We confirmed the tagged individual as a parent of the nest by checking the strength of the received radio signal when the bird approached the nest or by directly observing the attached transmitter. Unfortunately, four transmitters had fallen off, and one tag had stopped working shortly before we found a nest close to the last recent localizations of the respective individual. Therefore, we confirmed with binoculars if a bird that approached the nest had a non-working transmitter on the back or a ring on the leg, strongly suggesting a tracked bird as a parent. We also searched for Skylark nests of untagged individuals across the study area from April to August, as we also intended to analyze seasonal changes in nest success (i.e., the success of single nests) based on a larger dataset. Our efforts resulted in a total of 96 nests, 31 of which were breeding attempts of radio-tagged Skylarks. Nest contents of all nests were checked on average every third day to document the nest outcome. A distinction between predation and success (i.e., chicks had left the nest) was usually simple due to visual and/or acoustic cues (predation: messy nesting material, remains of eggs, injured dead chicks; success: warning or food carrying adults, cheeping chicks or their feces close to the empty nest). In case of no apparent signs, we counted empty nests whose

chicks were younger than the seventh day as predated (Donald et al. 2002a). The state of physical development was used for aging and determined according to Pätzold (1983). Nests with eggs were counted as abandoned if we had not observed any activity at the nest, and chicks had not hatched within two weeks after the nest was found because incubation lasts 13 days at most (Donald 2004). Besides nest outcome, we documented the clutch size, nesting habitat, and the distance to the next tramline and field edge for nests in winter cereals. To back-calculate the date of the first egg, we assumed a laying rate of one egg per day, ten days for incubation (excluding the day of laying the last egg and the day of hatching), and synchronous hatching (Donald 2004; Donald et al. 2002a). In the case of nests with eggs predated before hatching, we could not consider the chick age for our calculations. Then we chose the midpoint between the earliest and latest possible first-egg date, which depended on the number of days that a nest was known to be active.

### 2.3.3. Data analysis

*Individual breeding activity*

As a first step to analyze how Skylarks behave when winter cereal vegetation becomes denser, we checked if the tagged individuals ceased breeding activity clearly before the end of the breeding season. We defined the absence of breeding activity before July 1st as premature termination because May and June are usually the months when most breeding attempts occur in Central Europe (Donald 2004). Signs of breeding activity were (i) active nests of the respective individuals and (ii) the defense of a territory which in turn was inferred from direct observations of song flights or antagonistic behavior against neighboring Skylarks (Schläpfer 1988). Even though Skylarks or pairs that do not breed can defend a territory as well (Delius 1965; Wilson et al. 1997), these birds abandon their territories in the course of the breeding season (Delius 1965). Therefore, holding a territory indicates at least a high interest in breeding. We only considered the 15 male individuals that could be tracked until the end of July for our analysis.

Moreover, we investigated the onset of breeding attempts during the breeding season. We used a mixed-effect logistic regression model (GLMM) to test whether radio-tagged Skylarks were less likely to start a breeding attempt later in the breeding season. First, we calculated the 2.5 to 97.5 percentile range of first-egg dates based on all 96 nests we had found. Only nests of tagged individuals with first-egg dates within this range, i.e., between April 14th and July 10th, were included in the model. Then, we further subdivided the period into equal intervals of 22 days (phase 1: April 14th to May 5th; phase 2: May 6th to May 27th; phase 3: May 28th to June 18th; phase 4: June 19th to July 10th). A time interval of 22 days was chosen

because it represents the average duration of an entire breeding cycle, with 14 days of the egg-laying and incubation stage and eight days of the nestling stage (Praus et al. 2014). The phase was used as a categorical predictor for modeling, while the onset of a breeding attempt (yes/no) was taken as a binary dependent variable. Additionally, the year was included as a fixed effect and the individual as a random effect. The specific phase of a radio-tagged Skylark was only considered in the model when the respective individual (i) was not involved in an active breeding attempt for at least four days because this is the minimum time it takes a female to start a new attempt (Delius 1965), and (ii) showed breeding activity as defined above. For female Skylarks that do not defend a territory by song flights, we interpreted the observation of mate guarding by males as an additional sign of breeding activity (Donald 2004). Overall, data from 30 tagged individuals, including three pairs, were used for modeling. Skylarks were equally weighted in the analysis, with pairs defined as a single unit.

*Home range shifts*

Before examining the choice of nesting habitats during the breeding season, we wanted to identify those radio-tagged birds that had shifted their home ranges. First, we digitalized the localizations of all tracked individuals in *ArcGIS* (version 10.3.1; Esri Inc. 1999-2015; WGS 84/UTM zone 32N). The underlying map of the study area was based on field shapefiles provided by the *Servicezentrum Landentwicklung und Agrarförderung*. Then, we used *R* (version 4.0.3, R Core Team 2020) to perform a modified approach of Filla et al. (2017) for the detection of home range shifts. Instead of analyzing the size of minimum convex polygons (MCP95, Mohr 1947) over time, we examined centroid shifts of tracking data, which allowed for the combination of data from a tagged pair (see below).

The centroid of the first 30 localizations of a bird after the onset of breeding activity (see section *Individual breeding activity*) was defined as the centroid of the original home range. We chose 30 localizations to reach the minimum number of 20 to 30 for representing a Skylark home range (discussed in Jeromin 2002) without overestimating its size due to possible early home range shifts. Next, we added the two localizations of the subsequent tracking day, re-calculated the centroid of all 32 data points, and measured the distance between the new and the original centroid. This procedure was repeated until we reached the date with the last sign of breeding activity. Finally, plotting the centroid distances over time revealed the home range shifts as they became apparent with a continual increase in distance (S2.1). This pattern could only occur when a bird had settled in a new area and was almost exclusively located there with each additional tracking day, thus inducing a continuous centroid shift. Preliminary tests showed that discrepancies between our documented localizations and the "true" position (with exact coordinates of the transmitter position) had a 95th percentile of 39 m, so we considered

a steady increase above this distance as a true home range shift. Only 12 birds tagged during April and with breeding activity beyond July 1st were considered. Additionally, we combined tracking data from a female (W03), which had lost its transmitter in June, with the tracking data of its partner (M12), which had been radio-tagged immediately after the loss. Even though partners may have home ranges of different sizes (Jeromin 2002), we did not expect an influence on our analysis of centroids.

To deduce if detected home range shifts were related to the decreasing habitat suitability of winter cereals, we compared the composition of home ranges between birds with and without home range shifts. For tracked Skylarks with stable home ranges (i.e., without clear centroid shifts), we used all localizations within the individual period of breeding activity to calculate the composition of the MCP95s. Despite its limitations, the boundaries of MCPs are adequate to outline the available habitat for individuals (Horne et al. 2020; Horne et al. 2009). For birds that shifted their home range, we calculated the composition of an early and a late MCP95. To assign localizations, we examined the plots of centroid distances. Localizations of dates before the beginning of the continual increase (i.e., before the onset of the home range shift) were used to calculate the early MCP95. Localizations of dates above a centroid distance of 39 m were used to calculate the late MCP95. All other localizations were defined as transitional habitat use and not considered for any MCP95 calculations (S2.1).

*Nest habitats, nest success, and breeding success*

After we had grouped the radio-tagged Skylarks with sufficient tracking data into groups of birds that prematurely ceased nesting activity, shifted their home range later in the breeding season, or kept their home range, we analyzed the choice of nesting habitats over time. For individuals that nested in cereals, we checked if later breeding attempts were positioned closer to tramlines or field edges than early breeding attempts. Moreover, we compared the pattern of nesting habitats of radio-tagged Skylarks with the nesting site phenology of all nests we had found.

Similarly, we examined if successful nests of tagged individuals were more frequent in the early breeding season and checked our conclusions based on an analysis of the daily nest survival (DNS) that considered the dataset of all nests we had found. More precisely, we used the program *MARK* (White and Burnham 1999) via the *RMark* package (Laake 2013) to perform Mayfield logistic regressions (Hazler 2004). A binary categorization of nest outcome (1 = success; 0 = failure) was used as a response variable. We built two types of models: a *habitat model* and a *seasonal model*. In the habitat model, we included the nesting habitat as a nominal predictor variable to analyze if certain habitat types were more dangerous than

others. Sites where we had found nests were grouped into the habitat categories: *winter cereals*, *sugar beet*, *corn, other summer crops* (broad bean, strawberry, summer wheat), *mowed areas* (clover, grassy area of trial plots), and *set-aside* (fallow land, flower strips). We included only those nests in the category *winter cereals* that were positioned farther than 0.5 m to the next field edge or tramline. Nests in winter cereals closer than/at 0.5 m distance were sorted into the additional category *linear structures* according to Püttmanns et al. (2021). In the *seasonal model*, we used the day of the breeding season (day one: April 11th as our earliest calculated first-egg date) as a predictor to test if the DNS, and thus the overall nest success, decreased during the breeding season. The year and the radio-tagging (yes/no) were included in both models as fixed effects. Because we collected our data in two years of extremely dry weather (Deutscher Wetterdienst 2021a; Zscheischler and Fischer 2020) without detrimental rainfall that may have affected nest outcome (Donald et al. 2001a), we did not adjust for changing weather conditions. To calculate the chance for nests to survive a complete breeding cycle, we raised the DNS to the power of 22, representing the average duration of a full breeding cycle (see section *Individual breeding activity*). Four abandoned nests were not included in our analysis due to the difficulty of defining the date of abandonment (see section *Nest monitoring*). A further eight nests were not considered because the nest became inactive shortly before the find (six), or the nest outcome was influenced by human intervention (two).

For inferences on the breeding success, we calculated the average number of successful breeding attempts together with the average number of chicks that had left the nest per radio-tagged individual (or pair) and breeding season. Only the 17 birds tagged during April, including two pairs, with tracking data until the end of July, were considered for the calculations.

## 2.4. Results

### 2.4.1. Individual breeding activity

Only one of the 15 male Skylarks we tracked until the end of July showed no sign of breeding activity from the beginning of June onwards (M24). For 12 males (80%), we documented the last sign of breeding activity within the five days around July 15th (Figure 2.2).

Male M24 had an active nest until the end of May 2019. After nest predation around June 1st, it started to roam across the eastern half of the study site. From July on, localizations were again concentrated in a distinct area, at which a second bird regularly accompanied M24. A restart of breeding activity could not be observed (Figure 2.3).
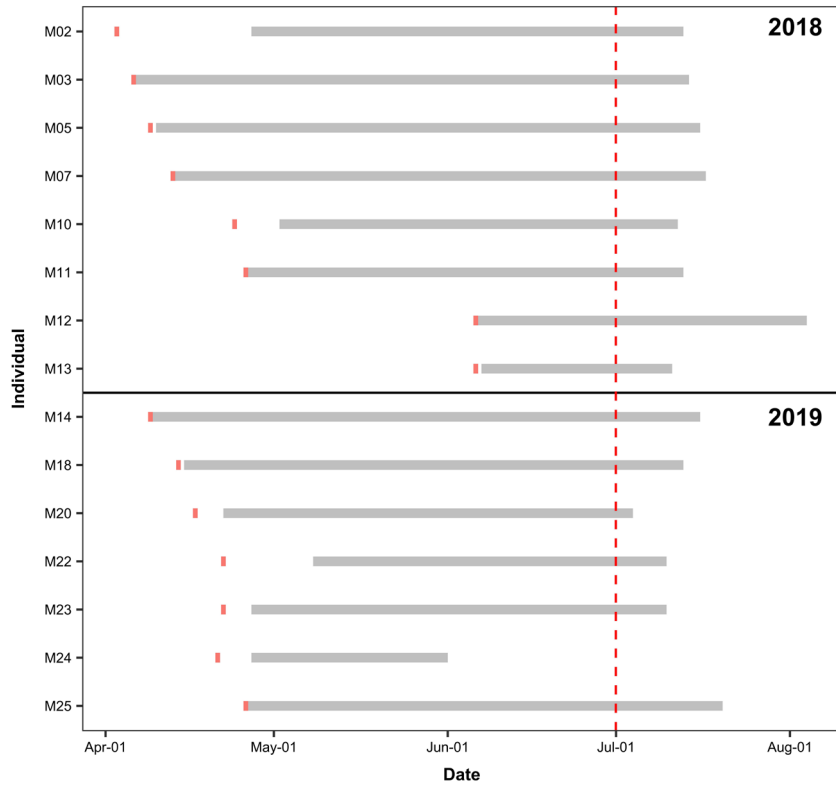
**Figure 2.2.** Duration of breeding activity of 15 radio-tagged male Skylarks (*Alauda arvensis*). Grey bars cover the period between the first and the last sign of breeding activity. Red markers indicate the start of radio-tracking. The absence of breeding activity before July 1st, indicated by the red dashed line, was defined as premature termination
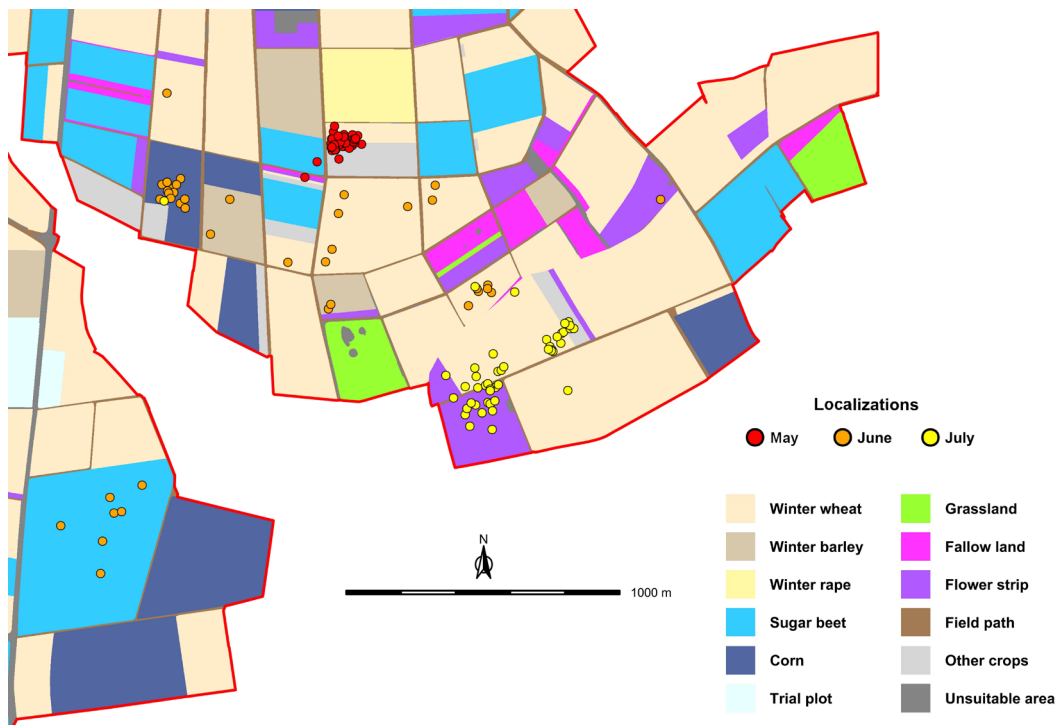


**Figure 2.3.** Localizations of Skylark (*Alauda arvensis*) male M24 within the study area (red line) from May to July 2019. Other crops = asparagus, broad bean, clover, cup plant, potato, strawberry, summer barley, summer wheat, winter rye, and winter triticale; Unsuitable area = building, company site, highway, water body, and wood

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Our GLMM revealed that the probability for radio-tagged Skylarks to start a breeding attempt during the second phase (May 6th to May 27th) did not differ significantly from the probability of starting a breeding attempt during the third phase (May 28th to June 18th) or fourth phase (June 19th to July 10th). Phase 1 (April 14th to May 5th) had a clear negative effect on the probability of starting a breeding attempt compared to the second phase without statistical significance. The year had no significant effect. (Table 2.1).

**Table 2.1.** Summary of the mixed-effect logistic regression model describing the effect of the ongoing breeding season on the probability for radio-tagged Skylarks (*Alauda arvensis*) to start a breeding attempt. Phase 2 (May 6th to May 27th) was set as the reference time because it covers the beginning of the main breeding season in Central Europe (Donald 2004). Phase 1 = April 14th to May 5th; Phase 3 = May 28th to June 18th; Phase 4: June 19th to July 10th. The estimates (Est.), standard errors (SE), lower 95% confidence intervals (Lower 95% CI), upper 95% confidence intervals (Upper 95% CI), z-values (*z*), and *p*-values (*p*) are given for each fixed effect. The standard deviation of the random effect (Bird ID) was 0.366. *n* = 77 phases of 30 radio-tagged Skylarks, including three pairs

| Fixed effect | Est. | SE | Lower 95% CI | Upper 95% CI | z | p |
|---|---|---|---|---|---|---|
| Intercept | -0.173 | 0.515 | -1.295 | 0.841 | -0.336 | 0.737 |
| Phase 1 | -0.990 | 0.632 | -2.311 | 0.220 | -1.566 | 0.117 |
| Phase 3 | 0.382 | 0.725 | -1.017 | 1.895 | 0.527 | 0.598 |
| Phase 4 | -0.583 | 0.756 | -2.148 | 0.921 | -0.771 | 0.441 |
| Year: 2019 | -0.147 | 0.523 | -1.276 | 0.958 | -0.280 | 0.779 |

2.4.2. Home range shifts

Nine of the 12 males that had been tagged during April and with tracking data beyond July 1st, as well as the Skylark pair with combined tracking data, stayed in the same home range throughout the breeding season. One of these nine individuals (M18) expanded its home range during early May. For three males, we documented clear home range shifts (S2.1). The shifting started between the end of May and the beginning of June. On average, the centroids between the early and the late home range were 230 m apart (Table 2.2).

**Table 2.2.** Overview of the three detected home range shifts by radio-tagged Skylarks (*Alauda arvensis*). The distance between the centroids of the early and the late MCP95 was defined as the distance between the home ranges

| Bird ID | Onset of home range shift | Distance between home ranges (m) |
|---|---|---|
| M03 | June 8th, 2018 | 184 |
| M05 | June 1st, 2018 | 305 |
| M10 | May 22nd, 2018 | 200 |
| **Mean** | **May 31st, 2018** | **230** |

All, except two of the analyzed home ranges, were composed of at least winter cereals and either a summer crop, trial plot, or flower strip (Figure 2.4). The average proportion of winter cereals in the early home ranges of the three shifting individuals was 27.20% (± 32.42 standard deviation). Skylarks that kept their home range during the breeding season had a higher winter cereal proportion of 48.31 ± 15.60%. The early home range of male M03 had a smaller proportion of winter cereals than its late home range (Figure 2.4).

### 2.4.3. Nest habitats

Of the 96 active nests we found during data collection in 2018 and 2019, 49 nests were initiated in winter cereals with eight nests close to linear structures, 18 in sugar beet, and 13 in set-aside. A further seven nests were built in less common summer crops (broad bean: four, summer wheat: two, strawberry: one), five on mowed areas, and four in corn.

Among radio-tagged Skylarks, winter cereals were clearly the dominating nest habitat during the early breeding season (Figure 2.5). Other nest habitats like sugar beet, corn, mowed areas, and set-aside outnumbered the use of winter cereals from the end of May onwards. Moreover, nests on linear structures in winter cereal fields first appeared during the second half of May (Figure 2.5).

When considering all the nests we had found, winter cereals and sugar beet, the two dominating crop types in the study area, were also the two most important nesting habitats with a clear time-shift in use (Figure 2.6). The use of winter cereals as nest habitat reached its peak during the first half of May and then strongly decreased, whereas the use of sugar beet reached its peak during the first half of June. Corn and linear structures were less frequently used and did not appear as nest habitat before the second half of May. Nests in other summer crops, mowed areas, and set-aside were found constantly throughout the breeding season, but likewise to a smaller extent (Figure 2.6).

**Figure 2.4.** Home range composition of radio-tagged Skylarks (*Alauda arvensis*). E = composition of the early MCP95 before the shift; L = composition of the late MCP95 after the shift. Unsuitable area = building, company site, highway, water body, and wood. Sample sizes (*n*) refer to the number of points used to calculate the MCP95
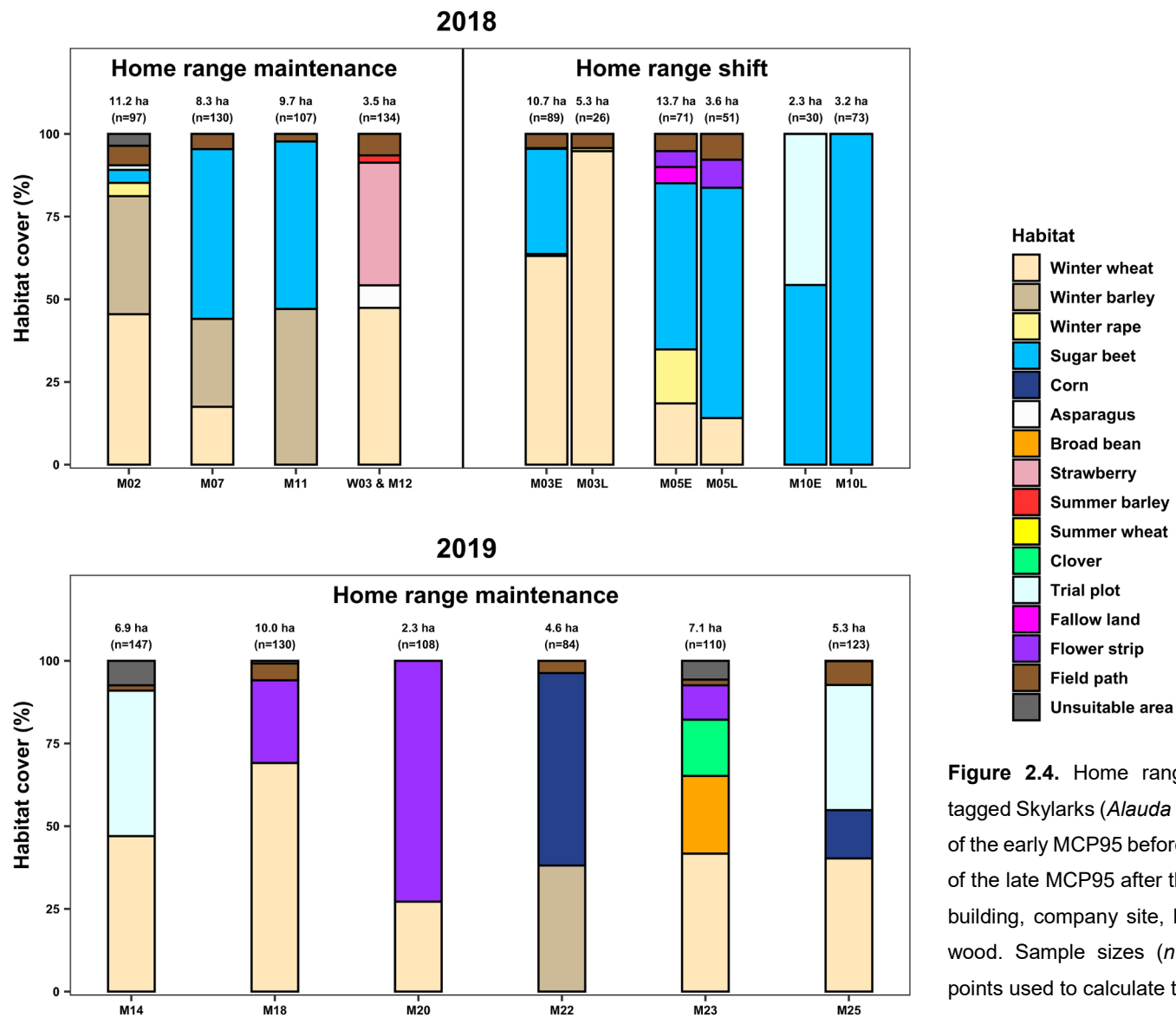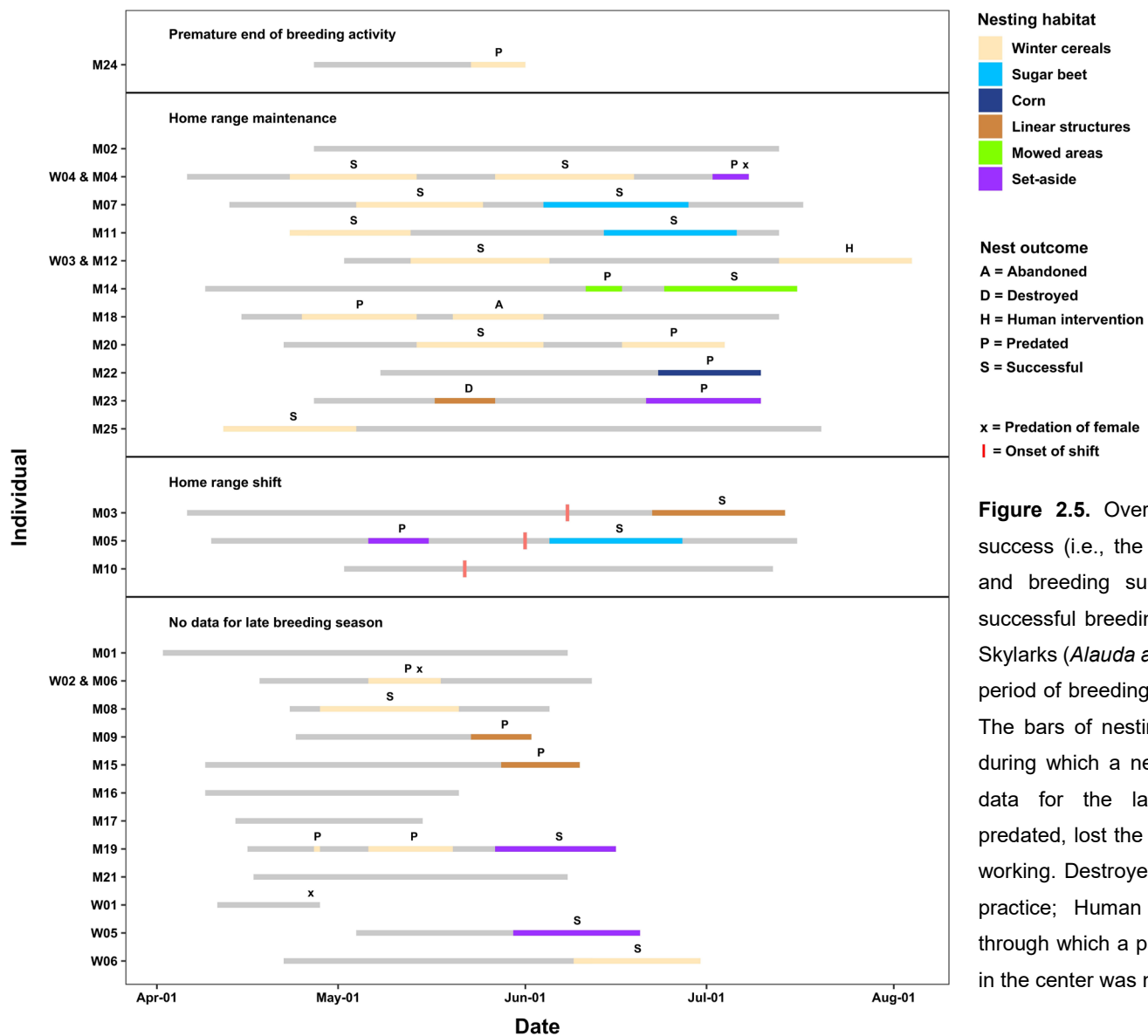
**Figure 2.5.** Overview of nest habitats, nest success (i.e., the survival of individual nests), and breeding success (i.e., the number of successful breeding attempts), of radio-tagged Skylarks (*Alauda arvensis*). Grey bars cover the period of breeding activity without active nests. The bars of nesting habitats cover the period during which a nest was active. Birds without data for the late breeding season were predated, lost the radio tag, or the tag stopped working. Destroyed = destroyed by agricultural practice; Human intervention = intervention through which a parcel of cereals with the nest in the center was not harvested
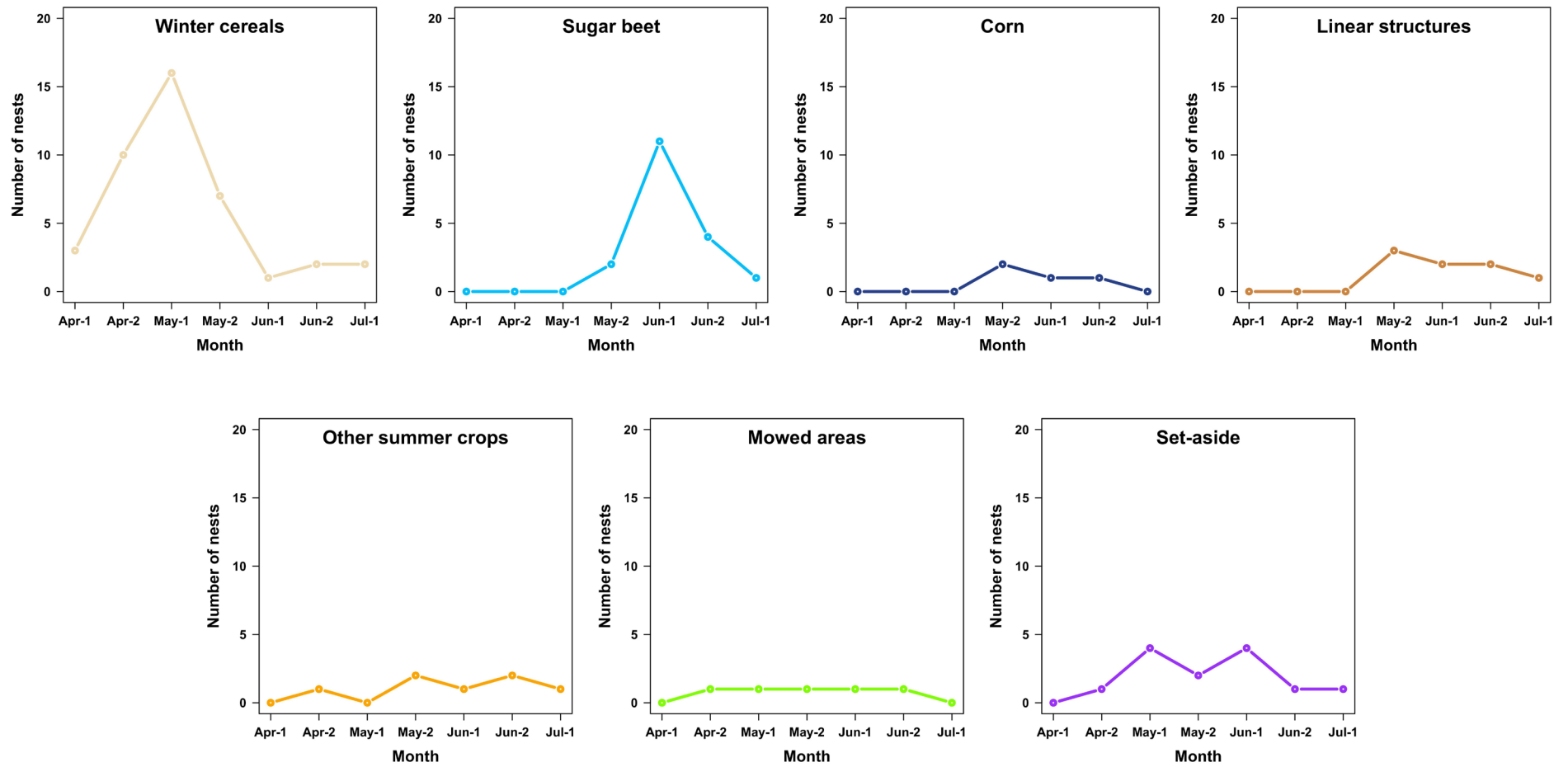
**Figure 2.6.** Nesting habitats of Skylarks (*Alauda arvensis*) for the duration of the breeding season. Month-1 = month 1st to 15th; Month-2 = month 16th to 30th/31st. Nests were assigned according to their first-egg dates. *n* = 96 (including the nests of radio-tagged individuals)

2.4.4. Nest success

Considering all 96 nests, 68 were successful, 20 were predated, four were abandoned, one was destroyed by agricultural practice, and one nest was unsuccessful because the chicks failed to hatch. In two cases, the nest outcome was influenced by human intervention through which a parcel of cereals with the nest in the center was not harvested.

Nest success did not decrease during the breeding season in the case of the radio-tagged Skylarks. Half of the nests with first-egg dates before June 1st were successful, and half of the nests were successful after this date (Figure 2.5).

Our Mayfield logistic regressions revealed no significant effect of the time of the breeding season on the DNS. However, the habitat of nesting sites affected nest success. The choice of corn and linear structures as nesting habitats reduced the DNS compared to winter cereals with statistical significance. Radio-tagging of Skylarks likewise had a negative effect. Other nesting habitats and the year had no statistically significant influence on the DNS (Table 2.3, Table 2.4). Overall, the average DNS of the habitat model was 0.9734 (standard error = 0.0080; 95% CI = 0.9524 to 0.9853) with a 55.29% (SE = 9.99; 95% CI = 35.54 to 73.51) chance for nest survival. According to the seasonal model, the average DNS was 0.9707 (SE = 0.0075; 95% CI = 0.9516 to 0.9823) with a 51.93% (SE = 8.89; 95% CI = 34.65 to 68.77) chance for nests to survive a complete breeding cycle.

**Table 2.3.** Summary of the Mayfield logistic regression describing the effect of different nesting habitats on daily nest survival of Skylark (*Alauda arvensis*) nests. Winter cereals were set as reference habitat. The estimates (Est.), standard errors (SE), lower 95% confidence intervals (Lower 95% CI), upper 95% confidence intervals (Upper 95% CI), and *p*-values (*p*) are given for each fixed effect. $n_{(nests)} = 84$

| Fixed effect | Est. | SE | Lower 95% CI | Upper 95% CI | *p* |
|---|---|---|---|---|---|
| Intercept | 4.672 | 0.667 | 3.366 | 5.979 | <0.001 |
| Sugar beet | 0.056 | 1.122 | -2.142 | 2.254 | 0.960 |
| Corn | -2.937 | 0.984 | -4.865 | -1.010 | 0.003 |
| Other summer crops | -0.846 | 1.161 | -3.121 | 1.429 | 0.466 |
| Mowed areas | -1.643 | 0.899 | -3.404 | 0.118 | 0.067 |
| Set-aside | -0.593 | 0.745 | -2.053 | 0.867 | 0.426 |
| Linear structures | -2.009 | 0.687 | -3.356 | -0.663 | 0.003 |
| Year: 2019 | -0.289 | 0.564 | -1.393 | 0.816 | 0.608 |
| Radio-tagging: yes | -1.205 | 0.556 | -2.294 | -0.116 | 0.030 |

**Table 2.4.** Summary of the Mayfield logistic regression describing the effect of the ongoing breeding season on daily nest survival of Skylark (*Alauda arvensis*) nests. The estimates (Est.), standard errors (SE), lower 95% confidence intervals (Lower 95% CI), upper 95% confidence intervals (Upper 95% CI), and *p*-values (*p*) are given for each fixed effect. $n_{(nests)}$ = 84

| Fixed effect | Est. | SE | Lower 95% CI | Upper 95% CI | *p* |
|---|---|---|---|---|---|
| Intercept | 4.362 | 0.647 | 3.095 | 5.630 | <0.001 |
| Day of breeding season | -0.006 | 0.011 | -0.028 | 0.017 | 0.601 |
| Year: 2019 | -0.522 | 0.508 | -1.517 | 0.473 | 0.304 |
| Radio-tagging: yes | -0.979 | 0.460 | -1.882 | -0.077 | 0.033 |

### 2.4.5. Breeding attempts and breeding success

On average, we documented 1.53 (± 0.83 standard deviation) breeding attempts per radio-tagged Skylark individual or pair and year. Most birds made two breeding attempts (seven tagged individuals; one tagged pair), followed by individuals with one breeding attempt (four) or none (two). For one pair, we documented a total of three breeding attempts (Figure 2.5).

Of all breeding attempts, 0.79 ± 0.80 were successful, producing an average of 2.38 ± 2.79 chicks that left the nest. In 2018, the number of successful breeding attempts was 2.7 times higher, and the number of chicks was 3.4 times higher compared to 2019 (Table 2.5).

**Table 2.5.** Average breeding success (± standard deviation) of radio-tagged Skylarks (*Alauda arvensis*) per breeding pair and year. Only tagged individuals/pairs that were tracked beyond July 1st were considered for calculations

| Year | *n* | No. breeding attempts | No. successful breeding attempts | No. of chicks per pair and year |
|---|---|---|---|---|
| 2018 | 8 | 1.50 ± 1.07 | 1.14 ± 0.90 | 3.83 ± 3.37 |
| 2019 | 7 | 1.57 ± 0.53 | 0.43 ± 0.53 | 1.14 ± 1.46 |
| 2018 & 2019 | 15 | 1.53 ± 0.83 | 0.79 ± 0.80 | 2.38 ± 2.79 |

**2.5. Discussion**

2.5.1. Individual breeding activity

Winter cereals pose an increasing challenge to the ground breeding Skylark due to their dense-growing sward structure (Donald and Morris 2005). One reaction to that problem might be a premature termination of breeding activity (Daunicht 1998; Donald 2004). However, this could not be observed in the present study. Almost all radio-tagged individuals showed breeding activity beyond the beginning of July. Moreover, our GLMM revealed that the probability of starting a breeding attempt during the main breeding season of Skylarks in Central Europe (i.e., during May and June; Donald 2004), did not decrease over time.

Only one male abandoned its territory shortly after its nest had been predated. Roaming across large parts of the study area ended with the companionship of a second bird. This behavior resembled Delius' (1965) description of wandering non-breeders searching for opportunities to replace territorial Skylarks. Former breeders that turn into floaters (see Penteriani et al. 2011) after nest- and probably mate loss are already known from other bird species (e.g., from the Middle Spotted Woodpecker *Dendrocoptes medius*, Robles and Ciudad 2020). Thus, we contend that territory abandonment was not motivated by cessation of breeding activity but by the search for new breeding opportunities after nest predation and potential predation of the mate.

2.5.2. Home range shifts

Seasonal shifts of Skylark territories away from winter cereals are well documented and typically associated with the decreasing suitability of the vegetation structure for breeding (Eggers et al. 2011; Jenny 1990b; Koleček et al. 2015; Schläpfer 1988). However, only three of 13 radio-tagged Skylarks shifted their home range and thus their territory. We do not think these shifts were triggered by sward development in our study area. Even though the onset of shifting coincided with when winter cereals exceeded the typical vegetation height for nests (Donald et al. 2002a; Püttmanns et al. 2021), home ranges of shifting individuals were not characterized by strikingly high winter cereal proportions. Moreover, in one case, the proportion of winter cereals was even higher after the shift. The respective individual chose a tramline for nesting in its new home range, which was an easily available micro-habitat already before the shift.

Instead, we conclude that home range shifts were triggered by the absence of breeding success, as we could not document a successful breeding attempt of any shifting individual during the early breeding season. Schläpfer (1988) already relates territorial stability in Skylarks to breeding success, and Hiron et al. (2012) suggest nest failure behind the seasonal

decline of Skylarks in winter cereals. Additionally, nest site shifts after breeding failure are reported for several other bird species and summarized as the *win–stay:lose–switch rule* (e.g., Chalfoun and Martin 2010; Kearns and Rodewald 2013). Nevertheless, our small sample size impedes safe conclusions except that home range shifts did not frequently occur in our study area.

As home ranges of Skylarks are typically larger than the defended territory (Donald 2004; Jeromin 2002), we might have missed more subtle changes of territory borders. However, it is generally difficult to define the clear boundaries of Skylark territories, so different studies have used various estimation methods, complicating comparison (Donald 2004). We believe that an analysis of home range centroids over time was suitable for detecting home range (and thus territory) shifts relevant to our research questions.

### 2.5.3. Nest habitats and nest success

Even though most radio-tagged Skylarks did not shift their home range over the course of the breeding season, our results support earlier studies that describe shifts in nesting sites when winter cereal vegetation becomes denser (Fischer et al. 2009; Ottens et al. 2013; Schläpfer 1988). Both the use of more openly structured crops like corn (Schläpfer 1988), as well as the switch to linear structures of winter cereal fields (Donald et al. 2002a; Donald and Vickery 2000), occurred among tagged individuals from the end of May onwards. Furthermore, our data confirm the negative influence of nesting in corn (Praus and Weidinger 2015) and closeness to linear structures (Donald et al. 2002a; Fischer et al. 2009; Püttmanns et al. 2021) on nest success. Nevertheless, no indications of a seasonal decrease in nest success were found, which can be explained by the dominant use of sugar beet and the minor role of corn and linear structures during the late breeding season. Jenny (1990b) found only a few nests in sugar beet, but these had the highest nest success compared to all other crops. According to our Mayfield logistic regressions, the choice of sugar beet for breeding had no negative effect on the DNS compared to winter cereals. Similarly, set-aside (including flower strips) was not a particularly high-risk nesting habitat. Several radio-tagged Skylarks used set-aside for later breeding attempts, and overall, it was consistently used as nesting habitat. Thus, our findings emphasize the value of uncropped land, which is a common measure to support farmland bird populations (Meichtry-Stier et al. 2018; PARTRIDGE 2021; Schmidt et al. 2022). The small proportion of grassland in our study area likely had positive effects on nest survival because it reduced the opportunity for Skylarks to breed in this high-risk habitat due to frequent silage-cutting (Kuiper et al. 2015; Ottens et al. 2016; Ottens et al. 2013). However, the lower DNS of mowed areas compared to winter cereals was not a result of nest destruction in our study area, but of predation events, as two of the five nests in that habitat were predated (one nest before

the mowing, one nest shortly after mowing). Altogether, the calculated nest success of ca. 52 to 55% is, to our knowledge, the highest value reported for breeding Skylarks from farmland thus far (compilation in Praus et al. 2014). We are confident that these results were not strongly biased by selective nest searching. We either searched for nests after behavioral observations (e.g., collecting of nesting material or food) that were mainly independent of the actual nesting site or focused on radio-tagged Skylarks and their neighboring territories.

The negative effect of the radio-tagging itself on the DNS might be traced back to the intensive observations of tagged individuals that could have led to an increased number of documented nesting attempts lost early after initiation. Additionally, our regular presence in proximity to/within home ranges due to tracking, observation, and nest search might have posed a disturbance that reduced energetic and time capacities for nest guarding. It is also possible that the tag increased the predation risk for incubating females, as three of six tagged females were predated: two of them during incubation. In both cases, feather remains were in the direct nest surroundings, but no remnants of adults around predated nests of untagged birds were found. These results highlight the importance of scientists considering the potential effects of transmitter devices on data interpretation (Barron et al. 2010).

## 2.5.4. Breeding attempts and breeding success

A temporal restriction of successful breeding attempts to the early breeding season is thought to be a major driver behind the dramatic decline of European Skylarks (Donald 2004; Wilson et al. 1997). In contrast, neither the breeding activity was terminated prematurely nor the nest success decreased over time, so we found no time constraints for successful reproduction. The average number of breeding attempts (1.5) was moderately lower compared to the estimates of other studies conducted in farmland (Daunicht 1998: 1.8; Jenny 1990b: 1.9 to 2.3; Ottens et al. 2013: 2.2). However, we likely missed several breeding attempts of radio-tagged Skylarks that were lost shortly after nest initiation. If Jenny's (1990b) calculation that a maximum of 20% of breeding attempts remains undetected also applies to our study area, then Skylarks made on average 1.8 breeding attempts. When comparing this result in conjunction with previous estimations to the average number of 2.7 breeding attempts in undisturbed coastal dunes (Delius 1965), it becomes clearer that the farmland environment likely reduces the number of breeding attempts in general (Donald 2004). Schläpfer (1988) suggests that the condition of females in agricultural landscapes does not allow a quick restart of breeding after a previous breeding attempt. However, this would not necessarily result in a population decline, as the number of successful breeding attempts, and not breeding attempts in general, is more relevant for population dynamics.

Apart from early nest losses, we are confident that we found almost all successful nests of radio-tagged Skylarks because of more conspicuous behavior during chick feeding. Therefore, we believe that the documented breeding success, with 0.8 successful nests producing 2.4 chicks that left the nest per pair and year, is reliable for the tagged individuals. The value is similar to the 2.7 chicks per pair and year reported by Schläpfer (1988) and higher than the 1.8 chicks per pair and year documented in Jenny (1990b). It is noteworthy that the average breeding success in our study area might have been higher if the radio-tagging itself reduced nest and female survival. Kuiper et al. (2015) estimate that three chicks per pair and year are necessary to keep the local population at their study site stable, which agrees with the preliminary results of population viability analyses based on our dataset (Lehmann 2019, Martens 2019, unpublished data). As the breeding success of tagged individuals strongly varied between 2018 and 2019, longer time series of data are required to make valid predictions about the population stability. These need to be complemented by studies like Ottens et al. (2016) and Helmecke et al. (2005), which analyze the survival rate of chicks between leaving the nest and fledging.

## 2.5.5. Conclusions

When combining all our results on radio-tagged Skylarks and nests we had monitored, it is possible to outline a breeding season for most breeding pairs in our study area:

Most home ranges were comprised of winter cereals and at least one further habitat type. After a first breeding attempt in winter cereals, the pairs initiated a second breeding attempt in a more accessible habitat, most likely sugar beet or (to a smaller extent) set-aside. Nesting in corn or on linear structures, which were associated with a high nest predation risk, played a minor role. The switch of nesting habitats took place within the original home ranges and not as a result of home range shifts. Both breeding attempts had a relatively high chance of success, so chicks of one attempt left the nest successfully.

Even though frequent variations of this outline hamper firm conclusions on the actual population trend, our data strongly suggests the absence of temporal restrictions for successful reproduction. This is most likely a result of the advantageous composition of our study area. The two prevailing crops appeared to be suitable nesting habitats for early (winter cereals) and late (sugar beet) breeding attempts. Uncropped land and less frequent summer crops like broad bean further enriched the habitat heterogeneity, which is also reflected in the diverse composition of most Skylark home ranges. To us, this easy access to safe nesting sites is the prerequisite to constantly high nest success. At the same time, intensively managed grassland and thus the risk for nests of being destroyed by agricultural practice is scarce.

Taken together, our study demonstrates the often-discussed advantages of heterogeneous farmland for Skylarks and birds in general (e.g., Eraud and Boutin 2002; Flade et al. 2003; Miguet et al. 2013; Püttmanns et al. 2022; Schläpfer 1988; Tscharntke et al. 2021) by directly analyzing individual fates throughout the breeding season. As Hiron et al. (2012) have suspected, winter cereals are not a problem *per se,* but they can contribute to a successful breeding season when they are embedded in a diversified agricultural landscape. Nevertheless, follow-up studies are required to prove the long-term viability of the study population directly.

## 2.6. Acknowledgements

## 2.7. Supplementary material



**Supplementary material S2.1.** Distances between the centroid of the original home range (C1) of radio-tagged Skylarks (*Alauda arvensis*) and the centroids based on stepwise addition of daily localizations over time (C2). Individuals were grouped according to their home range maintenance (a) or shift (b) during the breeding season. Home range shifts were defined as a steady increase in distance exceeding the dashed line at 39 m. In the case of home range shifts, the first 30 localizations used to calculate C1 were always considered for the calculations of the early MCP95. The sharp increase in distance by M18 that levels off afterward indicates that the bird expanded the home range early in the breeding season but still used the original area

# Chapter 3

## Seasonal dynamics of foraging habitats and food availability for breeding Eurasian Skylarks

## 3.1. Abstract

Reduced food availability during chick raising is a major driver of farmland bird declines. For the Eurasian Skylark (*Alauda arvensis*), food availability is determined by various factors (i.e., arthropod abundance/diversity, accessibility of the vegetation, distance to foraging sites). In modern farmland, it is supposed to decrease over the breeding season due to less penetrable vegetation. We explored foraging habitat selection by chick-raising Skylarks with a focus on the seasonal dynamics of habitat use and food availability. We investigated (i) habitat selection concerning prey biomass/diversity, vegetation cover, and distance to foraging sites, (ii) the overall and seasonal habitat use, and (iii) seasonal developments of foraging parameters (e.g., the feeding frequency) as indicators of food availability. We collected data on foraging habitats and foraging parameters of chick-raising Skylark pairs at 51 nests from a Central European population in 2018 and 2019. Prey biomass/diversity and vegetation cover were measured for all habitats around 42 of these nests. As revealed by multivariate and compositional analyses, Skylarks mainly selected foraging habitats based on the proximity to nests. The most frequent habitats within home ranges could not be ranked according to an overall importance for foraging and their use partially changed over time. The feeding frequency increased throughout the breeding season, while other foraging parameters did not show significant changes. In contrast to our expectations, our data indicated therefore an increase, not a decrease in food availability in the late breeding season. This also implies that the way in which Skylarks used habitats was constantly suitable to raise offspring. We interpret this to be a consequence of the heterogeneous farmland composition of the study area that enabled Skylarks to establish a diverse home range and to benefit from the synergetic effects of neighboring habitat types. Thus, our findings provide support for the high importance of crop diversity in Skylark conservation.

## 3.2. Introduction

Over the last 50 years, agricultural intensification in Europe has negatively affected the living conditions of numerous farmland-associated birds, leading to severe population declines (Donald et al. 2006; Emmerson et al. 2016; Krebs et al. 1999). A primary driver behind these declines is reduced food availability, together with a loss of suitable nesting habitats (Butler et al. 2007). Food availability, and therefore the ability to feed chicks, does not only depend on the sheer abundance of food but also on the accessibility and the distance to food sources, as in the case of the Eurasian Skylark (*Alauda arvensis*) (Jeromin 2002; Wilson 2001). Even though this species is still widespread across European agricultural land, its population in Europe has decreased by 54% since 1980 (Hagist and Zellweger-Fischer 2020; PECBMS 2021).

Like many other songbirds (O'Connor 1984), Skylarks mainly feed arthropods to their chicks (Poulsen et al. 1998; Weibel 1999), and a diverse invertebrate diet is beneficial for chick development (Donald et al. 2001c). Plant-based alternatives, even though regular components of the diet of Skylark nestlings (Ottens et al. 2014), are believed to be inferior food due to their poorer nutritional value (Douglas et al. 2012; Ricklefs 1983). However, modern pesticides reduce the number and diversity of prey items either directly by killing insect pests together with collateral species or indirectly by killing undesirable weeds, which are a food resource of many arthropods (Boatman et al. 2004; Hallmann et al. 2014; Odderskær et al. 1997a). Furthermore, arthropod-rich habitats, like fallow land, have strongly decreased in the European Union (EU) over the last decades (Tarjuelo et al. 2020). Besides the reduction of arthropod abundance and diversity, food accessibility can be lowered by unfavorable vegetation structure. Skylarks are passerines that collect food directly from the ground or near-ground plant parts and thus depend on open vegetation that does not hamper mobility (Jenny 1990a; Pätzold 1983). However, many crops in modern agriculture become too dense during the breeding season of Skylarks, resulting in a decreasing amount of area that is available for foraging (Donald 2004; Jenny 1990a; Weibel 1998). Especially Skylarks that settle in winter cereals are thought to suffer increasing food shortage later in the breeding season due to the growing sward structure (Donald and Morris 2005). Therefore, conservation measures that prolong the access to food within winter cereals by implementing undrilled patches result in higher breeding productivity and better nestling condition (Morris et al. 2004). At the same time when the accessibility to foraging habitats decreases, the area of available breeding ground is highly reduced because Skylarks also build their nests on the ground in sparse vegetation (Donald 2004; Jenny 1990b). Thus, it is still unclear whether the lack of suitable nesting sites or the lack of suitable foraging sites explains the seasonal fall in territory density in winter cereals (Donald 2004). Reduced food availability in farmland is further caused by landscape homogenization with an increase in field size and a decrease in crop diversity (Benton et al.

2003). These developments greatly limit the choice of foraging habitats because Skylarks rarely fly more than 300 m between their nest and a foraging site (Jeromin 2002; Wilson 2001).

Consequently, analyses of habitat selection by chick-raising Skylarks based on food availability should consider prey abundance and diversity, accessibility of vegetation, and the distance to a foraging site. Moreover, temporal effects on food availability should be included because arthropod abundance and vegetation structure per habitat type might change throughout the breeding season (Donald and Morris 2005; Jenny 1990a; Kuiper et al. 2013; Morris et al. 2004). Several researchers previously investigated foraging habitats of chick-raising Skylarks and considered some of the influential parameters in various combinations (Jenny 1990a; Jeromin 2002; Kuiper et al. 2013; Murray 2004; Weibel 1998; Wilson 2001). To our knowledge, however, studies that take into account all the mentioned determinants of food availability and measure their relative importance for habitat selection are still missing. Additionally, changes in habitat use over time have rarely been considered on a continuous scale, even though time-scale dependencies are crucial for a better understanding of habitat selection (Miguet et al. 2013). Based on all the above, our study aimed to analyze the selection of foraging habitats by Skylarks in our Central European study area with a special focus on temporal dynamics. Furthermore, we aimed to find indications of a lowered food availability later in the breeding season due to grown vegetation that limited the access to food.

We divided our study into three parts. First, we analyzed the habitat selection of Skylarks with respect to arthropod abundance, insect diversity, vegetation structure, and distance to foraging sites and measured their relative importance for habitat choice. Second, we investigated both the overall and the seasonal use of different habitat types and interpreted it against the background of detected preferences from the step before. Finally, we checked if the ability of Skylarks to feed chicks decreased over time as a consequence of denser vegetation restricting the access to prey. We thus analyzed three foraging parameters as indicators of food availability. In a scenario with a decreasing amount of area that is available for foraging, we expected (i) the feeding frequency to decrease because feeding Skylarks would need more time to find sufficient food. Furthermore, we expected both (ii) the distance flown to foraging sites and (iii) the actual area searched for food to increase throughout the breeding season to compensate for the overall loss of suitable foraging habitats.

### 3.3. Methods

3.3.1. Study area

Fieldwork was conducted in the farmland south of the city Göttingen in Lower Saxony, Germany (N51° 29.650, E9° 56.635). Located in the transitional zone from maritime to

continental climate of temperate latitudes, the area around Göttingen is relatively dry (mean annual temperature: 8.7°C, mean annual total precipitation: 644.9 mm) compared to other regions in Germany (Vohl 2020). In the approx. 8.2 km² study site, the proportion of cropland (82.9%) outweighed the proportion of grassland (2.6%). Organic farming was practiced in 3.7% of the area. The average arable field size was 5.1 ha. Among the cultivated crops in 2018 and 2019, winter wheat (33.8% of the whole study site averaged over both years), sugar beet (19.9%), corn (9.0%), winter barley (7.8%), and winter rape (7.0%) were dominating. Other crops such as asparagus, broad bean, clover, strawberry, and summer wheat covered no more than 1.3% in each case. Moreover, the Faculty of Agricultural Sciences from the University of Göttingen cultivated 2.3% with trial plots of various crops. Sown flower strips (3.0%) together with fallow land (1.4%) were predominantly present in the eastern part. There, our study area partly intersected with a demonstration site of the Interreg North Sea Region project PARTRIDGE, which aims to increase biodiversity by establishing flower strips (PARTRIDGE 2021). Field paths summed up to a network with a total length of ca. 32.8 km. Overall, the composition of the study area was heterogeneous without vast areas of monocultures (Figure 3.1). The estimated density of Skylarks at the study area was three to four territories per 10 ha (based on Langer 2017 and Meineke 2018, unpublished data).

## 3.3.2. Data collection

*Bird data*

From April to August in 2018 and 2019, we searched for Skylark nests in our study area by observing Skylarks that clearly showed breeding behavior. The observation of adults carrying nesting material or prey items and of females returning to their nest for incubation were the main indicators to find the nests. In about one-quarter of findings, rope dragging to flush incubating females supported the search. Moreover, the nest localization itself was facilitated by the use of a thermal binocular (Pulsar Accolade XQ38) in individual cases.

After a nest was found, nest content was checked on average every third day. In the case of nests with chicks, we used the state of physical development for aging as described in Pätzold (1983). Nest outcome was usually obvious, that is, predation could be confirmed due to injured/dead chicks or messy nesting material, while success could be confirmed by observing cheeping chicks in the nest surroundings or adults uttering warning calls when the nest was empty. Nests without a clear sign of outcome were interpreted as predated if chicks had not reached the age of the seventh day because Donald et al. (2002a) found this to be the earliest age at which a nest was left successfully.

As a commonly used method for analyzing foraging habitats of chick-raising Skylarks and other farmland birds (e.g., Douglas et al. 2009; Fischer et al. 2009; Kuiper et al. 2013), we directly observed foraging flights of feeding adults. When a Skylark returned to its nest with prey, the subsequent foraging flight was tracked with binoculars (8–10x magnification) until the bird landed. We documented the landing position on a map together with the habitat at that point and then directly focused observations on the nest again, waiting for the next foraging flight to start. A bamboo stick placed at a few meters distance to the nest helped the observer to visually locate it. In general, we carried out one observation session per nest with chicks per day. Each single observation session lasted until ten foraging flights were recorded, up to a maximum of 90 min. The first observation session of a nest started as soon as possible, that is, not later than the day after a nest with chicks was found or after the regular nest control revealed that the chicks had already hatched. The series of observation sessions per nest ended when we found the nest to be predated or left successfully during a nest control or when the observer noticed deviant behavior. This included no activity at the nest indicating predation or feeding adults not landing at the nest anymore, but in the nest surroundings, indicating success. The following nest control then confirmed the observer's impression. Observations took place from an average distance of approx. 150 m to the nest in a hide like a car or camouflaged tent with a full view of all potential foraging habitats. We conducted our observation sessions at varying times during daylight and under all weather conditions with good sight, only avoiding storm, heavy rainfall, and the hottest hours of a day with low feeding activity. Temperature and wind speed during the observations were taken as weather indicators. Data on these two variables were retrospectively downloaded from the Climate Data Center of the *Deutscher Wetterdienst* (Deutscher Wetterdienst 2021b). We used the data from a weather station located within our study area (national station code: 1691). Data gaps (June 9th to June 17th in 2018 and on May 2nd in 2019) were filled with data from a weather station in ca. 28 km distance (national station code: 2925), as daily temperature and wind speed were highly correlated between the stations in both years (Pearson's correlation coefficient for temperature = 0.993 and for wind speed = 0.852).

*Arthropod data*

In order to analyze the foraging habitats of Skylarks against the background of food availability, we needed detailed information on arthropod biomass and prey diversity for all different habitats within a home range. Following the explanations by Kuiper et al. (2013) and Morris et al. (2007), vacuum sampling was chosen as the most suitable sampling method to gather data on relevant prey for Skylarks. We sampled each agricultural field (crop cultivation, grassland) and each non-cropped field (flower strip, fallow land) that was at least partly inside a 300-m

radius around nests with chicks, as almost all foraging flights of Skylarks occur within that radius (Jeromin 2002; Wilson 2001). Because we assumed a homogenous distribution of arthropods per habitat unit, all individual fields were sampled only once. Additionally, we took one sample per 300-m radius from the field path vegetation and, if occurring, from extensive areas of stunted growth within a field. One sample consisted of vacuuming the vegetation at no more than knee height down to the ground twenty times along a transect with a 1-m distance to the preceding touchdown of the suction tube. As arthropod abundance and diversity can differ between the field edge and the field center (Batáry et al. 2012), we kept at least a 5-m distance from the habitat edge whenever possible. The samples were taken with an *ecoVac* (EcoTech Umwelt-Meßsysteme, ⌀ 14 cm suction tube in 2018) and modified leaf vacuums (Stihl, ⌀ 11 cm in 2018; Stihl, ⌀ 14.5 cm in 2019) between 12:00 and 18:00 under dry weather conditions. Sampling took place, on average, two days after the chicks had left the nest or the nest had been predated. We froze the arthropod samples at −20° C for several days and then cleaned them from soil and debris. During the following counting of arthropods per sample, we identified each insect specimen to order level by the usage of a binocular microscope. Next, the samples were dried in drying cabinets at 105°C for 65 h and subsequently weighted with a precision balance (Sartorius).

Besides mapping prey within the area around Skylark nests, we aimed to systematically monitor the development of arthropod biomass and insect diversity for the most important habitat types of Skylark home ranges. The first preliminary results in 2018 had indicated winter wheat, sugar beet, corn, annual flower strips, and field paths as the main habitats. Thus, we took arthropod samples as described above in four fields of each main crop per half of a month (on the 7th and 23rd) between May and July in 2019. Similarly, we sampled annual flower strips and field path vegetation at four different sites. In general, sample sites were chosen at the greatest possible distance to each other to ensure spatial independence. Data on arthropod number, taxonomic order in the case of insects, and dry weight were collected with the same methodology that we used for habitats around nests.

*Vegetation data*

We measured vegetation openness for each habitat within the 300-m radius around nests that we had vacuum-sampled. As a proxy for openness, we used fractional vegetation cover (hereafter abbreviated as FVC or vegetation cover), which represents the proportion of ground covered by the vertical projection of foliage (Chianucci et al. 2018). The choice of this proxy was based on the assumption that Skylarks do not only depend on open vegetation to walk on the ground but also to land in a specific habitat in the first place so that we needed an indicator that considered the vertical vegetation structure as a whole. We took photos from each field

with a straight-down perspective at chest height, similar to the photos that are required to measure FVC with automated tools (Patrignani and Ochsner 2015). However, we estimated the vegetation cover visually. The use of automated tools was deemed unsuitable for our study because they focus on green vegetation while ignoring, for instance, brownish cereals later in the season. Visual estimations of FVC were independently conducted by three people using intervals of 10% in the range between 0% and 100%, thus following the recommendations by Hahn and Scheuring (2003) for cover estimation. The mean value was then calculated for subsequent analyses. FVC for habitats with a vegetation height up to 5 cm was set to zero because we did not expect a hampering effect of vegetation very close to the ground level. Similarly, we set the vegetation cover of field paths to zero, as Skylarks usually landed on their open ground and then walked to the wayside vegetation to forage.

We also documented the changes in the FVC at all sites chosen to systematically monitor arthropods for the most important habitat types. We measured the vegetation cover at the same time when arthropod samples were taken, that is, in each half of a month (on the 7th and 23rd) between May and July 2019.

### 3.3.3. Data analysis

*Dataset*

We found 96 active nests (i.e., nests with at least one laid egg) during the breeding seasons of 2018 and 2019. Of these, 22 nests became inactive (predation: 16, abandonment: four, destruction by agricultural practices: one, failed to hatch: one) before a record of foraging flights could start, 15 nests had a nest surrounding that was not observable, for example, due to hills, and eight nests had chicks that were close to leaving or already sitting outside the nest at find. For the remaining 51 nests (Figure 3.1), we collected 2,243 landing points of foraging flights. However, because the exact landing point was ambiguous in 2.4% of the cases, we only used the 2,190 safe landing points for further analyses. We collected arthropod and vegetation data within a 300-m nest radius for 42 of the 51 nests with documented foraging flights.

All recorded nest locations and safe landing points were digitized in *ArcGIS* (version 10.3.1; Esri Inc. 1999–2015; WGS 84/UTM zone 32N). For the digital map of the study area in 2018 and 2019, we used shapefiles of the agricultural fields provided by the *Servicezentrum Landentwicklung und Agrarförderung* and modified them manually (e.g., by adding field paths). All subsequent analyses were conducted in *R* (version 4.0.3, R Core Team 2020).
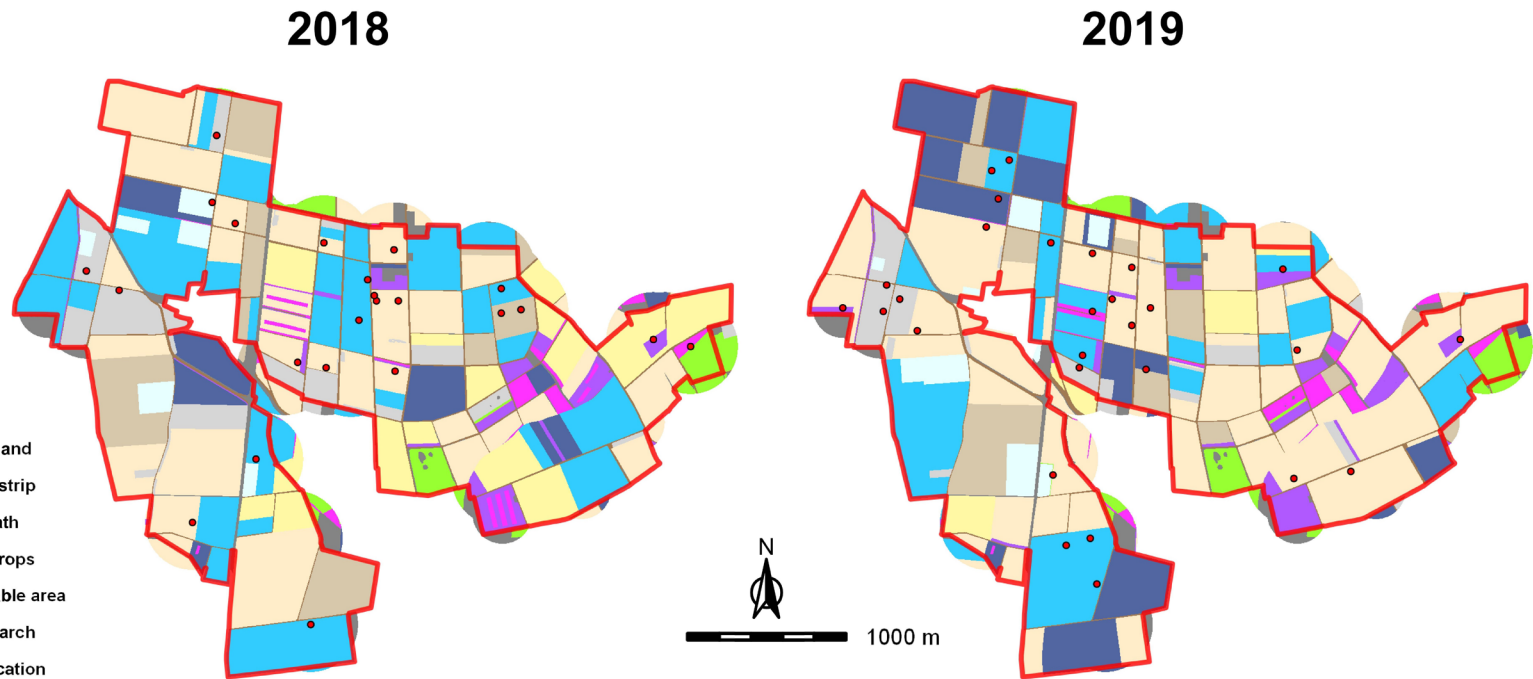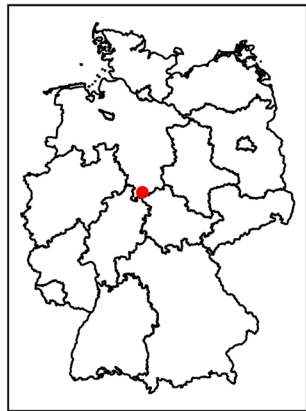
**Figure 3.1.** Location of the study area (red dot) within Germany (upper left corner) and its composition in 2018 and 2019. Other crops = asparagus, broad bean, clover, cup plant, potato, strawberry, summer barley, summer wheat, winter rye, and winter triticale; Unsuitable area = building, company site, highway, water body, and wood. Only the area within the red line was searched for Skylark nests; arthropod and vegetation data were also collected outside the red line. Nest locations represent those nests with documented foraging flights. Shapefiles of individual fields were provided by the *Servicezentrum Landentwicklung und Agrarförderung*, shapefiles of Germany and its federal states by (DIVA-GIS 2021)

*Habitat selection: Influence of prey biomass and diversity, vegetation structure, and foraging distance*

To understand how Skylarks select foraging sites, we combined our collected data on foraging flights, arthropods, and vegetation structure in the surroundings of Skylark nests. As a first step, we had to define a home range accessible for chick-raising Skylarks. Following Kuiper et al. (2013), we calculated the 95th percentile of all recorded distances between a nest and the corresponding landing points of foraging flights in both study years. Distances were determined with equal weighting to nests. The circular area around a nest with the resulting length of 188 m as radius was then defined as the home range. For the 42 nests of which we had mapped the surroundings in detail, we created digital shapefiles of the home ranges and intersected all habitats within this radius with the associated data on vegetation structure, arthropod biomass, and arthropod abundance. As a measure of insect diversity, we calculated the Shannon Index per individual habitat. In cases where part of the data was missing (e.g., because cows on a pasture prevented arthropod sampling), we used the mean values of the same habitat type within the home range if present. Otherwise, we kept the data gap.

Our analysis of habitat selection was conducted following the approach and explanations of Filla et al. (2021), that is, for each digital home range, we drew 240 random pseudo-absence points to reach the recommended number of 10,000 points for good model performance (Barbet-Massin et al. 2012). Landing points of foraging flights within the home range (1,779) and all pseudo-absence points (10,080) were intersected with the corresponding habitat characteristics. Next, we analyzed the influence of vegetation cover, arthropod biomass, insect diversity, and distance between the nest and the point location on habitat selection with a generalized additive mixed model (GAMM). As pointed out by Guisan et al. (2002), general additive models are well suited to study ecological data due to their capacity for modeling nonlinear relationships. The point type (documented landing point = success, pseudo-absence point = failure) was used as a binary response, while the individual nest was included as a random effect. Between predictors, Pearson's correlation coefficient was smaller than |0.3| in all cases, so that we did not expect multicollinearity to severely affect the explanatory power (Dormann et al. 2013). We weighted nests equally, and pseudo-absence points obtained the same total weight as documented landing points (Barbet-Massin et al. 2012). The relative importance of all model variables for habitat selection was then analyzed with the random permutation procedure by Thuiller et al. (2009), as described in Filla et al. (2021).

*Habitat selection: Overall and seasonal use of habitats*

Before we investigated the seasonal habitat use of chick-raising Skylarks, we first examined whether certain habitat types are generally more important for foraging than others during a whole breeding season. Therefore, we analyzed how the overall use of habitats differed from their availability within home ranges (third-order habitat selection, Johnson 1980). Again, we defined the circular area around a nest with a radius of 188 m as the home range. Then, we calculated the proportion of habitat types within this area for each of the 51 nests with documented foraging flights. We used the weighted surface area instead of the mere proportion to adjust for distance-dependent habitat selection following Kuiper et al. (2013). Next, we calculated the relative use of habitats per nest by subdividing the number of documented foraging flights to the respective habitat by the total number of observed landing points. Only landing points within the respective home range were included. A compositional analysis, according to Aebischer et al. (1993), was conducted to test for significant deviation from random habitat use and to rank habitats according to their relative importance as foraging habitat. *p*-values were obtained by randomization (Manly and Navarro Alberto 2020) with 1,000 iterations. Specific categories were created for habitats present in at least one-third of all home ranges, that is, *winter wheat*, *sugar beet*, *corn*, *annual flower strips*, and *field paths*. All other habitats were jointly analyzed under the category *other*.

To analyze the habitat use in relation to the time of the breeding season, we used mixed-effect logistic regression models (GLMMs). For each previously analyzed habitat category except *other*, landing points within the home ranges were grouped into two categories: The habitat of the landing point equals the habitat in focus (i.e., success), or the habitat of the landing point does not equal the habitat in focus (i.e., failure). This binary categorization was then taken as the dependent variable, while the day of observation (day one: April 25th as our earliest documented hatching date) was used as a predictor and the individual nest as a random effect. Additionally, we adjusted for the year and for the varying availability by including the weighted surface area. Correlation coefficients of Pearson's correlations between predictors were smaller than |0.5|, indicating no serious distortion of model estimation through multicollinearity (Dormann et al. 2013). Nests with no occurrence of the focal habitat within their home range were excluded from the analysis, while the remaining nests (winter wheat: 45, sugar beet: 39, corn: 19, annual flower strip: 30, field path: 49) were equally weighted per day of observation.

We also intended to explain changes in habitat use based on the preferences in prey biomass and diversity as well as in the vegetation structure that we had analyzed before. That is, we visualized the temporal pattern of arthropod biomass, insect diversity, and vegetation cover per focal habitat using the data from our systematic monitoring.

*Foraging parameters*

Based on the 51 nests with documented foraging flights, we analyzed the development of three foraging parameters throughout the breeding season as indicators of food availability: the feeding frequency, the distance flown to a foraging site, and the actual area that Skylarks searched for food.

To calculate the feeding frequency, we divided the number of recorded landing points of foraging flights per observation session by the minutes of observation. Consequently, our feeding frequency represented only a minimum value because it did not consider nest visits by feeding Skylarks with subsequent behavior other than foraging (e.g., males that started a song flight after feeding). Only observation sessions were included that ended before sunset, as feeding activity ceased during dawn (personal observation). This resulted in the full exclusion of one nest. Feeding frequencies of another nest were not considered because the number of fed offspring was unclear due to the unknown fate of several chicks that had disappeared (partial brood loss vs. chicks left the nest asynchronously). For the remaining 49 nests, we calculated both the feeding frequency per hour as well as the feeding frequency per hour and chick. Our analysis of the distance flown to foraging sites was based on the distances that we had calculated between the 51 nests and the corresponding landing points of foraging flights.

For the actual area used for foraging, we defined the minimum convex polygon for 95% (MCP95) of all documented foraging flights per nest. We only considered those nests with at least 20 data points (46 nests) in our analysis. From then on, we did not see an increase in the used area with the number of landing points after visual inspection of this relationship. The feeding frequency per hour, the feeding frequency per hour and chick, and the distance flown were modeled with linear mixed-effect models (LMMs). As predictors, we included the day of observation, the chick age, the starting time of the observation, both the temperature as well as the wind speed during the observation, and the year in all three models. Because 12 of the 51 nests with documented foraging flights had one radio-tagged parent (with a tag weighing ca. 3% of the body weight) due to a parallel running telemetry study, we additionally included the radio-tagging (yes/no) as a predictor. Two of these nests were subsequent breeding attempts of the same bird. All nests were equally weighted, and the individual nest was included as a random effect.

For the analysis of the MCP95 size, we used a linear regression model (LM) with the day of hatching, the average temperature and wind speed during the observations, the radio-tagging, and the year as predictors. To account for the varying daytime when the observation sessions took place, we found that averaging the starting time of the observations would be biologically meaningless. Instead, we grouped data points that were part of the MCP95 into *early* (collected during an observation session that started before noon, 12:00) and *late* observations (collected

during an observation session that started after noon). Then, we calculated the proportion of early observations per MCP95 as a further predictor. After each modeling, we used residual plots to check for homoscedasticity and both histograms and Q-Q plots to check for normality of residuals. Pearson's correlations had coefficients smaller than |0.6| in all models so that we did not expect a serious bias of model estimation due to multicollinearity (Dormann et al. 2013).

## 3.4. Results

### 3.4.1. Habitat selection

*Influence of prey biomass and diversity, vegetation structure, and foraging distance*

Our GAMM model revealed a statistically significant effect of the following predictors: vegetation cover, insect diversity, and distance on the habitat selection of chick-raising Skylarks. Only the effect of arthropod biomass was statistically insignificant (Table 3.1). Skylarks preferred a vegetation cover below 67% and avoided habitats with a cover above 70% (Figure 3.2a). While our results did not clearly point at habitat selection based on arthropod biomass (Figure 3.2b), Skylarks preferred habitats with a Shannon index between 1.2 and 1.4 and avoided habitats with a lower Shannon index, that is, between 0.5 and 1.0 (Figure 3.2c). Locations within a radius of 112 m around nests where preferred foraging habitats, and locations outside a radius of 121 m around nests were avoided (Figure 3.2d).

**Table 3.1.** Summary of the generalized additive mixed model describing the selection of foraging habitats by chick-raising Skylarks (*Alauda arvensis*) with vegetation cover, arthropod biomass, insect diversity, and distance as predictors and the individual nest as a random effect. The model was based on 1,779 landing points of 42 nests and 10,080 pseudo-absence points. Penalized regression splines with maximum likelihood estimators were used for parameter smoothing. The estimated degrees of freedom (edf), reference degrees of freedom (Ref.df), chi-square test statistics ($\chi^2$), and *p*-values (*p*) are given. The model explained 16.9% of the deviance

| Variable | edf | Ref.df | $\chi^2$ | *p* |
|---|---|---|---|---|
| Vegetation cover | 1.001 | 1.001 | 74.208 | <0.001 |
| Arthropod biomass | 1.000 | 1.000 | 0.934 | 0.334 |
| Insect diversity | 3.036 | 3.691 | 10.723 | 0.017 |
| Distance | 3.702 | 4.595 | 579.760 | <0.001 |
| Nest | 13.535 | 41.000 | 20.345 | 0.019 |
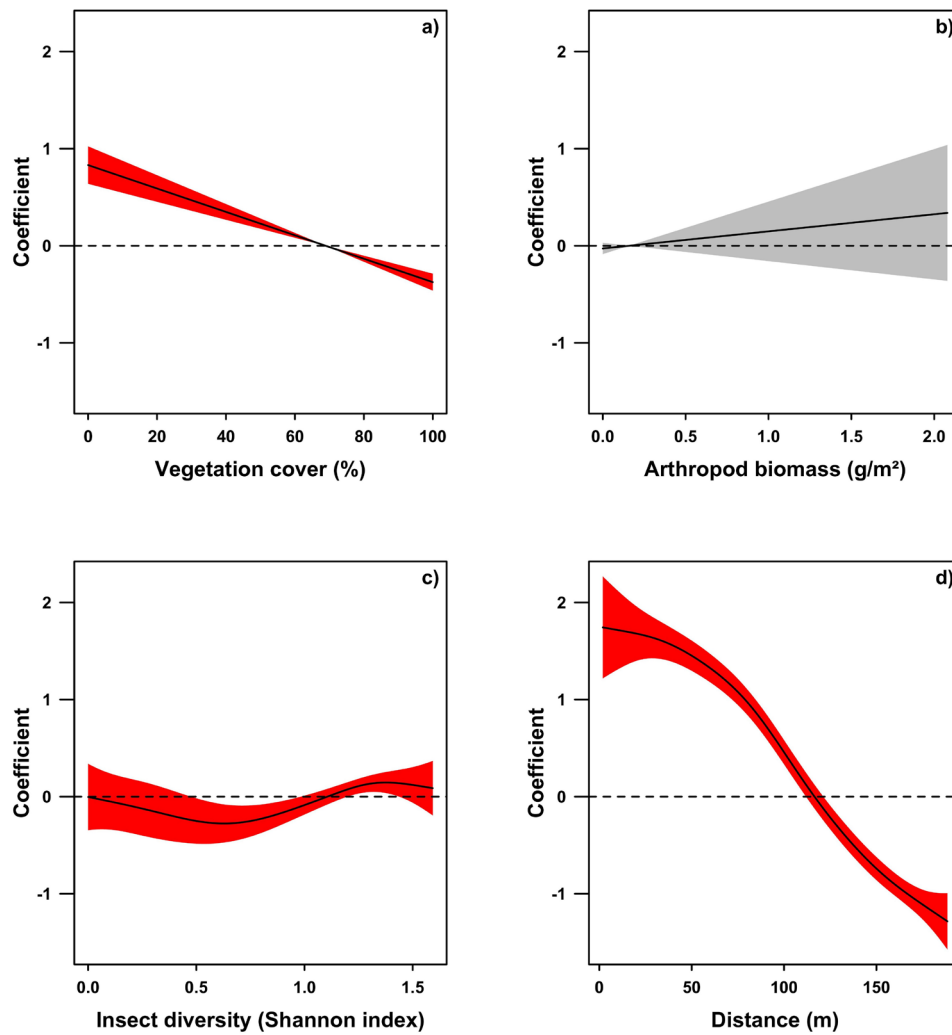
**Figure 3.2.** Selection of foraging habitats by chick-raising Skylarks (*Alauda arvensis*) according to the generalized additive mixed model, which is based on 1,779 landing points of 42 nests and 10,080 pseudo-absence points. Penalized regression splines with maximum likelihood estimators were used for parameter smoothing. Plots show the selection (with 95% CI) with respect to vegetation cover (a), arthropod biomass (b), insect diversity (c), and distance to the foraging habitat (d). Lower confidence intervals above the horizontal dashed line indicate statistically significant preference; upper confidence intervals below the dashed line indicate statistically significant avoidance. The confidence intervals of significant variables are red

According to our analysis of the relative variable importance, the distance between the nest and the habitat was clearly the dominating parameter influencing habitat selection (87.8%), followed by vegetation cover (9.9%). All other parameters had a relative importance below 1.5% (Table 3.2).

**Table 3.2.** Relative variable importance of the predictors (vegetation cover, arthropod biomass, insect diversity, distance) and the random effect (nest) in the generalized additive mixed model. The model describes the selection of foraging habitats by chick-raising Skylarks (*Alauda arvensis*) based on 1,779 landing points of 42 nests and 10,080 pseudo-absence points

| Variable | Relative importance (%) |
|---|---|
| Vegetation cover | 9.9 |
| Arthropod biomass | 0.1 |
| Insect diversity | 1.4 |
| Distance | 87.8 |
| Nest | 0.8 |

### *Overall and seasonal use of habitat types*

Across all 51 nests with documented foraging flights, the average home range consisted to the extent of ca. 75% out of the five most frequent habitats, with ca. 35% winter wheat, 25% sugar beet, and roughly 5% corn, annual flower strips, and field paths in each case (Figure 3.3). About one-quarter of foraging flights per nest was on average directed to both winter wheat and sugar beet, which therefore were not only the two most frequently available, but also the two most frequently used habitats. Approximately 10% of foraging flights were directed to both annual flower strips and field paths, clearly exceeding their respective availability. Further 7% of foraging flights per nest ended in corn, a use that is similar to its weighted surface area (Figure 3.3). Overall, within home ranges, habitat use of the whole breeding season did not differ significantly from random according to compositional analysis (Wilk's $\lambda = 0.544$, $p = 0.119$), making a ranking of the relative importance of habitats redundant.
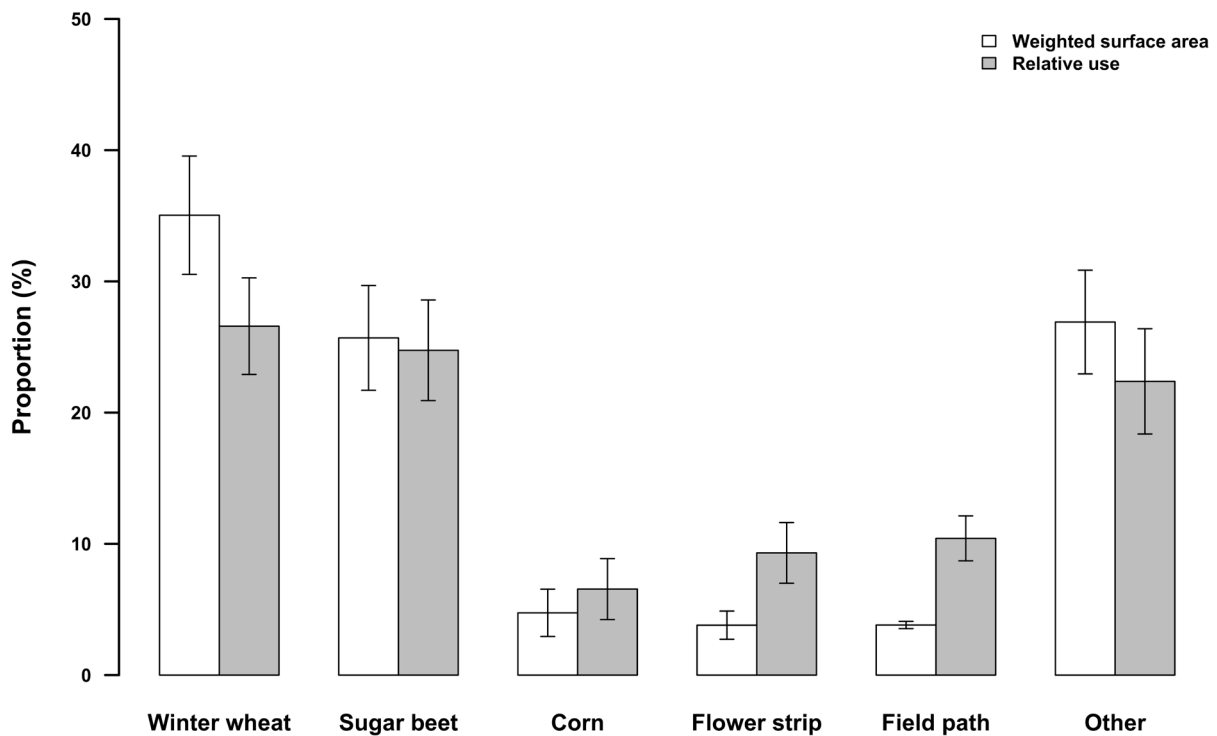
**Figure 3.3.** Average (± SE) weighted surface area compared to the average (± SE) relative use per habitat type and nest within home ranges of chick-raising Skylarks (*Alauda arvensis*) over the whole breeding season. *n* = 51

When the data on habitat availability and use per nest were grouped based on the month of hatching, seasonal patterns became apparent (Figure 3.4). Changes in the average availability over time were a result of varying nest site locations of the nests we had found. Winter wheat and sugar beet were the most frequently used habitat types in all months, but the use of winter wheat in relation to its availability increased while the use of sugar beet decreased. Likewise, annual flower strips were less used in relation to their availability later in the season due to an increasing proportion of the weighted surface area. The relation between the availability and use of field paths stayed constant. Corn was almost absent in the analyzed home ranges of Skylarks, whose chicks hatched during July, resulting in a lack of use.

The corresponding GLMMs in which we had adjusted for the weighted surface area detected statistically significant changes in the relative use of winter wheat, sugar beet, and annual flower strips in the course of the breeding season (Table 3.3, Figure 3.5a, b, d). Winter wheat was avoided as a foraging habitat until the end of June and from then on used according to its availability. The predicted use of sugar beet matched almost the complete opposite time-dependency with use according to its availability until mid-June and an avoidance afterward. Similarly, the selection of annual flower strips as foraging habitats decreased over time. The model predicted a preference until mid-May, use according to their availability until the end of June, and then avoidance until the end of the breeding season. The models of corn and field

paths did not show a statistically significant effect of the day of the breeding season (Table 3.3, Figure 3.5c, e). Except for field paths, increasing habitat availability led to an increased use with statistical significance in all habitat models. Annual flower strips were significantly less used in 2019 compared to 2018 (Table 3.3).
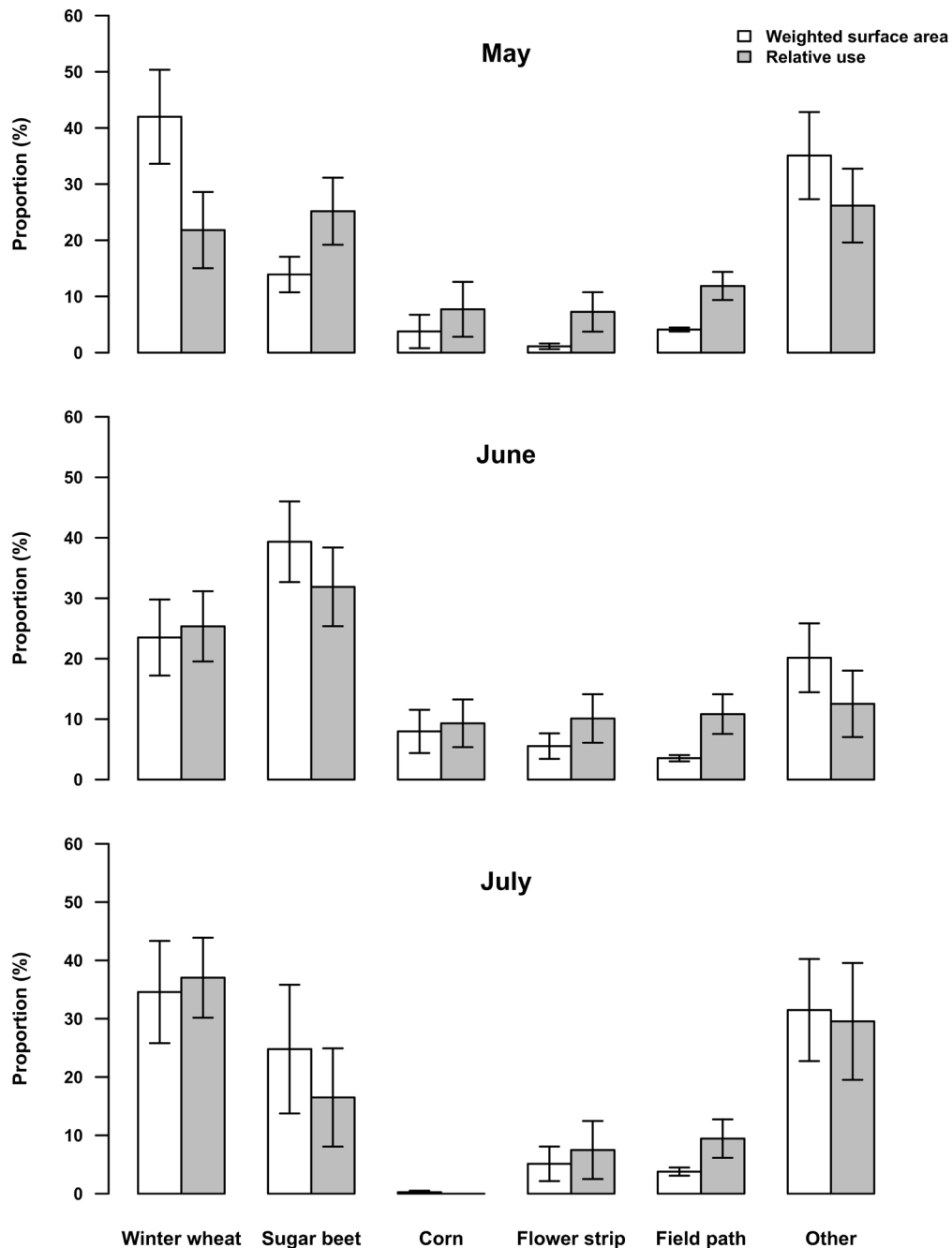


**Figure 3.4.** Monthly average (± SE) weighted surface area compared to the monthly average (± SE) relative use per habitat type and nest within home ranges of chick-raising Skylarks (*Alauda arvensis*). The assignment of nest data to a month was based on the month of hatching. $n_{(May)} = 17$; $n_{(June)} = 21$; $n_{(July)} = 10$. Data from nests whose chicks hatched during April are not shown due to the small sample size ($n = 3$)

**Table 3.3.** Summary of the mixed-effect logistic regression models describing the relative use of habitats by chick-raising Skylarks (*Alauda arvensis*) depending on the time of the breeding season. The sample sizes, estimates (Est.), standard errors (SE), z-values (*z*), and *p*-values (*p*) are given for each model

| Model | Sample size | Fixed effect | Est. | SE | z | p |
|---|---|---|---|---|---|---|
| Winter wheat | 1,830 landing points of 45 nests | Intercept | −4.850 | 0.838 | −5.791 | <0.001 |
| | | Day of breeding season | 0.035 | 0.011 | 3.251 | 0.001 |
| | | Weighted surface area (%) | 0.045 | 0.008 | 5.361 | <0.001 |
| | | Year: 2019 | −0.032 | 0.458 | −0.070 | 0.944 |
| Sugar beet | 1,566 landing points of 39 nests | Intercept | −0.965 | 0.616 | −1.568 | 0.117 |
| | | Day of breeding season | −0.049 | 0.013 | −3.752 | <0.001 |
| | | Weighted surface area (%) | 0.069 | 0.010 | 6.553 | <0.001 |
| | | Year: 2019 | −0.432 | 0.474 | −0.913 | 0.361 |
| Corn | 742 landing points of 19 nests | Intercept | −5.480 | 1.664 | −3.293 | 0.001 |
| | | Day of breeding season | 0.000 | 0.027 | 0.010 | 0.992 |
| | | Weighted surface area (%) | 0.070 | 0.030 | 2.329 | 0.020 |
| | | Year: 2019 | 2.172 | 1.327 | 1.637 | 0.102 |
| Annual flower strip | 1,160 landing points of 30 nests | Intercept | −0.934 | 0.774 | −1.207 | 0.228 |
| | | Day of breeding season | −0.055 | 0.016 | −3.455 | 0.001 |
| | | Weighted surface area (%) | 0.198 | 0.039 | 5.033 | <0.001 |
| | | Year: 2019 | −1.232 | 0.627 | −1.965 | 0.049 |
| Field path | 2,000 landing points of 49 nests | Intercept | −3.012 | 0.815 | −3.696 | <0.001 |
| | | Day of breeding season | 0.005 | 0.010 | 0.454 | 0.649 |
| | | Weighted surface area (%) | 0.031 | 0.129 | 0.238 | 0.812 |
| | | Year: 2019 | 0.050 | 0.466 | 0.108 | 0.914 |

Almost all analyzed habitats were within the preferred range of either vegetation cover or insect diversity for a certain time period, but not within both at the same time (Figure 3.6a, b). Throughout the breeding season, the vegetation cover of winter wheat was ca. 90% and thus always within the range that Skylarks avoided during foraging (70% to 100%). The vegetation cover of annual flower strips exceeded the preferred range, that is, cover below 67%, during early June, the vegetation cover of sugar beet during Mid-June, and of corn during Mid-July. The Shannon index of sugar beet was smaller than 1.0 except during the first half of June and therefore within the range that Skylarks avoided (0.5 to 1.0), while the Shannon index of both winter wheat and annual flower strips was greater than 1.0 during most of the breeding season. Corn showed a steady increase in insect diversity with a Shannon index greater than 1.0 from

the end of June onwards. The Shannon index of field paths was ca. 1.3 until mid-July, which represented the highest insect diversity of monitored habitats and was within the range of Shannon indices that Skylarks preferred during foraging (1.2 to 1.4). Field paths also had the highest arthropod biomass until mid-July (≥0.20 g/m²), followed by winter wheat and corn with intermediate biomass (0.05 to 0.20 g/m²) and sugar beet and corn with low biomass (≤0.05 g/m²) (Figure 3.6c).
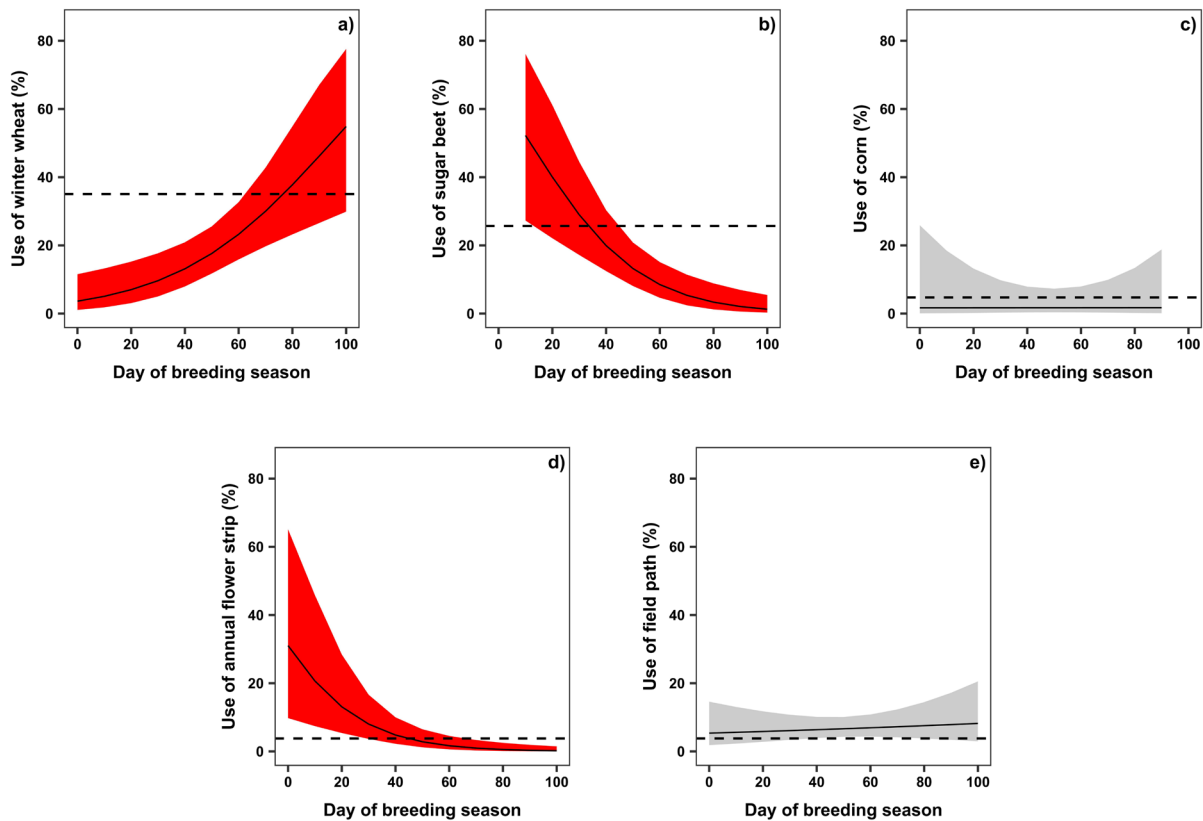


**Figure 3.5.** Relative habitat use (with 95% CI) of winter wheat (a), sugar beet (b), corn (c), annual flower strips (d), and field paths (e) by chick-raising Skylarks (*Alauda arvensis*) throughout the breeding season according to the predictions by mixed-effect logistic regression models. A significant influence of the time is indicated by red confidence intervals. The predictions were made for the average weighted surface area, illustrated by the horizontal dashed line. Lower confidence intervals above the dashed line indicate statistically significant habitat preference; upper confidence intervals below the dashed line indicate statistically significant habitat avoidance. April 25th was set as the first day of the breeding season. Only data of home ranges were included where the respective habitat type was present. For sample sizes, see Table 3.3. Plots were created with the *ggemmeans* function of the R package *ggeffects* (Lüdecke 2018)
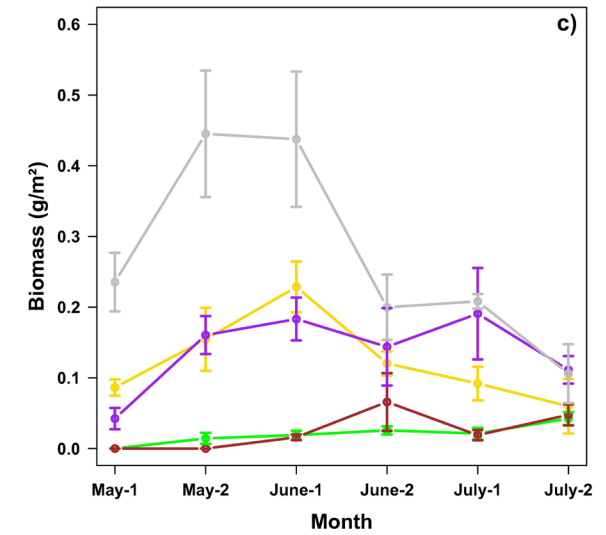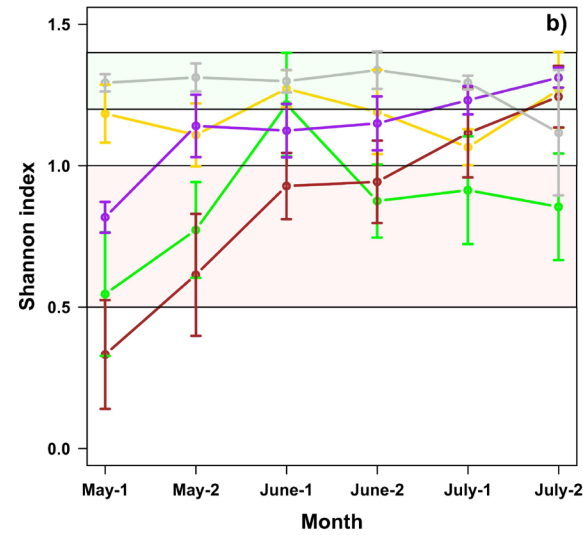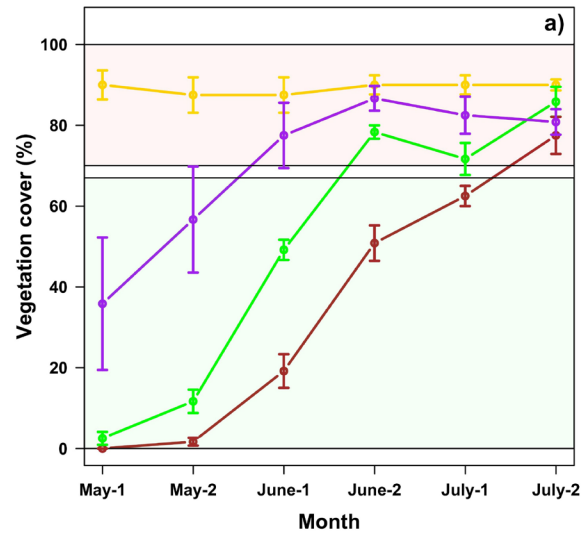
**Figure 3.6.** Average (± SE) vegetation cover (a), Shannon index (b), and arthropod biomass (c) of the main habitats within Skylark (*Alauda arvensis*) home ranges during the breeding season. Yellow line = winter wheat, green line = sugar beet, brown line = corn, purple line = annual flower strip, grey line = field path. Month-1 = 7th; Month-2 = 23rd. $n_{\text{(per habitat and half of month)}}$ = 4. Green boxes indicate the range that chick-raising Skylarks preferred during foraging, red boxes indicate the range of avoidance. The vegetation cover of field paths was not visualized, as it had been defined as zero (see Methods)

### 3.4.2. Foraging parameters

Skylarks in our study area fed their chicks with an average frequency of 11.33 visits (± 5.31 standard deviation) per hour and an average frequency of 3.43 ± 1.60 visits per hour and chick. The feeding frequency per hour increased with statistical significance throughout the breeding season. In contrast, the feeding frequency per hour and chick did not change over time. Older chicks led to a statistically significant increase in both the feeding frequency per hour as well as the feeding frequency per hour and chick (Table 3.4, Figure 3.7a, b).
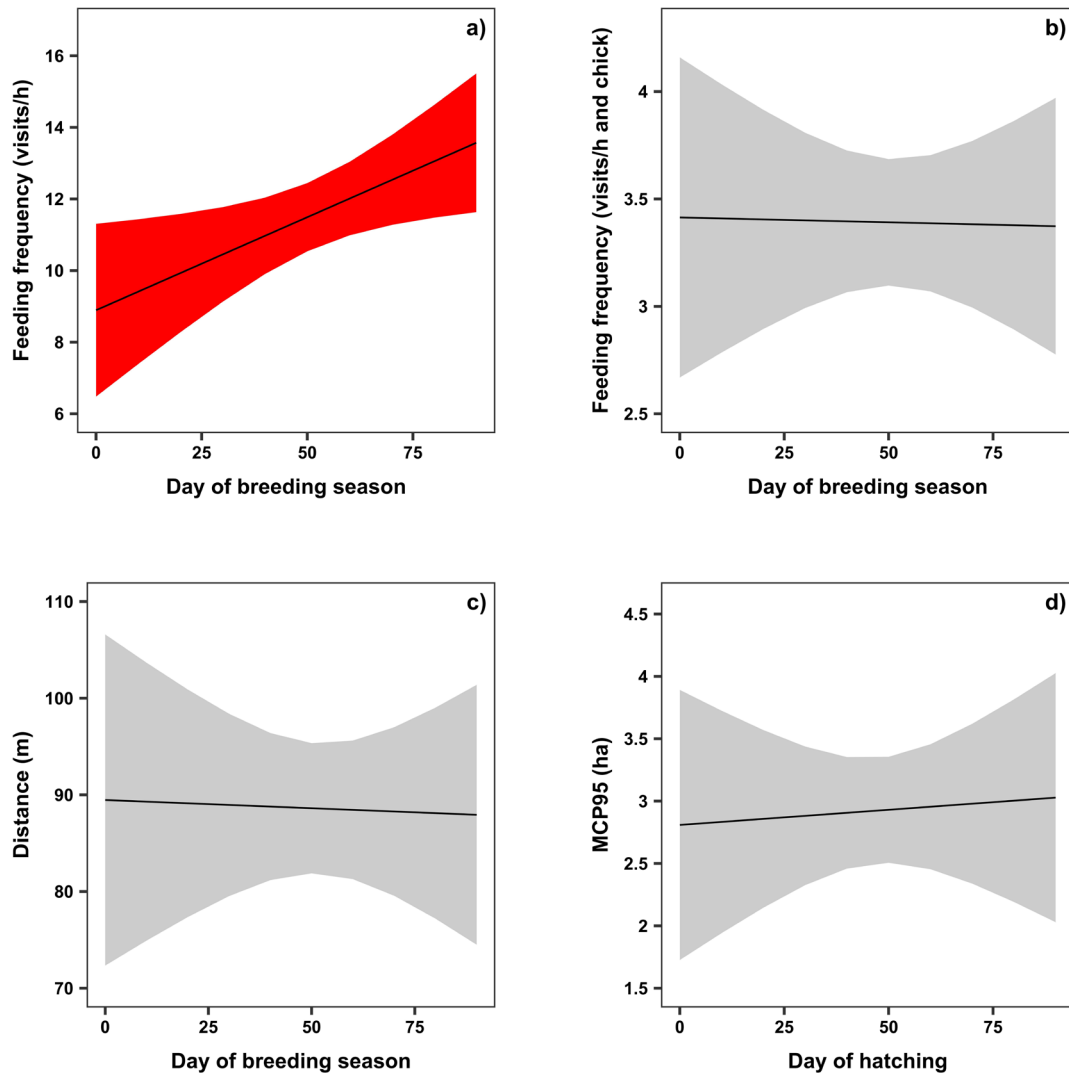


**Figure 3.7.** Development (with 95% CI) of the foraging parameters feeding frequency per hour (a), feeding frequency per hour and chick (b), distance flown (c) and area searched for food (d) of chick-raising Skylarks (*Alauda arvensis*) throughout the breeding season according to predictions by linear mixed-effect models (a, b, c) and a linear regression model (d). April 25th was set as the first day of the breeding season. A significant influence of the time is indicated by the red confidence interval. For sample sizes, see Table 3.4. Plots were created with the *ggeffect* function of the R package *ggeffects* (Lüdecke 2018)

**Table 3.4.** Summary of the linear-mixed effect models and the linear model describing the effects that influence the foraging parameters of chick-raising Skylarks (*Alauda arvensis*). The sample sizes, estimates (Est.), standard errors (SE), degrees of freedom (df) in the case of the linear mixed effect models, *t*-values (*t*), and *p*-values (*p*) are given for each model

| Model | Sample size | Fixed effect | Est. | SE | df | *t* | *p* |
|---|---|---|---|---|---|---|---|
| Feeding frequency (visits/h) | 221 feeding frequencies of 49 nests | Intercept | 6.421 | 2.282 | 178.084 | 2.814 | 0.005 |
| | | Day of breeding season | 0.052 | 0.022 | 46.463 | 2.362 | 0.022 |
| | | Chick age (days) | 1.042 | 0.179 | 211.364 | 5.825 | <0.001 |
| | | Daytime (min) | −0.002 | 0.002 | 208.713 | −1.309 | 0.192 |
| | | Temperature (°C) | −0.101 | 0.076 | 206.231 | −1.331 | 0.185 |
| | | Wind (km/h) | −0.039 | 0.054 | 208.646 | −0726 | 0.469 |
| | | Radio-tagging: yes | −1.139 | 1.173 | 50.567 | −0.971 | 0.336 |
| | | Year: 2019 | −0.631 | 0.994 | 46.912 | −0.634 | 0.529 |
| Feeding frequency (visits/h and chick) | 221 feeding frequencies of 49 nests | Intercept | 2.100 | 0.667 | 174.291 | 3.148 | 0.002 |
| | | Day of breeding season | 0.000 | 0.007 | 47.451 | −0.067 | 0.947 |
| | | Chick age (days) | 0.331 | 0.051 | 209.065 | 6.460 | <0.001 |
| | | Daytime (min) | −0.001 | 0.000 | 205.328 | −1.160 | 0.248 |
| | | Temperature (°C) | −0.029 | 0.022 | 211.100 | −1.336 | 0.183 |
| | | Wind (km/h) | −0.011 | 0.015 | 205.404 | −0.699 | 0.486 |
| | | Radio-tagging: yes | 0.056 | 0.360 | 53.242 | 0.154 | 0.878 |
| | | Year: 2019 | 0.281 | 0.307 | 47.758 | 0.915 | 0.365 |
| Distance flown to foraging habitat (m) | 2,190 distances of 51 nests | Intercept | 85.670 | 12.521 | 190.473 | 6.842 | <0.001 |
| | | Day of breeding season | −0.017 | 0.155 | 46.820 | −0.109 | 0.913 |
| | | Chick age (days) | 1.898 | 0.748 | 1736.592 | 2.537 | 0.011 |
| | | Daytime (min) | −0.008 | 0.005 | 2131.123 | −1.548 | 0.122 |
| | | Temperature (°C) | 0.719 | 0.309 | 1639.687 | 2.322 | 0.020 |
| | | Wind (km/h) | 0.075 | 0.212 | 2128.517 | 0.355 | 0.722 |
| | | Radio-tagging: yes | −2.664 | 7.620 | 68.677 | −0.350 | 0.728 |
| | | Year: 2019 | −32.321 | 6.939 | 47.032 | −4.658 | <0.001 |

| Model | Sample size | Fixed effect | Est. | SE | df | t | p |
|---|---|---|---|---|---|---|---|
| Area searched for food (ha) | 46 MCPs | Intercept | 6.365 | 1.893 | – | 3.363 | 0.002 |
| | | Day of hatching | 0.002 | 0.010 | – | 0.233 | 0.817 |
| | | Observations before noon (%) | 0.002 | 0.008 | – | 0.253 | 0.802 |
| | | Mean temperature (°C) | −0.038 | 0.072 | – | −0.527 | 0.601 |
| | | Mean wind (km/h) | −0.096 | 0.071 | – | −1.360 | 0.182 |
| | | Radio-tagging: yes | −0.608 | 0.534 | – | −1.140 | 0.261 |
| | | Year: 2019 | −2.704 | 0.490 | – | −5.522 | <0.001 |

Neither the distance flown nor the area searched for food was affected by the ongoing breeding season, but instead by other predictors included in the respective model (Table 3.4, Figure 3.7c, d). The average distance flown to a foraging habitat was 86.17 ± 53.82 m. Distances significantly increased with chick age and temperature. Moreover, Skylarks flew significantly shorter distances in 2019 compared to 2018. The area that was actually used for foraging had a size of 2.92 ± 1.88 ha and was significantly smaller in 2019 than in 2018. None of the four models showed a statistically significant effect of the radio-tagging (Table 3.4).

## 3.5. Discussion

### 3.5.1. Habitat selection

*Influence of prey biomass and diversity, vegetation structure, and foraging distance*

Skylarks that search for food for their chicks have to consider the amount of prey, the accessibility of the vegetation, and the distance to a site when selecting a foraging habitat (Jeromin 2002). In our study area, Skylarks based their selection mainly on two factors (Tables 3.1 and 3.2, Figure 3.2): the distance from the nest to the foraging habitat (87.8% relative importance) and the vegetation cover (9.9%).

The clear preference of foraging habitats closer than 112 m to the nest and avoidance of habitats beyond is in agreement with several other studies. For example, Kuiper et al. (2013) found an almost identical threshold for chick-raising Skylarks in the Netherlands, where arthropod-rich field margins were rarely used with distances to the nest above 100 m, while they were the preferred foraging habitat below that distance. Likewise, average flight distances recorded by Donald et al. (2001c), Jeromin (2002), and Murray (2004) were all beneath 100 m, although Poulsen (1996) found considerably higher distances averaging between 120 m and 230 m. As the flown distance is related to costs in time and energy (Poulsen 1996), long extra-territorial foraging flights are interpreted as signs of food shortage or the exploitation of very

profitable food sources (Jenny 1990a; Jeromin 2002). Additionally, longer distances automatically reduce the time for birds to guard their nest, so that nest guarding is thought to be one positive side effect of the short flight distances by female Skylarks (Jeromin 2002). Because distances above approx. 120 m were avoided, our results also indicate that measurements improving foraging habitat quality can only be successful if they are evenly implemented across landscapes. Supporting this, Kuiper et al. (2013) showed for their study area that breeding ground from where Skylarks reach field margins with short flights could have been almost doubled if field margins were implemented more systematically.

Vegetation cover was the second most important factor determining foraging habitat selection. Based on our results, Skylarks preferred vegetation cover below 70% for foraging and avoided higher FVC. The preference for sparse vegetation is also confirmed by several other studies and is strongly related to the foraging behavior of Skylarks (Jenny 1990a; Murray 2004; Odderskær et al. 1997b; Wilson 2001). As they search for their prey on the ground during walking, Skylarks rely on vegetation that does not hamper mobility (Donald 2004; Jenny 1990a).

We found that insect diversity (1.4%) and arthropod biomass (0.1%) had the lowest relative influence on foraging habitat selection by Skylarks, with biomass being the only predictor without a statistically significant effect. The fact that Skylarks preferred habitats with higher insect diversity (Shannon index between 1.2 and 1.4) and avoided less diverse habitats (Shannon index between 0.5 and 1.0) can be explained by the beneficial effects of a varied diet on chick growth and condition (Borg and Toft 2000; Donald et al. 2001c). Even though we did not detect an influence of arthropod biomass on habitat selection (in accordance with Murray 2004), it is evident that a sufficient amount of arthropods is needed for breeding Skylarks. Several studies proved the negative impact of insecticides on insectivorous bird populations, including the Skylark (Hallmann et al. 2014; Odderskær et al. 1997a). Instead, we think that chick-raising Skylarks must consider first and, most importantly, the energetic costs of their foraging flight, and second arthropod reachability in terms of open vegetation, before they can profit from diverse and abundant prey items. This is also supported by Odderskær et al. (1997b), who frequently recorded foraging Skylarks on unvegetated tramlines later in the season, although arthropod abundance was higher within the dense crop itself. Moreover, since short distances clearly were the single most important determinant of habitat selection in our study area, we believe there was sufficient food availability within the direct nest surroundings.

*Overall and seasonal use of habitat types*

Ranking the five most common habitat types within Skylark home ranges (winter wheat, sugar beet, corn, annual flower strips, and field paths) according to their general importance as foraging habitat was not possible. The reason for this was that habitat use within home ranges over the whole breeding season did not differ significantly from random, which contrasts with other studies using compositional analysis (Fischer et al. 2009; Kuiper et al. 2013; Weibel 1998). However, this result depended on the number of habitat categories we included. When post hoc not only considering habitats as own category that were present in one-third of all home ranges, but one-quarter (so that winter barley was also a category of its own), the difference became significant (S3.1). Nevertheless, the ranking of the five most frequent habitats was mainly not supported with statistical significance, that is, ranks were mostly interchangeable. To us, this reflects the difficulty of grouping them into overall suitable and unsuitable foraging habitats. Throughout the breeding season, habitats offered either open vegetation or a high insect diversity/arthropod biomass, but rarely both (Figure 3.6). Moreover, we detected significant changes in the use of habitats over time in our GLMM models with adjustments for availability (Table 3.3, Figure 3.5). Vegetation that became too dense is likely the reason for the decreasing use of sugar beet and annual flower strips. The time when they were used less than available from the middle/end of June onwards coincided with the time when vegetation cover exceeded 70%. Douglas et al. (2009) found a similar shift in the use of field margins due to less accessible vegetation. As extensively used structures are very common measures to support Skylarks and farmland birds in general (Fischer et al. 2009; Kuiper et al. 2013; Ottens et al. 2014; PARTRIDGE 2021), these results emphasize the relevance of low seeding densities when implementing flower strips. Our analyses further revealed increased use of winter wheat later in the breeding season. Inevitably, reduced use of certain habitats leads to increased use of others. However, we were surprised about the intensified use of winter wheat, as the average vegetation cover was always within the avoided range (Figure 3.6). Additionally, winter wheat was of minor importance or clearly avoided as a foraging habitat in various studies (Jenny 1990a; Kuiper et al. 2013; Wilson 2001), and it is the most common example of a habitat that becomes unsuitable for foraging due to the growing sward structure (e.g., Donald and Morris 2005). The bare tramlines, which are frequently used micro-habitats within cereals (personal observation, Odderskær et al. 1997b), may have been sufficiently profitable in our study area to be more exploited later in the season. This also demonstrates the limits of our study, as the vegetation and arthropod data that we extrapolated to field level cannot grasp fine-scale differences influencing habitat use. In general, we believe that changing habitat characteristics and, therefore, the varying use of specific habitats over time impede an overall ranking and stretches the importance of considering time-dependencies in analyses of habitat use.

Another important factor influencing the use of habitats is the nest site selection within the study area itself (second-order habitat selection, Johnson 1980) due to the strong distance-dependent habitat choice. At first glance, for example, the decreasing use of sugar beet over time for a given availability (Figure 3.5b) seems to contradict its status as the constantly most frequented foraging habitat together with winter wheat (Figure 3.4). However, this can be traced back to the increased availability of sugar beet within home ranges later in the breeding season that was especially pronounced in June because higher availability automatically led to intensified use (Table 3.3). At the same time, the average weighted surface area of winter wheat within home ranges was much smaller in June compared to May. We are aware that time patterns in the availability of habitats strongly depend on the nesting sites of the nests we found. Nevertheless, we think that the increasing availability of sugar beet/decreasing availability of winter wheat reflects the seasonal shifting of nest locations from winter cereals to summer crops well known from other studies (Schläpfer 1988). As the increased availability of sugar beet over time did not come along with a proportional increase in its use, we believe that a shift in the nesting site was not triggered by foraging habitat preferences but by demands on the nesting site itself. As with foraging habitats, Skylarks depend on open vegetation that allows free access to the nest (Donald 2004; Jenny 1990b). However, from late May onwards, winter cereal vegetation becomes too dense, and Skylarks are forced to breed close to the bare tramlines or switch to a different crop (Donald 2004; Donald et al. 2002a; Fischer et al. 2009). Because tramlines are high-risk nesting sites that Skylarks try to avoid (Püttmanns et al. 2021), sugar beet with a lower vegetation cover was probably more suitable than winter wheat.

3.5.2. Foraging parameters and food availability

Skylarks in modern agriculture are thought to experience a food shortage later in the breeding season due to the growing vegetation that hampers access to prey (Donald 2004; Jenny 1990a; Weibel 1998). In contrast to this and our hypotheses, we did not find indications of a seasonal decrease in food availability (Table 3.4, Figure 3.7). Instead, the feeding frequency per hour showed a significant increase during the breeding season, implying an even greater food availability later in the season. When we modeled the feeding frequency per hour and chick, we found that this did not change significantly over time. Evidently, Skylarks invested the surplus of food in greater clutches later in the season, an effect already reported in the literature (Donald et al. 2001a), which caused an increase in the feeding frequency per hour. The lack of significant changes in the distance flown and the area searched for food at least do not support a food shortage scenario over time. We are aware that we did not collect data on chick weight, and therefore we cannot provide direct evidence that the food availability in

our study area was sufficient for a healthy condition of chicks. However, only 1.7% of chicks (3 of 178) likely died because of starvation, while other studies documented higher losses (Jenny 1990b; Poulsen et al. 1998; Wilson et al. 1997). The average values that we found for all foraging parameters were very similar to those reported in Jeromin (2002), who worked at a study site that was managed for farmland bird conservation. Furthermore, we think that the foraging parameters we analyzed have the potential to detect more subtle differences in food availability than the measurement of chick weight, as Skylark parents might be able to bear the costs of food shortage by an increase in feeding effort (Bradbury et al. 2003).

Besides our analyses of time effects, we found no significant influence of radio transmitters on any foraging parameter. Consequently, our results support other studies that could not document a detrimental effect of low-weight tagging on the behavior of the focal species (e.g., Hegemann 2012; Hegemann et al. 2010). Nevertheless, the negative impact of additional weight might be complex and more subtle (Hegemann et al. 2013), which was not possible to test in the framework of this study. Therefore, researchers should always consider potential costs for the bird and bias in data collection when using transmitters (Barron et al. 2010).

As we found no signs of a food shortage later in the season but indications of an increase in food availability and thus feeding ability, we interpret the way in which Skylarks used habitats throughout the breeding season as constantly suitable to raise offspring. Even though higher vegetation cover was probably the reason for the reduced use of sugar beet and annual flower strips over time relative to their availability, accessible prey was apparently still numerous enough. We do not believe, however, that our findings can be readily transferred to other regions but result from the heterogeneous composition of the study area. The farmland south of Göttingen was characterized by a spatial arrangement in which winter crops and summer crops were often cultivated in fields next to each other (Figure 3.1). The implementation of several large flower strips, especially in the eastern part of the study area (PARTRIDGE 2021), further enriched habitat diversity. Therefore, almost all Skylarks were able to compose a home range via a nest-site selection that included several habitat types (S3.2). This, in turn, enabled the use of spatial synergetic effects (Miguet et al. 2013), that is, to combine the advantages and outweigh the disadvantages of neighboring habitats at a given time with the potential for flexible adaptations of habitat use to changing conditions. A balanced home range composition with habitat complementation, therefore, prevented any deterioration of foraging parameters from our point of view. It is important to note, though, that we collected our data in two years of extremely dry weather (Deutscher Wetterdienst 2021a; Zscheischler and Fischer 2020) and that we could not consider the – often detrimental – effects of heavy rainfall (Donald et al. 2001a). Future research is required to compare our results with data both from more homogeneous landscapes and from years with changing weather conditions to corroborate our interpretations.

### 3.5.3. Conclusions

The results of this study support the often discussed benefits of heterogeneous farmland (Eraud and Boutin 2002; Jeromin 2002; Miguet et al. 2013; Schläpfer 1988) with respect to foraging habitats of Eurasian Skylarks. In contrast to most other studies that infer positive effects of crop diversity indirectly from analyzing abundance patterns (Hiron et al. 2012), we draw our conclusions based on direct observations of habitat use in combination with measurements of food availability. As we could show, Skylarks acted on comparatively small spatial scales, avoiding distances to food sources longer than 120 m. We suggest that spatial synergetic effects of different habitats within a home range secured sufficient food availability throughout the breeding season. Foraging habitats with vegetation cover below 70% are of special importance, an aspect that should be considered when implementing conservation measures such as flower strips.

We find it encouraging to see that it can be possible for chick-raising Skylarks to find enough food throughout the breeding season even in conventionally managed farmland – under the premise of habitat heterogeneity.

## 3.6. Acknowledgements

## 3.7. Supplementary material

**Supplementary material S3.1.** Compositional analysis matrix of the means of log-ratio differences and ranking of the habitats that were available within one-quarter of Skylark (*Alauda arvensis*) home ranges. The habitat use differed significantly from random (Wilk's λ = 0.320, *p* = 0.047). Numerator habitats are in rows; denominator habitats are in columns. Numbers in brackets represent the sample size to calculate the respective means of log-ratio differences. *\*p* < 0.05

| | Winter wheat | Field path | Annual flower strip | Sugar beet | Corn | Winter barley | Other | Rank |
|---|---|---|---|---|---|---|---|---|
| **Winter wheat** | 0.000 | 0.766 [43] | 0.538 [27] | 1.301 [33] | 2.943 (*) [15] | 4.293 [10] | 2.190 (*) [45] | 6 |
| **Field path** | | 0.000 | 0.411 [29] | 1.307 [38] | 2.764 [19] | 3.654 (*) [14] | 1.532 [47] | 5 |
| **Annual flower strip** | | | 0.000 | 0.506 [21] | 1.141 [12] | 1.679 [7] | 2.490 (*) [29] | 4 |
| **Sugar beet** | | | | 0.000 | 0.366 [16] | 1.605 [10] | 2.054 [37] | 3 |
| **Corn** | | | | | 0.000 | 5.148 (*) [8] | 1.632 [17] | 2 |
| **Winter barley** | | | | | | 0.000 | 0.181 [13] | 1 |
| **Other** | | | | | | | 0.000 | 0 |

**Supplementary material S3.2.** Weighted surface area (%) of the main habitats within Skylark (*Alauda arvensis*) home ranges and the total number of different habitats per home range with a weighted surface area ≥1% (No. habitats). It is given the minimum number of different habitats because the category *other* might have consisted of more than one habitat type

| Nest | Winter wheat | Sugar beet | Corn | Annual flower strip | Field path | Other | No. habitats |
|---|---|---|---|---|---|---|---|
| N02.18 | 9.3 | 25.3 | 0.0 | 0.0 | 4.2 | 61.2 | 4 |
| N03.18 | 75.9 | 3.1 | 5.4 | 3.9 | 2.7 | 9.0 | 6 |
| N04.18 | 77.7 | 9.8 | 3.6 | 1.7 | 5.6 | 1.6 | 6 |
| N05.18 | 57.2 | 27.6 | 0.0 | 8.1 | 4.7 | 2.4 | 5 |
| N09.18 | 66.6 | 29.9 | 1.6 | 0.0 | 0.6 | 1.4 | 4 |
| N10.18 | 0.0 | 32.1 | 0.0 | 0.0 | 2.7 | 65.2 | 3 |
| N12.18 | 56.8 | 2.9 | 0.0 | 1.7 | 4.7 | 34.0 | 5 |
| N13.18 | 0.0 | 15.5 | 0.0 | 0.1 | 2.6 | 81.9 | 3 |
| N14.18 | 3.8 | 0.0 | 0.0 | 0.4 | 4.8 | 91.0 | 3 |
| N16.18 | 53.8 | 26.8 | 0.0 | 0.0 | 8.1 | 11.3 | 4 |
| N18.18 | 75.4 | 1.3 | 0.5 | 0.0 | 5.3 | 17.6 | 4 |

| Nest | Winter wheat | Sugar beet | Corn | Annual flower strip | Field path | Other | No. habitats |
|------|------|------|------|------|------|------|------|
| N20.18 | 12.0 | 69.9 | 0.0 | 0.0 | 0.0 | 18.1 | **3** |
| N22.18 | 42.1 | 34.8 | 0.3 | 14.5 | 5.3 | 3.0 | **5** |
| N23.18 | 4.3 | 20.0 | 0.0 | 2.6 | 3.6 | 69.4 | **5** |
| N24.18 | 3.2 | 0.0 | 0.0 | 23.6 | 1.3 | 72.0 | **4** |
| N25.18 | 8.8 | 56.7 | 2.4 | 22.0 | 7.5 | 2.6 | **6** |
| N26.18 | 4.9 | 68.5 | 0.0 | 0.0 | 3.4 | 23.2 | **4** |
| N27.18 | 21.6 | 62.6 | 0.0 | 0.0 | 5.3 | 10.5 | **4** |
| N30.18 | 9.9 | 86.1 | 0.0 | 0.1 | 2.9 | 1.0 | **4** |
| N32.18 | 81.2 | 3.0 | 0.0 | 9.2 | 3.6 | 2.9 | **5** |
| N33.18 | 32.3 | 5.2 | 0.0 | 0.0 | 4.4 | 58.2 | **4** |
| N35.18 | 54.1 | 0.6 | 0.0 | 12.8 | 5.8 | 26.7 | **4** |
| N36.18 | 30.5 | 7.0 | 2.5 | 0.0 | 4.1 | 55.9 | **5** |
| N02.19 | 85.0 | 0.0 | 0.0 | 1.8 | 3.7 | 9.6 | **4** |
| N04.19 | 70.9 | 0.0 | 8.0 | 0.0 | 5.0 | 16.1 | **4** |
| N05.19 | 78.4 | 0.0 | 0.0 | 5.5 | 3.9 | 12.2 | **4** |
| N08.19 | 62.5 | 19.1 | 0.0 | 0.8 | 4.3 | 13.3 | **4** |
| N09.19 | 77.4 | 0.0 | 0.0 | 0.0 | 4.7 | 17.9 | **3** |
| N12.19 | 88.4 | 0.0 | 0.0 | 0.5 | 3.3 | 7.8 | **3** |
| N17.19 | 52.5 | 32.2 | 0.0 | 0.0 | 5.8 | 9.6 | **4** |
| N26.19 | 5.7 | 6.4 | 0.0 | 0.0 | 4.4 | 83.6 | **4** |
| N27.19 | 82.7 | 0.0 | 0.2 | 0.3 | 7.0 | 9.8 | **3** |
| N30.19 | 4.8 | 1.6 | 50.9 | 0.1 | 3.3 | 39.3 | **5** |
| N31.19 | 0.0 | 29.9 | 2.2 | 2.0 | 6.3 | 59.7 | **5** |
| N34.19 | 2.7 | 0.0 | 0.0 | 0.5 | 4.3 | 92.6 | **3** |
| N35.19 | 54.2 | 5.8 | 0.0 | 16.7 | 4.3 | 19.0 | **5** |
| N36.19 | 89.5 | 0.3 | 2.4 | 0.4 | 4.7 | 2.8 | **4** |
| N37.19 | 0.0 | 61.2 | 30.4 | 0.1 | 5.5 | 2.8 | **4** |
| N38.19 | 0.0 | 69.7 | 26.9 | 0.0 | 3.4 | 0.0 | **3** |
| N40.19 | 65.7 | 0.0 | 27.4 | 0.2 | 0.8 | 5.9 | **3** |
| N41.19 | 65.0 | 0.0 | 0.0 | 28.3 | 0.0 | 6.8 | **3** |
| N43.19 | 10.7 | 88.0 | 0.0 | 0.0 | 1.3 | 0.0 | **3** |
| N44.19 | 20.0 | 78.1 | 0.4 | 0.0 | 1.1 | 0.5 | **3** |

| Nest | Winter wheat | Sugar beet | Corn | Annual flower strip | Field path | Other | No. habitats |
|---|---|---|---|---|---|---|---|
| N45.19 | 0.0 | 60.5 | 8.4 | 0.0 | 1.3 | 29.9 | **4** |
| N46.19 | 1.4 | 16.6 | 65.0 | 1.3 | 1.9 | 14.0 | **6** |
| N47.19 | 10.8 | 57.7 | 0.0 | 0.0 | 1.7 | 29.8 | **4** |
| N48.19 | 9.7 | 49.1 | 0.0 | 30.9 | 2.1 | 8.1 | **5** |
| N51.19 | 0.3 | 68.1 | 3.5 | 3.2 | 3.8 | 21.1 | **5** |
| N52.19 | 11.8 | 69.7 | 0.0 | 0.0 | 6.1 | 12.4 | **4** |
| N54.19 | 53.8 | 0.0 | 0.0 | 0.0 | 0.6 | 45.6 | **2** |
| N57.19 | 2.4 | 7.8 | 0.0 | 0.7 | 6.9 | 82.2 | **4** |

# Chapter 4

## Additional tramline fragments: an example of science-based conservation management

## 4.1. Abstract

Linear structures in winter cereals like tramlines are frequently used but high-risk nesting sites for Eurasian Skylarks when crop vegetation becomes impenetrable during May. However, their influence on nest-site selection before vegetation greatly limits choice is less studied. Between 2017 and 2019, we located 32 nests in winter cereals during the early breeding season and show that Skylarks nested 2 m further away from linear structures than expected if nest location was random. We interpret this avoidance as anti-predation behavior and propose additional tramline fragments for conservation management. Moreover, we confirm earlier findings about a higher nest predation risk on linear structures and a shifting of nesting sites towards them in the later breeding season.

## 4.2. Introduction

Winter cereals are a critical breeding habitat for the European population of Eurasian Skylarks (*Alauda arvensis*) during the breeding season from April to July (Donald 2004). Field edges and implemented tramlines (hereinafter referred to as *linear structures*) profoundly influence their breeding success. Skylark nests close to linear structures experience a particularly high predation risk (Donald et al. 2002a; Fischer et al. 2009; Weibel 1999). Research has shown that the proportion of nests in the proximity of these high-risk areas rapidly increases from late May onwards (Donald 2004; Donald and Vickery 2000; Morris and Gilroy 2008). At this point, other areas of winter cereals are less accessible for nest building due to impenetrable vegetation, leaving Skylarks little choice for nest-site selection within that crop type.

Less evidence exists about the relevance of linear structures for the nest-site selection of Skylarks in the early breeding season. Donald and Vickery (2000) found only a few nests directly on tramlines from April to May. Whereas this pattern might suggest an avoidance behavior, their observation could also be the result of random nest distribution because linear structures only account for a small proportion of area per field.

The avoidance of breeding on linear structures by Skylarks in the early breeding season, if occurring, could indicate that they are capable of assessing the higher predation risk associated with linear structures. Proactive avoidance of nest predation through the choice of

nesting sites is a known anti-predation strategy in various birds (Lima 2009). Previous studies have already identified avoidance of high-risk areas, such as fox dens (Tryjanowski et al. 2002) or avian predator nests (Hromada et al. 2002; Martínez-Padilla and Fargallo 2008; Suhonen et al. 1994), as an anti-predation behavior in Skylarks.

Thus, the main goal of our study was to investigate whether Skylarks actively avoid breeding close to linear structures in the early breeding season as a potential expression of an anti-predation behavior. In addition, we checked whether we can confirm previous findings about a higher nest predation risk on linear structures and the shifting of nesting sites towards them in the later breeding season.

## 4.3. Methods

### 4.3.1. Data collection

Data collection took place between April and July from 2017 to 2019. Within the 8-km² study site in farmland south of Göttingen, Lower Saxony, in Germany, winter cereals (winter wheat, winter barley) were the dominating crops (49%), followed by sugar beet (20%), corn (10%), and winter rape (7%). Approximately 300 pairs of Skylarks breed at the study site (based on Langer 2017 and Meineke 2018, unpublished data). We searched areas in conventionally managed winter cereals for nests after we had observed Skylarks out of a car or camouflaged tent returning to the nest for nest building, incubation, or chick feeding. The distance from the nest to the closest linear structure (i.e., tramline or field edge) was measured and rounded to the nearest half meter. We pooled these two types of linear structures based on their association with a high nest predation risk (e.g., Fischer et al. 2009). Nests were visited on average every third day to check for predation. Following Donald et al. (2002a), nests found empty before the chicks had reached the age of the seventh day were counted as predated. After this age, nests were counted as successful as long as at least one chick had left the nest and no indications of predation were visible. For the back-calculation of first-egg laying dates, we assumed laying at a rate of one egg per day, an incubation period of ten days, and that all chicks hatched within one day (Donald 2004; Donald et al. 2002a). The age of chicks was estimated by the state of physical development according to Pätzold (1983).

### 4.3.2. Data analysis

As a measure of nest predation risk, we used the daily mortality rate (DMR) for nests on linear structures (closer than/at 0.5 m from a linear structure) and away from them (farther than 0.5 m), assuming that most predators walking along linear structures can easily find nests

within 0.5 m distance to these. DMR was calculated for each successful or predated nest according to the equation presented in Morris and Gilroy (2008): $\text{Outcome}_{[\text{failure}=1; \text{success}=0]}$/exposure days, with exposure days being the number of days a nest was under observation (Mayfield 1975). Then, a one-sided Mann–Whitney $U$ test was used to compare the DMRs of the two distance categories.

To check for a shifting of nesting sites towards linear structures from late May onwards, we used May 21st to subdivide our dataset into nests with a first-egg laying date before (early breeding season) and on or after this date (later breeding season). At that time, the average height of winter cereals in our study area exceeded 60 cm, which is the upper limit of the typical range of Skylark nest vegetation for this crop type (Donald et al. 2002a). For the comparison of nest distances to the next linear structure between early and later breeding season, we used a one-sided Mann–Whitney $U$ test again.

To assess whether Skylarks avoided linear structures, the actual nest-site selection was contrasted with a random nest distribution for nests of the early breeding season. First, we manually digitized all linear structures of fields with nests using *ArcGIS* (version 10.3.1; Esri Inc. 1999–2015; WGS 84/UTM zone 32 N). Because we aimed to base our field delineations on aerial photos from the year a nest was found, we used different image providers: the imagery base map in *ArcGIS*, *Google Earth Pro* (version 7.3.2; Google LLC. 2019) and the *Landesamt für Geoinformation und Landesvermessung Niedersachsen*. Next, we drew 10,000 random points per nest within the respective fields and measured the distance between the random points and the closest linear structure rounded to the nearest half meter using *R* (version 3.4.3; R Core Team 2017; packages *rgdal*, *raster, rgeos* and *sp*). For each field, we assumed a homogeneous vegetation structure except for the tramlines. We considered the bare ground of these structures to be an unsuitable nesting site with no concealment for nests. Therefore, no random points were generated directly on tramlines. We calculated the expected nesting distance by taking the mean distance of all random points. The observed mean nest distance to linear structures was then compared with the expected nesting distance using a two-sided one-sample $t$ test.

We assumed a random nest sampling for all statistical tests because nests were almost always found after clear behavioral indications independent of the ease to detect the nest. Moreover, we assumed data from nests of the same year to be independent, which is well justified for analyses considering only the early breeding season. During that period, most nests were found in fields far apart (i.e., in different territories) and/or were simultaneously active. For analyses considering the full breeding season, we cannot exclude the risk of non-independence because Skylarks have multiple breeding attempts. However, as pointed out by Morris and Gilroy (2008), the risk of pseudoreplication is minimized because nesting sites, and

thus predation risk, should vary independently between sequential nesting attempts given that changes are externally induced by vegetation structure.

Our decisions for the usage of a Mann–Whitney $U$ test for non-parametric data or a $t$ test for parametric data were based on the results of a Shapiro–Wilk test checking normal distribution. All statistical tests were performed with $R$ for all sampling years together and, for the analysis of avoidance behavior in the early breeding season, for each year separately. Finally, we used the Bonferroni–Holm correction to control for false positives through multiple testing.

## 4.4. Results

In total, we found 54 nests in winter cereals from 2017 to 2019. Forty of them were either successful or predated and could be considered for the analysis of DMR (see S4.1 for the nest outcome of the 14 other nests). Nests located directly on linear structures ($n_{(successful)} = 5$; $n_{(predated)} = 3$) had a mean DMR of 8.58% (± 17.31 standard deviation), while the mean DMR of nests farther away ($n_{(successful)} = 28$; $n_{(predated)} = 4$) was 1.56 ± 4.71%. The difference was not statistically significant ($W = 161.5$; $p = 0.092$).

For 32 out of the 54 nests found in total, the first-egg laying date was before May 21st, and for 22 nests after this date. Nests from the later breeding season had an average distance of 2.64 ± 3.06 m to the next linear structure and were on average positioned 3.91 m closer to them than nests from the early breeding season ($W = 572.5$; $p < 0.001$) (Figure 4.1).

To test for an avoidance behavior, only the 32 nests of the early breeding season were considered. Their distance to the closest linear structure was 6.55 ± 3.63 m. Separated per year, the mean distance was 5.38 ± 5.94 m in 2017 ($n = 4$), 7.68 ± 2.90 m in 2018 ($n = 11$), and 6.09 ± 3.49 m in 2019 ($n = 17$).
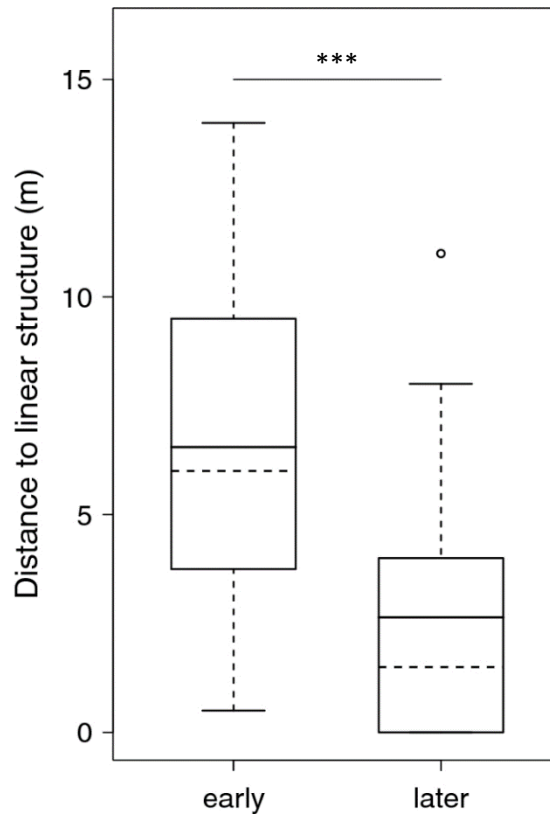
**Figure 4.1.** Distance to the closest linear structure of Skylark (*Alauda arvensis*) nests found in the early (first egg laid before May 21$^{st}$) and in the later breeding season (first egg laid on or after May 21$^{st}$) from 2017 to 2019. Boxes indicate the first and third quartile, lower whiskers the minimum distance, and upper whiskers the maximum distance or the third quartile + 1.5*IQR. Solid horizontal lines within the boxes indicate the mean, dashed horizontal lines indicate the median. Asterisks indicate a significant difference (***$p < 0.001$) according to Mann–Whitney $U$ test. $n_{(early)} = 32$; $n_{(later)} = 22$. Created in $R$ (version 3.4.3)

In contrast, the expected nesting distance if nest distribution was random (i.e., the mean distance of the 320,000 generated random points to the closest linear structure) was 4.66 ± 3.39 m. When we considered only random points drawn for nests of a certain year, the expected nesting distance varied with 4.70 ± 3.32 m in 2017, 4.47 ± 3.23 m in 2018, and 4.77 ± 3.49 m in 2019. Thus, the distance of observed nests to linear structures was always higher than expected according to a scenario of random nest distribution. The differences were statistically significant for both data from all years together ($t = 2.94$; $p = 0.018$; 95% CI = 4.92 to 8.17) and when considering only data from 2018 ($t = 3.67$; $p = 0.017$; 95% CI = 5.02 to 10.34). In 2019, the difference was not statistically significant ($t = 1.55$; $p = 0.140$; 95% CI = 4.30 to 7.88) (Figure 4.2). For data from 2017, we did not conduct a $t$ test due to the small sample size.
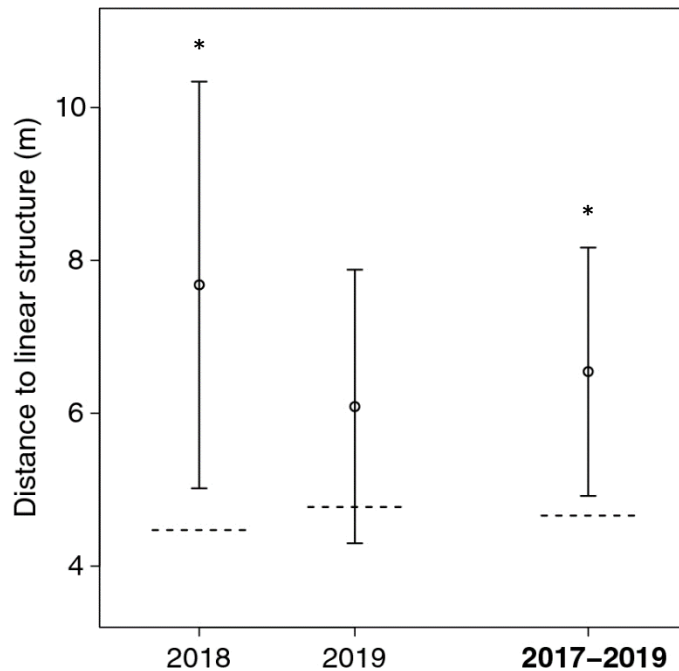
**Figure 4.2.** Mean distance to the closest linear structure of Skylark (*Alauda arvensis*) nests found in 2017 to 2019 (with 95% CI) compared to the expected mean of random nest distribution. Only nests found in the early breeding season (first egg laid before May 21$^{st}$) were considered for analysis. Points indicate the mean, whiskers the upper and lower confidence interval. The dashed horizontal lines indicate the expected distance. Asterisks indicate a significant difference (*$p < 0.05$) according to one-sample *t* test. Data from 2017 were not analyzed separately due to the small sample size ($n = 4$). $n_{(2018)} = 11$; $n_{(2019)} = 17$; $n_{(2017–2019)} = 32$. Created in *R* (version 3.4.3)

## 4.5. Discussion

Comparing nest-site selection during the early breeding season with a scenario of random nest distribution, we found that Skylarks actively avoided breeding close to linear structures in winter cereals. The behavior occurred in all analyzed years with statistical significance in 2018 and in the whole study period (i.e., 2017 to 2019). All years combined, the observed mean distance was about 2 m further away than for random points. Our results are in line with Donald and Vickery's (2000) observation that only a few Skylarks nest directly on tramlines at the beginning of the breeding season.

We contend that anti-predation behavior is the most plausible cause of the observed avoidance of linear structures. First, many previous studies have found an association of linear structures with a high nest predation risk (Donald et al. 2002a; Fischer et al. 2009; Morris and Gilroy 2008; Weibel 1999). Similarly, the data from our study area confirms a higher DMR for nests positioned directly on linear structures, even though the sample size was rather small, and the effect was not statistically significant. Secondly, Skylarks are known for their ability to perceive

areas of high predation risk and use avoidance as an anti-predation behavior (Hromada et al. 2002; Martínez-Padilla and Fargallo 2008; Suhonen et al. 1994; Tryjanowski et al. 2002).

In addition, we conclude that the lack of potential nest concealment on unvegetated tramlines cannot be responsible for the avoidance because we did not generate random points directly on this type of linear structure. Consequently, the detected effect does not only indicate avoidance by Skylarks of breeding directly on them but also of breeding close to the surroundings of linear structures. An alternative explanation of our results could be that nests close to linear structures were depredated very early and thus were not observed by us. However, we consider this to be unlikely because the number of days between laying the first egg and the date of finding the nest did not correlate with the distance to the closest linear structure (Spearman's rank correlation coefficient for data from the early breeding seasons 2017 to 2019: $r = -0.05$; $p = 0.79$, $n = 32$). Thus, the stage of the breeding cycle at the time we found the nest was not associated with the distance to linear structures.

For the later breeding season, earlier studies showed that winter cereal vegetation becomes impenetrable, and Skylarks that do not switch to a different crop are forced to breed on linear structures, which in turn leads to low breeding success (Donald et al. 2002a; Fischer et al. 2009). Our results confirm both a shift of nesting sites of ca. 4 m towards linear structures in the later breeding season as well as a higher nest predation risk on them. This pattern comes along with a curtailment of the breeding season, which is one of the major reasons for the dramatic population decline of Skylarks in Europe (Donald 2004). Therefore, unsown areas in winter cereals as conservation measure have been designed and implemented in various sizes and shapes, including undrilled patches commonly known as Skylark plots (Morris et al. 2004), wide-spaced drill rows sown at double the normal width (Morris et al. 2007; Morris et al. 2004), or additional tramlines (Schmidt et al. 2017). These conservation measures have the potential to prolong the breeding season of Skylarks by providing access to breeding (Fischer et al. 2009) and foraging habitats (Fischer et al. 2009; Morris et al. 2004). However, Schmidt et al. (2017) reported difficulties for farmers with the creation of Skylark plots. Similarly, there are concerns about the amount of land that is taken out of production and potentially overgrown with weeds when implementing double-spaced rows or additional tramlines (Morris et al. 2007; Schmidt et al. 2017).

Because we interpret the detected avoidance behavior as a further example for the ability of Skylarks to assess predation risk at fine spatial scales, we conclude that less uncultivated land may be required to benefit this species. More specifically, we propose the testing of a modified design of additional tramlines that would overcome the above issues. Instead of providing many pairs of two long and unsown ca. 30 cm wide strips (Schmidt et al. 2017), we recommend creating several small fragments of strips of few meters in length. The implementation of these

additional tramline fragments should be similarly easy to that of additional tramlines (Schmidt et al. 2017) for drills with computer-based tramline control. Moreover, due to their smaller size, the amount of unsown land would be greatly reduced. Additional tramline fragments should be positioned maximizing the distance between regular tramlines and unconnected to the field edge, as already recommended for Skylark plots and additional tramlines (Morris et al. 2004; Schmidt et al. 2017). This would make them less accessible for mammalian carnivores, and their small width would likely hamper avian predators to land. Whereas additional tramline fragments also constitute linear structures, we argue that it is the higher nest predation risk close to field edges and tramlines, but not necessarily linear structures *per se* that triggers avoidance behavior. Consequently, we contend that additional tramline fragments give Skylarks the opportunity to avoid high-risk linear structures also from late May onwards and may be actively selected as safe access points for breeding. Besides, we observed that many Skylark nests were built within 2 m distance to occasionally occurring small linear spots of patchy vegetation (e.g., at least seven of the 17 nests in 2019) so that we do not expect an avoidance of additional tramline fragments because of their small size.

In summary, a proven preference of additional tramline fragments over regular tramlines for breeding would not only further support our interpretation that the avoidance of linear structures is an anti-predation behavior in Skylarks but also contribute to the conservation of this species.

## 4.6. Acknowledgements

## 4.7. Supplementary material

All data analyzed and all codes used for analysis during this study are included in this published article and its supplementary information files.

**Supplementary material S4.1.** Data on individual Skylark (*Alauda arvensis*) nests found during the breeding seasons 2017 to 2019. The difference in days between the date of the first egg and the date of finding (Difference find – 1. egg (d)) was set to zero if the nest was found during nest building. Nest outcome with the annotation _i refers to a human intervention through which a parcel of cereals with the nest in the center was not harvested. LS = Linear structure

| Nest_ID | Year | Crop | Breeding stage at find | Date of find | Date of 1. egg | Breeding season | Difference find – 1. egg (d) | Nest outcome | Exposure days | Distance to LS (m) | LS |
|---------|------|------|------------------------|--------------|----------------|-----------------|------------------------------|--------------|---------------|--------------------|-----|
| N01.17 | 2017 | winter wheat | egg | 22.05.2017 | 14.05.2017 | early | 8 | abandoned | NA | 3 | tramline |
| N02.17 | 2017 | winter wheat | egg | 26.05.2017 | 17.05.2017 | early | 9 | successful | 14 | 0.5 | tramline |
| N03.17 | 2017 | winter wheat | chick | 27.05.2017 | 08.05.2017 | early | 19 | successful | 2 | 4 | tramline |
| N04.17 | 2017 | winter wheat | chick | 29.05.2017 | 08.05.2017 | early | 21 | unknown | NA | 14 | tramline |
| N07.17 | 2017 | winter wheat | building | 17.06.2017 | 19.06.2017 | later | 0 | abandoned | NA | 3 | tramline |
| N11.17 | 2017 | winter wheat | building | 23.06.2017 | 27.06.2017 | later | 0 | unknown | NA | 3 | tramline |
| N12.17 | 2017 | winter wheat | chick | 08.07.2017 | 19.06.2017 | later | 19 | successful | 3 | 4 | tramline |
| N13.17 | 2017 | winter wheat | chick | 14.07.2017 | 25.06.2017 | later | 19 | successful | 4 | 4 | tramline |
| N14.17 | 2017 | winter wheat | chick | 14.07.2017 | 26.06.2017 | later | 18 | successful | 3 | 0 | tramline |
| N0A.18 | 2018 | winter wheat | chick | 08.05.2018 | 16.04.2018 | early | 22 | successful | 0 | 6 | tramline |
| N0D.18 | 2018 | winter wheat | chick | 26.05.2018 | 04.05.2018 | early | 22 | successful | 0 | 3.5 | field edge |
| N03.18 | 2018 | winter wheat | egg | 30.04.2018 | 29.04.2018 | early | 1 | successful | 21 | 11 | tramline |
| N04.18 | 2018 | winter wheat | egg | 30.04.2018 | 28.04.2018 | early | 2 | successful | 21 | 8.5 | tramline |
| N05.18 | 2018 | winter wheat | chick | 08.05.2018 | 23.04.2018 | early | 15 | successful | 6 | 9 | tramline |
| N08.18 | 2018 | winter barley | chick | 09.05.2018 | 23.04.2018 | early | 16 | successful | 4 | 10 | tramline |
| N09.18 | 2018 | winter wheat | chick | 11.05.2018 | 23.04.2018 | early | 18 | successful | 4 | 5.5 | tramline |
| N10.18 | 2018 | winter barley | egg | 11.05.2018 | 04.05.2018 | early | 7 | successful | 14 | 11.5 | tramline |

| Nest_ID | Year | Crop | Breeding stage at find | Date of find | Date of 1. egg | Breeding season | Difference find – 1. egg (d) | Nest outcome | Exposure days | Distance to LS (m) | LS |
|---------|------|------|----------------------|--------------|----------------|-----------------|------------------------------|--------------|---------------|--------------------|-----|
| N12.18 | 2018 | winter wheat | egg | 18.05.2018 | 13.05.2018 | early | 5 | successful | 18 | 7 | tramline |
| N13.18 | 2018 | winter barley | chick | 23.05.2018 | 05.05.2018 | early | 18 | successful | 3 | 9.5 | tramline |
| N16.18 | 2018 | winter wheat | egg | 27.05.2018 | 25.05.2018 | later | 2 | successful | 19 | 1.5 | tramline |
| N17.18 | 2018 | winter wheat | egg | 31.05.2018 | 23.05.2018 | later | 8 | predated | 2 | 0.5 | tramline |
| N18.18 | 2018 | winter wheat | chick | 04.06.2018 | 15.05.2018 | early | 20 | successful | 4 | 3 | tramline |
| N21.18 | 2018 | winter wheat | chick | 13.06.2018 | 24.05.2018 | later | 20 | successful | 2 | 2 | tramline |
| N22.18 | 2018 | winter wheat | chick | 14.06.2018 | 27.05.2018 | later | 18 | successful | 5 | 1.5 | tramline |
| N29.18 | 2018 | winter wheat | chick | 03.07.2018 | 14.06.2018 | later | 19 | successful | 1 | 0 | tramline |
| N32.18 | 2018 | winter wheat | chick | 10.07.2018 | 22.06.2018 | later | 18 | successful | 4 | 0 | tramline |
| N34.18 | 2018 | winter wheat | chick | 14.07.2018 | 22.06.2018 | later | 22 | successful | 1 | 7.5 | tramline |
| N35.18 | 2018 | winter wheat | chick | 15.07.2018 | 25.06.2018 | later | 20 | successful | 2 | 0 | tramline |
| N38.18 | 2018 | winter wheat | egg | 18.07.2018 | 13.07.2018 | later | 5 | successful_i | 17 | 3 | tramline |
| N01.19 | 2019 | winter wheat | building | 25.04.2019 | 27.04.2019 | early | 0 | predated | 0 | 4 | tramline |
| N02.19 | 2019 | winter wheat | chick | 28.04.2019 | 13.04.2019 | early | 15 | successful | 8 | 12 | tramline |
| N03.19 | 2019 | winter wheat | egg | 28.04.2019 | 25.04.2019 | early | 3 | predated | 15.5 | 11 | tramline |
| N04.19 | 2019 | winter wheat | chick | 28.04.2019 | 12.04.2019 | early | 16 | successful | 6 | 6 | tramline |
| N05.19 | 2019 | winter wheat | chick | 29.04.2019 | 11.04.2019 | early | 18 | successful | 4 | 12 | tramline |
| N06.19 | 2019 | winter wheat | egg | 30.04.2019 | 23.04.2019 | early | 7 | abandoned | NA | 3.5 | field edge |
| N08.19 | 2019 | winter wheat | egg | 05.05.2019 | 03.05.2019 | early | 2 | successful | 20 | 5.5 | tramline |

| Nest_ID | Year | Crop | Breeding stage at find | Date of find | Date of 1. egg | Breeding season | Difference find – 1. egg (d) | Nest outcome | Exposure days | Distance to LS (m) | LS |
|---|---|---|---|---|---|---|---|---|---|---|---|
| N10.19 | 2019 | winter wheat | egg | 06.05.2019 | 03.05.2019 | early | 3 | abandoned | NA | 4 | field edge |
| N11.19 | 2019 | winter wheat | egg | 09.05.2019 | 06.05.2019 | early | 3 | predated | 10.5 | 7 | tramline |
| N12.19 | 2019 | winter wheat | building | 12.05.2019 | 15.05.2019 | early | 0 | successful | 20 | 8 | tramline |
| N13.19 | 2019 | winter wheat | chick | 13.05.2019 | 26.04.2019 | early | 17 | successful | 6 | 1 | tramline |
| N14.19 | 2019 | winter wheat | building | 14.05.2019 | 20.05.2019 | early | 0 | abandoned | NA | 3.5 | tramline |
| N16.19 | 2019 | winter wheat | building | 15.05.2019 | 17.05.2019 | early | 0 | successful | 26 | 9.5 | tramline |
| N17.19 | 2019 | winter wheat | egg | 18.05.2019 | 13.05.2019 | early | 5 | successful | 18 | 6.5 | tramline |
| N19.19 | 2019 | winter wheat | egg | 21.05.2019 | 13.05.2019 | early | 8 | abandoned | NA | 5.5 | tramline |
| N22.19 | 2019 | winter wheat | egg | 24.05.2019 | 17.05.2019 | early | 7 | destroyed | 2.5 | 0.5 | tramline |
| N23.19 | 2019 | winter wheat | egg | 27.05.2019 | 23.05.2019 | later | 4 | predated | 4.5 | 8 | tramline |
| N24.19 | 2019 | winter wheat | chick | 28.05.2019 | 14.05.2019 | early | 14 | successful | 7 | 4 | tramline |
| N27.19 | 2019 | winter wheat | egg | 31.05.2019 | 25.05.2019 | later | 6 | successful | 15 | 6 | tramline |
| N29.19 | 2019 | winter wheat | egg | 01.06.2019 | 28.05.2019 | later | 4 | predated | 8.5 | 0 | tramline |
| N36.19 | 2019 | winter wheat | egg | 17.06.2019 | 13.06.2019 | later | 4 | predated | 14.5 | 0 | tramline |
| N40.19 | 2019 | winter wheat | chick | 23.06.2019 | 09.06.2019 | later | 14 | successful | 7 | 11 | tramline |
| N42.19 | 2019 | winter wheat | egg | 25.06.2019 | 17.06.2019 | later | 8 | predated | 8.5 | 1.5 | field edge |
| N55.19 | 2019 | winter wheat | egg | 16.07.2019 | 13.07.2019 | later | 3 | predated_i | 14 | 0 | tramline |
| N56.19 | 2019 | winter wheat | chick | 20.07.2019 | 02.07.2019 | later | 18 | successful | 3 | 1.5 | tramline |

For **supplementary material S4.2** (data on 320,000 random points generated for a scenario of random Skylark nest distribution) and **supplementary material S4.3** (*R* code for all analyses conducted in the study) see: https://doi.org/10.1007/s10336-020-01833-1

# Chapter 5

# Synopsis

## 5.1. Conventionally managed but heterogeneous farmland – the key to saving the Skylark?

Contradicting my expectations at the beginning of this PhD project, I could not find indications of worsening problems for breeding Skylarks during the breeding season from mid-April to the end of July.

Winter cereals were the dominating crops at the study site, covering ca. 40%, which is similar to the area of all cereals on arable land in the EU (Eurostat 2022). Therefore, consequences of the dense-growing crop vegetation for breeding Skylarks were clearly observable. For instance, I observed that the number of nests initiated within winter cereal fields rapidly decreased from the end of May onwards, supporting several earlier studies (e.g., Ottens et al. 2013; Schläpfer 1988). In parallel and accordance with Donald et al. (2002a), nests in winter cereals were positioned significantly closer to high-risk linear structures, like tramlines, during the later breeding season. Nevertheless, my co-authors and I did not detect a restriction for successful breeding attempts to the early breeding season (Chamberlain et al. 2000; Donald 2004; Wilson et al. 1997) or a seasonal decrease in food availability (Donald and Morris 2005; Jenny 1990a; Weibel 1998). I interpret these findings as clear effects of diverse habitat composition and, more importantly, diverse habitat configuration within the study area. Winter crops were typically cultivated in fields next to sugar beet, other summer crops, or set-aside, thus creating a mosaic of vegetation structures. Consequently, this mosaic made it possible for Skylarks to compose stable, diverse home ranges with suitable nesting and foraging sites throughout the breeding season. The calculated nest success of roughly 54%, to my knowledge, is outstanding as the highest value documented for breeding Skylarks on farmland.

Therefore, the studies that arose from my PhD project provide direct evidence for the positive synergetic effects of crop complementation, as suggested by Miguet et al. (2013). Other research has already pointed to the importance of habitat diversity for Skylarks and farmland birds in general (e.g., Eraud and Boutin 2002; Šálek et al. 2021; Schläpfer 1988; Sirami et al. 2019; Tscharntke et al. 2021), although not all studies come to this same conclusion (e.g., Hiron et al. 2015; Martin et al. 2020). The added value of the work presented in this dissertation is that we present positive effects of local crop diversity on the individual level and not based on breeding pair densities, thus filling the knowledge gap pointed out by Hiron et al. (2012). The few older, existing studies that followed Skylarks throughout the breeding season came to similar conclusions (Jenny 1990b; Schläpfer 1988), but at study sites with parcel sizes of only 0.4 to 2.3 ha. I find it encouraging that Skylarks can also benefit from crop diversity on farmland with an average field size of ca. 5 ha. As agrobiodiversity generally decreases with increasing field size (Fahrig et al. 2015), future research should search for thresholds of a maximum field size tolerable for Skylarks and other farmland taxa. The less structurally diverse

a Skylark home range in my study area was, the more extensive its size (Heinz, unpublished data), and it is possible the larger fields generally triggered the formation of larger territories or home ranges (Jenny 1990b; Schläpfer 1988). However, a comparison with other studies is difficult due to the various methods of territory/home range estimation (Donald 2004). At least, larger territories or home ranges cannot be deduced from the Skylark densities at my study site (3 to 4 breeding pairs/10 ha, calculations based on unpublished data by Langer 2017 and Meineke 2020), which are similar or even higher compared to those reported in the two Swiss publications (Jenny 1990b: 1.1 to 2.0 breeding pairs/10 ha; Schläpfer 1988: 0.9 to 3.0 breeding pairs/10 ha).

Overall, the results of my PhD project strongly suggest that a successful breeding season for Skylarks is also possible in conventionally managed farmland under the premise of compositional and configurational heterogeneity, including areas of set-aside. Tscharntke et al. (2021) already urged policy-makers to focus on the diversification of cropland and the reduction of field size to enhance biodiversity while sustaining high yields. It is important to emphasize that, while I do not want to argue against the value of organic farming and the efforts to increase its use, I believe from my research that a heterogenization of farmland could be the most practical step to counteract the decline of Skylarks.

Regarding single conservation measures, I suggest focusing on those that provide suitable nesting sites. In our study area, shifts of nesting habitats were likely triggered by demands on the nesting site itself and not by foraging habitat preferences. If this holds true for other regions, then the need for suitable nesting sites and not foraging habitats determines the dynamics of habitat use. Moreover, measures that increase food availability cannot compensate for nest failures due to agricultural practice and predation (Kuiper et al. 2015).

Although I am confident about the correctness of my conclusions, it is essential to note the intrinsic limitations of a short-term PhD project. The intensive and time-consuming fieldwork made it impossible to simultaneously collect data in more homogeneous farmland that could have been used as a reference. Moreover, 2018 and 2019 were extraordinarily hot and dry (Deutscher Wetterdienst 2021a; Zscheischler and Fischer 2020). Consequently, because data was only available for these years, my co-authors and I could not consider the detrimental effects of heavy rainfall (Donald et al. 2001a) or exclude behavioral adaptations of animals in response to the heat (Buchholz et al. 2019), e.g., changed activity patterns of predators that affected the predation risk. Finally, large fluctuations in the breeding success between 2018 (1.1 successful breeding attempts per pair) and 2019 (0.4), with a consistent total number of ca. 1.5 breeding attempts prevent firm conclusions regarding the self-sustainability of the Skylark population south of Göttingen. This knowledge would be the prerequisite to promoting my study area as a good example of modern farmland.

**5.2. Potential focuses for future research on Skylarks**

First, I would like to encourage studies that replicate my research but address the limitations mentioned above by collecting data with similar methods over several years and in various agricultural landscapes. Besides this, I suggest three primary research topics to generate practice and policy recommendations for supporting Skylark populations in European farmland.

(i) There is still a need for comprehensive knowledge of the demographic parameters shaping the population dynamics of Skylarks. My co-authors and I made contributions by providing data about the number of breeding attempts and chicks that leave the nest per pair and year, which Donald (2004) called the Holy Grail of modern Skylark research. However, little is known about the fate of chicks between leaving the nest and fledging. Available studies indicate higher losses than previously assumed, with only 19% to 27% of chicks outside the nest fledging (Helmecke et al. 2005; Ottens et al. 2016). Similarly, current data on the survival rates of first-year birds and adults are scarce. This data scarcity challenges the estimations of the impacts of legal Skylark hunting (Hirschfeld et al. 2019) on population viability. Moreover, demographic parameters cannot be generalized across populations because they heavily depend on numerous contextual factors (e.g., the composition of farmland in the breeding grounds or the risk of being killed during migration). Therefore, similar studies must be conducted across Europe. Bird ringing centers that explicitly ask European ringers to catch Skylarks to understand better their population dynamics have taken a crucial first step (Beringungszentrale Hiddensee 2021). Further insights can be expected from the next generation of small GPS transmitters that will be small enough to tag Skylarks (ICARUS 2022).

(ii) Scientists should investigate the impact of new land-use changes on Skylarks directly from the start. Over the next decades, climate change will force significant adaptations of agricultural practices in Europe (Anderson et al. 2020; European Environment Agency 2019; Iglesias et al. 2012). Measures, like the use of better climate-adapted crops, will affect agrobiodiversity and ecosystem services in a way that is not yet predictable and strongly depends on the associated agricultural practices (European Environment Agency 2019). At the same time, measures to mitigate climate change, such as increased renewable energy production, might also threaten Skylarks on farmland. For instance, habitat avoidance and increased mortality risk are frequently reported consequences of wind turbines for several bird species (Dai et al. 2015; Marques et al. 2020). First studies already documented male Skylarks as common victims of collisions due to their elevated song flights (Morinha et al. 2014) and a change in song characteristics due to the noise of wind farms (Szymański et al. 2017).

(iii) Conservation measurements to save the Skylark and other farmland taxa need to be regularly evaluated according to scientific standards and, if necessary, modified or replaced.

This adaptive management allows for detecting inefficient approaches, like the existing greening of the CAP (Pe'er et al. 2017). New measures should constantly be developed based on the latest scientific findings and more efficiently communicated with practitioners to better fill the science-practice gap in nature conservation (Fabian et al. 2019). Following the argument of Martin et al. (2020), which is used to promote a reduction in agricultural field sizes, I believe that scientists should first focus on efficient agrobiodiversity measures with minimal impact on agricultural production because I expect those measures to have the greatest chance of implementation. Considering this, I am looking forward to the upcoming experimental testing of additional tramline fragments, which my co-authors and I suggest as a modification of Skylark plots (Morris et al. 2004). This topic will be investigated at my study site in the breeding season of 2022.

I sincerely hope that these and all the other issues raised in my dissertation will contribute to the better conservation of this species so that future generations in Europe can experience the extraordinary beauty of a singing Skylark as well.

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