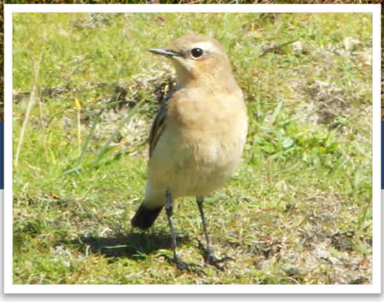

Conservation of threatened grassland birds – Large, nutrient-poor and heterogenous grasslands are of prime importance

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Front & back cover
Front: Natural dune grassland on the island of Spiekeroog and investigated species (from left to right): Wheatear (*Oenanthe Oenanthe*), Eurasien Curlew (*Numenius arquata*) and Short-eared Owl (*Asio flammeus*).
Back: Short-eard owl (*Asio flammeus*) in flight.

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Preface

The fascination with the diversity of life on our planet inspires people of all ages in all parts of the world. Nevertheless, the loss of biodiversity and the extinction of species by human activity continue to accelerate and are not reversible. So far, isolated successes in nature conservation measures have not been able to bring about any change in this trend. Wilson (2008) therefore states that:

> *"The history of conservation is a story of many victories in a losing war."*

It seems that only enlarging the area under protection from human intervention and advancing societal changes towards the sustainable use of resources considerate of the planetary boundaries might reverse this trend. Because this process will be lengthy, conservation efforts can be valuable in the immediate future, buying time to allow the recovery of species and ecosystems and provide important knowledge on effective conservation measures. This thesis aims to contribute to this process by analysing habitat requirements and ecology of threatened umbrella species as a basis for the development of effective conservation measures.

Chapter I

Introduction

Natural dune habitats on the East Frisian Island Spiekeroog. Extensive and nutrient-poor grasslands like natural dunes become rare due to land-use change in Europe. Therefore, numerous species dependent on such habitats are particularly threatened (Spiekeroog 29/06/2022).

Introduction

THE IMPORTANCE OF BIODIVERSITY

Biodiversity is the biological variety and variability of life on earth and encompasses genetic diversity within species, as well as diversity between species and of ecosystems (CBD 1992). Biodiversity plays a significant role in mankind's fascination with planet Earth resulting in an intrinsic value, which is subject to moral considerations (Fosci & West 2016). On the other hand, biodiversity performs important ecosystem services for the well-being of humanity on Earth. These ecosystem services can be grouped into provisioning (production of food and water), regulating (control of climate and disease), supporting (nutrient cycles and oxygen production), and cultural (spiritual and recreational) benefits (De Groot et al. 2002, Costanza 2017). The concept of ecosystem services enables the quantification of the value of biodiversity not only in moral or aesthetic but also in economic terms (e.g. Bartowksi 2017, Hanley & Perrings 2019). For instance, the value of insect pollination in Germany alone is estimated at 3.8 billion dollars per year (Lippert et al. 2021). Therefore, humankind is strongly dependent on intact and functioning ecosystems from an ecological and economic point of view (Burkhard & Maes 2017, Cardoso et al. 2020). Even though the approach of putting a price on earthly life is controversial, it can make arguments for the protection of biodiversity more convincing (Masood 2018). Irrespective of whether the value of biodiversity is considered from an intrinsic or an economic point of view, there is great agreement on the high value of biodiversity for humankind and the associated need to conserve and protect it (CBD 1992).

BIODIVERSITY IN THE ANTHROPOCENE

Loss of biodiversity

Although the value of biodiversity is mostly beyond debate, it is declining on a global scale and at rates unprecedented in human history (IPBES 2019). The current rate of extinction is estimated to be 1,000 times higher than natural background rates (Pimm et al. 2014, De Vos et al. 2014). Consequently, scientists recently warned that the planet is heading towards a sixth mass extinction (Barnosky et al. 2011, Cowie et al. 2022). Despite conservation efforts, there is no evidence of a slowdown in rates of change (Tittensor et al. 2014). In contrast, the rate of species extinction is still accelerating, with probable grave impacts on people around the world (Cook 2020). Knowledge of current threats suggests that extinction rates could rise to a level five times higher than observed in the recent past (Johnson et al. 2017). Consequently, loss of biodiversity is one of the most fundamental challenges facing humankind (Pimm et al. 2014, Cook 2020). At least since the adaption of the Convention on Biological Diversity in 1992, there has been a broad consensus that the progression of biodiversity loss must urgently be prevented to preserve the basis of life on earth (CBD 1992). However, targets defined in the Biodiversity Convention have so far largely been missed globally (Buchanan et al. 2020) due to a lack of action and knowledge (Mehring et al. 2017). To achieve biodiversity targets in the future, consistent political action and further research on drivers of biodiversity and its conservation are urgently needed.

Drivers of biodiversity loss

The current pressure of human civilization on nature is greater than ever and reaches an extent comparable to the effect of major geological forces (Storch et al. 2021). Traces of human activities can be found even in the most remote areas of the world and human influence is causing ecosystems and biodiversity to change at an unprecedented speed (Pearson 2020). Humans are effecting tremendous changes on the planet and have now become the dominant influence on the climate and environment. Consequently, the current geological age is referred to as the Anthropocene (Cook 2020, Pearson 2020).

The most important drivers of the current loss of biodiversity are human activities through alterations of the environmental conditions including overexploitation, conversion of habitat, climate change, the spread of non-native species, disease, pollution, and urban development (Sala et al. 2010, Butchart et al. 2010, Maxwell et al. 2016). Among these factors, habitat loss and degradation through land-use change were identified as the most important drivers of species decline in terrestrial ecosystems (Sala et al. 2010). Worldwide, 75 % of the terrestrial environment were severely altered to date by human actions, with an even higher proportion in Europe (Venter et al. 2016). However, the effects of human activities do not necessarily have exclusively negative impacts on biodiversity. This can be seen in the example of traditional and low-intensity agriculture in Central Europe. According to the megaherbivores theory, large herbivores had maintained open habitats through browsing and trampling of huge areas throughout Europe (Johnson 2009, Storch et al. 2021). At the end of the Pleistocene, many of these herbivores were extirpated probably through direct persecution by humans (Bulte et al. 2006). From that point on traditional and low-intensity agriculture prevented overgrowth by homogenous forests and was thereby crucial to preserve open, heterogeneous habitat mosaics with structural diversity (Bocherens 2018). In this way, cultural landscapes in Europe have always been in a state of change, but during the second half of the last century, the pace and extent of changes increased dramatically (Fuller 2012). Through the upcoming industrialisation of agriculture, the positive effect of agricultural activities disappeared and even reversed (Dobrovodská et al. 2019, Storch et al. 2021). Especially agricultural mechanization, increased input of agrochemicals like synthetic fertilizer and pesticides, increasing nitrogen depositions and the associated homogenization of the landscape caused a sharp decline in habitat diversity in agricultural landscapes (Sala et al. 2000, Robinson & Sutherland 2002, Henle et al. 2008, Butchart et al. 2010). Moreover, especially grasslands suffered either from intensification or abandonment (Veen et al. 2009). As a result, particularly species associated with low-intensity land use and nutrient-poor conditions suffered huge population declines across different taxa such as plants, insects, and birds (Vickery et al. 2001, Donald et al. 2006, Flohre et al. 2011).

Another example of man-made changes with fatal consequences for biodiversity on earth is the anthropogenic climate change (Sala et al. 2010, Bellard et al. 2012). Many studies provide evidence that global warming is already affecting species and ecosystems (Parmesan 2006, Chen et al. 2011, Fumy et al. 2021). Climate change not only causes changes in temperature and precipitation resulting in habitat degradation (Miller et al. 2020) but also affects species phenology and distribution and in this way alters trophic interactions between organisms (Millon et al. 2014, Poniatowski et al. 2020, Acácio et al. 2022). In migratory birds, migration patterns are found to be changing due to climate change and other environmental factors like food availability (Clausen et al. 2018, Lehikoinen et al. 2021). This includes not only changes in the timing of migration (Jenni & Kéry 2003, Conklin et al. 2021), but also in migration distances resulting in a shift of the wintering areas (Visser et al. 2009).

Consequently, anthropogenic climate change is having an increasing impact on biodiversity and is already causing large disruptions to species and ecosystems (Scheffers et al. 2016, Johnson 2017). Due to ongoing climate change, the long-term effect of global warming is expected to grow and even exceed those caused by land-use change on a global scale (Sala et al. 2000, Schefferset et al. 2016).

Because of various interactions between climate and species, the impact of climate change on species and ecosystems is hard to assess or even predict. This is further complicated by numerous interactions between climate change, land use change, loss of biodiversity, and other global changes, many of which are not yet fully understood (Prestele et al. 2017, Doelman et al. 2018).

BIODIVERSITY CONSERVATION

While some of the man-made, profound changes causing the loss of biodiversity are irreversible, it seems possible to halt or reverse some changes (Cook 2020). Although there are some encouraging results of conservation efforts around the world, there is still no sign of a global trend reversal, and pressure on biodiversity in the Anthropocene is predicted to continue, if not increase, over the coming decades (Heywood 2018, IPBES 2019). To counteract the ongoing loss of biodiversity, only far-reaching transformative societal changes towards a sustainable use of resources that considers the planetary boundaries can bring about a trend reversal on a global scale (Rockström et al. 2009, Johnson et al. 2017, IPBES 2019). Nonetheless, conservation efforts can be valuable in buying time that could allow recovery of species and ecosystems in the future and provide important knowledge on how conservation measures can be made more effective (Johnson et al. 2017). In view of the massive extinction of species, enlarging the area that is protected from human interventions and effective large-scale conservation measures appear to be the only way to slow down the loss of biodiversity and thus maintain the possibility of preserving biodiversity in the long term. Addressing these challenges requires detailed understanding of habitat requirements and ecology of threatened species. Such knowledge is essential to assess possible outcomes of different management decisions and prevent future loss of biodiversity (Wyborn et al. 2021). Even though large-scale measures are often perceived as very expensive, their benefits might outweigh the significant larger costs of the high socioeconomic damage caused by biodiversity loss (Lippert et al. 2021, Yao et al. 2019). However, there is still a lack of sufficient large-scale conservation measures and the knowledge required for their development.

Depending on how many habitats and landscapes have already been changed by human activities, two very different approaches to conservation can be considered. The first of these, ‘rewilding,’ is characterised by the reintroduction of large herbivores or key predators with the aim of bringing the ecosystem in the reserves into a natural balance. Together with a ban on human activities in this area, this approach is supposed to enable natural dynamics that promote biodiversity. This approach requires large areas and is designed, for example, in national parks, where a large part of the area is subject to natural processes (Carroll & Noss 2021). This approach is limited to human-altered habitats missing key species like top predators or megaherbivores and therefore natural dynamics.

The other approach is characterised by human measures to simulate natural processes disrupted or stopped by man-made environmental changes. Corresponding examples are the financial support for low-intensity farming practices or the integration of agri-environmental schemes in cultural landscapes (Cook 2020, Storch et al. 2021) but also the active (re)creation of functioning ecosystems (Perino et al. 2019). This approach of human conservation measures can also be implemented on smaller spatial scales and in areas with high levels of human activities. However, continuous, and sometimes costly human measures are necessary to preserve such habitats (Corlett 2016).

In both approaches, ecosystem engineers can play important roles to implement natural dynamics and provide key resources which are essential for other species. Ecosystem engineers are organisms that alter the availability of resources by modifying the physical state of biotic or abiotic materials (Jones et al. 1994). Popular examples are the Eurasian beaver (*Castor fiber*) (Brazier et al. 2020) and the European rabbit (*Oryctolagus cuniculus*) (Gálvez-Bravo et al. 2009) but also Ants (*Formicidae*) (Streitberger et al. 2017) and the European mole (*Talpe europaea*) (Streitberger & Fartmann 2013). Because ecosystem engineers can act as key stone species in both natural and human-altered habitats, they are important for biodiversity conservation in any case.

Given the ongoing declines in numerous species, the consistent protection of all habitats and required sites over the course of an annual cycle (breeding, migration, wintering) is urgently needed, regardless of the conservation approach chosen.

BIRDS AS INDICATORS

Birds and bird assemblages have been extensively studied around the world. Moreover, many studies found birds and bird assemblages around the globe to react sensitively to changes in land use and climate, demonstrating that ongoing processes of global change can be studied effectively on birds (e.g. Butet et al. 2022, Müller, et al. 2022, Romano et al. 2023). Therefore, they are excellent indicators for biodiversity at both habitat and landscape level (Donald et al. 2001, Gregory et al. 2003, Fartmann et al. 2018).

Land-use change was found to affect birds mainly through habitat degradation and destruction, especially due to land use intensification (Newton 2017) and associated reduction of feeding and breeding habitats as well as due to increasing numbers of mesopredators (Fuller 2012, Newton 2017, Roos et al. 2018, Butet et al. 2022). Especially for ground-breeding bird species predation and nest destruction through agricultural measures are among the most important factors reducing nest and fledglings' survival significantly (Roos et al. 2018). As a result, the reproduction rates of many species are not sufficient to ensure stable populations.

Consequently, many species are declining and threatened with extinction. In Germany, almost 30 % of bird species are considered vulnerable, endangered, or even threatened with extinction. 43 % of the native breeding birds have been placed in one of the Red List categories and are considered at least near threatened (Ryslavy 2021). While populations of many forest bird species are stable or even increasing, the proportion of threatened species is particularly high among farmland birds (Kamp et al. 2021). On the other hand, there are also species with the ability to adapt to anthropogenic changes (Otto 2018). In this way, working with birds as model organisms allows the study of different responses to human activities and underlying processes as a basis for the development of conservation measures.

ISLANDS AS REFUGES

Although islands make up only a small fraction of the Earth's landmass, they are home to a disproportionately large share of global biodiversity (Kier et a. 2009, Tershy et al. 2015). However, due to isolation, limited area, and natural fragmentation, island biodiversity is particularly vulnerable to the profound changes in habitats caused by global change (Chisholm et al. 2016; Spatz et al. 2017; Fernández-Palacios et al., 2021). Conversely, their isolation from many of the dominating processes threatening biodiversity on the adjacent mainland can allow islands to act as important natural refuges, harbouring rare or even endemic species. (Salz & Fartmann 2009, Roos et al. 2018, Gibson et al. 2017, Kämpfer & Fartmann 2022). Particularly for ground-breeding bird species, islands free of predatory mammals offer important retreat areas in which the reproductive success is significantly greater than on the surrounding mainland (Roos et al., 2018; Kämpfer et al., 2022). Thus, islands can harbour important source populations for endangered species.

Island biodiversity is changing especially with the introduction of non-native species becoming a part of many ecosystems, and humans shaping many ecological processes (Pearson 2020). Non-native species like mammals acting as predators are a major threat to ground-breeding (bird) species and, consequently, to biodiversity on islands. Thus, islands are microcosms for the emerging biodiversity and socioecological landscapes of the Anthropocene (Pearson 2020), which makes them an excellent model system for conservation (Kueffer et al. 2014).

STUDY AREA

The study area of this thesis comprises different grassland areas in Northwest Germany within the federal states of Lower Saxony, Bremen, and North Rhine-Westphalia with a focus on the East Frisian islands in the southern North Sea. Study sites on the mainland were characterized by different types of agricultural grasslands. Most of these are primarily used for intensive agriculture, especially haymaking and silage production but agri-environmental schemes are applied in some areas (Früh-Müller et al. 2019, Blickensdörfer et al. 2022). Most studies were conducted on the East Frisian Islands of Borkum, Juist, Norderney, Baltrum, Langeoog and especially Spiekeroog (Lower Saxony, Germany), which are a refuge habitat for many threatened species (Niedringhaus et al. 2008). The Wadden Sea Islands cover an area of about 120 km² and are sandy barrier islands, influenced by tides. The islands are characterized by high shares of natural and semi-natural habitats with low land-use intensity. They are dominated by beaches, mudflats, marshes, built-up areas, and dune grasslands and part of the Wadden Sea National Park of Lower Saxony and the Wadden Sea World Heritage site (Baird & Asmus 2020). In contrast to the mainland, disturbance through human activities occurs rarely. Only small parts are used for low-intensity agriculture and human access is prohibited in most areas through legal regulations of the national park. Except for Norderney, all islands are free from mesopredators like the Red Fox (*Vulpes vulpes*). Another mammal found in high densities on some of the islands while other islands are not populated is the non-native European rabbit (*Oryctolagus cuniculus*) (Niedringhaus et al. 2008).

AIM AND OUTLINE OF THE THESIS

As a result of the large-scale loss of open and extensively used grasslands in the second half of the 20th century mainly through land-use change (Henle et al., 2008, Stoate et al., 2009), many species associated with semi-natural grasslands are particularly threatened with extinction throughout Europe (Mahony et al. 2022). In birds, ground-breeding species are particularly affected (Kamp et al. 2021). Additionally, climate change puts further pressure on the remaining habitats and thus becomes another crucial driver of biodiversity loss (Sala et al. 2000, Pöyry et al. 2009).

Addressing these challenges requires detailed knowledge of species' ecological demands and how these might change in response to future environmental changes. Such knowledge is crucial to estimate potential threats and to develop evidence-based conservation strategies that anticipate future changes in resource availability (Senner et al. 2020, Verhoeven et al. 2021). To gain relevant knowledge, scientific studies on habitat preferences and habitat requirements are essential. However, investigating remnant populations that already suffered declines carries the risk of using habitats that are no longer suitable for successful reproduction as a reference for conservation measures. Because major habitat deterioration occurred during recent decades, the consequences of habitat changes may not have been fully realized. The occurrence of species might therefore represent an extinction debt (Tilman & Lehman 1994). Despite unsuitable conditions, species can still be found years after habitat conditions have deteriorated. In birds, this phenomenon is particularly evident in long-lived species and species showing breeding site fidelity like the Eurasian Curlew (*Numenius arquata*) (Valkama et al. 1998, Kueffer et al. 2014). Study sites that are used to identify habitat requirements as a basis for conservation measures must therefore be carefully selected and should not represent fragmented remnant populations, but rather core habitats that harbour healthy and constant populations. Therefore, this thesis seeks to gain insights into breeding habitat requirements and ecology of threatened species in natural dune grasslands with successful reproduction. Three bird species of conservation concern, inhabiting open grasslands were studied as model organisms that represent different ecological niches and habitat requirements. In detail the Wheatear (*Oenanthe Oenanthe*) was treated as a songbird feeding on small insects and larvae, the European Curlew (*Numenius arquata*) as a representative of grassland breeding waders feeding on vertebrates and earthworms and the Short-eared owl (*Asio flammeus*) as a raptor species feeding on voles (*Mircotus spec.*).

Overall, the thesis includes five studies covering different areas of habitat requirements, breeding ecology, and migration ecology. The first part of the thesis deals with breeding habitat requirements of threatened ground-breeding grassland birds on island refuges based on three model organisms with different ecology (chapter II). The aim of Paper 1 was to investigate the dependence of a threatened songbird on an ecosystem engineer, the European Rabbit (*Oryctolagus cuniculus*). In Paper 2 habitat and nest-site preferences of a declining grassland bird, the Eurasian Curlew, were studied in natural dune grasslands with successful reproduction. In Paper 3 habitat preferences of a raptor feeding on voles were investigated, drawing on the Short-eared Owl as a model organism in one of the last remaining permanent populations in Central Europe. Habitat and nest-site preferences of the Short-eared owl were determined using a large long-term monitoring dataset to analyse characteristics of consistently occupied habitats (Paper 3).

Chapter III deals with breeding and migration ecology of threatened grassland species. In Paper 4, nest and fledgling survival of the Short-eared owl were studied in relation to (i) habitat composition, (ii) vegetation structure, (iii) weather conditions and (iv) vole abundance. Because the consistent protection of species requires the protection not only of breeding habitats but also other areas and sites which are used over the course of an annual cycle, Paper 5 deals with the migration ecology of a threatened wader to identify important habitats outside the breeding area. Therefore, migration routes, wintering areas, and stopover sites of the Eurasian Curlew breeding in Northwest Germany were studied based on a large sample of GPS-tagged birds, which until now were exclusively analysed based on ring recoveries. The aim of this study was to identify essential areas for the protection and the development of conservation measures in stopover and wintering habitats. Of particular interest was the proportion of birds wintering in France, as France is currently considering a reintroduction of Curlew hunting based on an adaptive harvest management plan (AEWA Eurasian Curlew International Working Group 2019).

Based on the findings of the five studies, consequences for the protection of the investigated model organisms as umbrella species for open grasslands are discussed and recommendations for future conservation measures are given (chapter IV).

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Dune grasslands are characteristic habitats on the East Frisian Islands as part of the Wadden Sea National Park of Lower Saxony (Spiekeroog, 11/07/2018).

The dune chains in the north are followed by salt marshes in the southern parts of the islands (Spiekeroog, 28/08/2018).

Chapter II

Habitat requirements of threatened grassland birds on island refuges

Dune chain in the transition zone between saltmarsh and dune grassland (Spiekeroog, 01/08/2019)

Chapter II

Breeding habitat requirements of threatened grassland birds on island refuges

Paper 1

Breeding populations of a declining farmland bird are dependent on a burrowing, herbivorous ecosystem engineer

Paper 2

Natural coastal dunes on Wadden Sea islands as a refuge for an endangered wader species

Paper 3

Extensive dune grasslands largely lacking human disturbance are an important refuge for a vole-dependent raptor

(1) Breeding populations of a declining farmland bird are dependent on a burrowing, herbivorous ecosystem engineer

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ABSTRACT

In recent decades, numerous farmland birds have experienced considerable population declines. The loss of nutrient-poor habitats with short vegetation due to land-use intensification, abandonment or nitrogen deposition helps account for this decrease. Soil-disturbing ecosystem engineers can naturally create short and sparsely vegetated swards with beneficial effects for biodiversity. The aim of this study is to examine the influence of the European rabbit (*Oryctolagus cuniculus*) as an ecosystem engineer on breeding populations of the severely declining Northern Wheatear (*Oenanthe oenanthe*) on the East Frisian Islands (Lower Saxony, northern Germany). Rabbits were found to have had a considerable influence on the structure of the dune grassland, the main breeding habitat of the Wheatear: high rabbit abundance resulted in greater burrow density and more bare ground. Wheatears were also more abundant on islands with larger rabbit populations. At the plot level, Wheatear abundance increased with burrow density and the cover of potential foraging habitats (short vegetation). In addition, the likelihood of nest-building increased with burrow density and decreased with vegetation height. We thoroughly investigated the dependence of the northern Wheatear on large populations of the ecosystem engineer European rabbit. Through their digging and grazing activities, rabbits create two key resources for breeding Wheatears: (i) sufficient burrows as potential nesting sites and (ii) the availability of short vegetation as foraging habitats.

KEYWORDS

Dune grassland, European rabbit (*Oryctolagus cuniculus*), Habitat preference, Land-use change, Northern Wheatear (*Oenanthe oenanthe*), Vegetation structure

INTRODUCTION

Biodiversity loss in the Anthropocene constitutes a global concern (Rockström et al., 2009). Indeed, current extinction rates are 1,000 times higher than the natural background rate (De Vos et al., 2014). For terrestrial biomes, land-use change is assumed to be the main driver of species loss (Sala et al., 2000; Foley et al., 2005). Although most of Europe's biodiversity is associated with agricultural land (Donald et al., 2006; Henle et al., 2008; Kleijn et al., 2009), farmlands exhibit the largest decrease in biodiversity across different taxa such as plants, insects or birds (Donald et al., 2006; Flohre et al., 2011; Vickery et al., 2001). Two contrasting processes have been identified as the primary reasons for the recent loss of farmland flora and fauna: (i) the intensification of land use in productive areas; and (ii) the abandonment of marginal land (Foley et al., 2005; Henle et al., 2008; Kleijn et al., 2009). Both processes work alongside atmospheric nitrogen deposition (Wallis De Vries and Bobbink, 2017) to instigate a loss of nutrient-poor habitats with short vegetation, an important factor behind the steep decline of numerous farmland birds (Butler and Gillings, 2004; Devereux et al., 2004; Stillman and Simmons, 2006).

For grasslands, it has been shown that soil-disturbing ecosystem engineers can naturally create short and sparsely vegetated swards (Davidson et al., 2012; Streitberger et al., 2017). Ecosystem engineers are generally defined as organisms that alter the availability of resources by modifying the physical state of biotic or abiotic materials (Jones et al., 1994). Research on ecosystem engineers has particularly focused on soil-disturbing animals in the steppe and desert ecosystems of North America and Asia (Davidson et al., 2012). Nevertheless, in Central European grasslands, certain animal species also act as ecosystem engineers (e.g., ants, mole or wild boar) (Seifan et al., 2010; Streitberger et al., 2014; Streitberger and Fartmann, 2016; Streitberger et al., 2017; Schaetzen et al., 2017). Due to their burrowing and mound-building activities, they can create small-scale patches of open and short vegetation with beneficial effects for less competitive plant species or threatened butterfly species. Another example of an ecosystem engineer occurring in European grasslands is the European rabbit (*Oryctolagus cuniculus*), which is known to promote lizard diversity and density through its borrowing activities (Bravo et al., 2009; Grillet et al., 2010). Yet, systematic studies regarding the effects of rabbits on bird species in open landscapes have not been conducted.

The northern Wheatear (*Oenanthe oenanthe*) was formerly a widespread breeding bird of open habitats with sparse and short vegetation in Europe (Cramp, 1988; Bauer et al., 2012). However, due to the loss of such habitats, Wheatear populations have declined in many European countries (Burfield and Van Bommel, 2004; BirdLife International, 2015). In Germany, the decrease has been estimated at 21–50% for the period 1985–2009 (Gedeon et al., 2014; Birdlife International, 2015). Several authors perceive that Wheatears benefit from grazing by European rabbits through the creation of short vegetation for foraging (Brooke, 1979; Tye, 1980; Conder, 1989; Wilson et al., 2009; Newton, 2017). Furthermore, it has been shown that rabbit burrows are regularly used for nesting (Conder 1989; Blüml and Schönheim, 2006). Interestingly, in the Netherlands Wheatear decline appears to have followed rabbit population trends with a delay of five to ten years (Van Turnhout et al., 2007). However, a thorough investigation of the relationship between the occurrence of European rabbit and the northern Wheatear has yet to be undertaken.

The aim of this study is thus to examine the influence of European rabbits on breeding populations of the rapidly declining northern Wheatear. We selected the East Frisian Islands (Lower Saxony, northern Germany) for our study location, because the islands vary considerably in rabbit abundance. The influence of rabbit abundance on habitat structure and Wheatear populations was analysed by considering all eight East Frisian Islands. Detailed studies on the habitat preferences of breeding Wheatear were conducted on the Lower Saxonian abundance hotspot of the species, the island of Norderney.

MATERIALS AND METHODS

Study species

The northern Wheatear (*Oenanthe oenanthe*) is an insectivorous passerine bird with a Palaearctic and north Nearctic breeding range (Bauer et al., 2012). The wintering grounds of the European breeding population of this long-distance migrant are the sub-Saharan savannahs in Africa (Schmaljohann et al. 2012). The species breeds in open habitats with sparse and short vegetation (Cramp, 1988). For nesting the northern Wheatear relies on cavities such as rock crevices, niches and burrows (Conder, 1989). In the Central European lowland, breeding Wheatears mainly occur in human-made habitats, for instance clear-cuts, peat cuts, military training areas, surface-mining areas and vineyards (Bauer et al., 2012). In contrast, on the coastal islands of the North Sea the species primarily occurs in natural dune grasslands (Blüml and Schönheim, 2006). Due to steep declines the northern Wheatear is considered critically endangered in Lower Saxony (1990–2014: >50%) and Germany (1985–2008: >50–75%) (Grüneberg et al., 2015; Krüger and Nipkow, 2015, Sudfeldt et al. 2013).

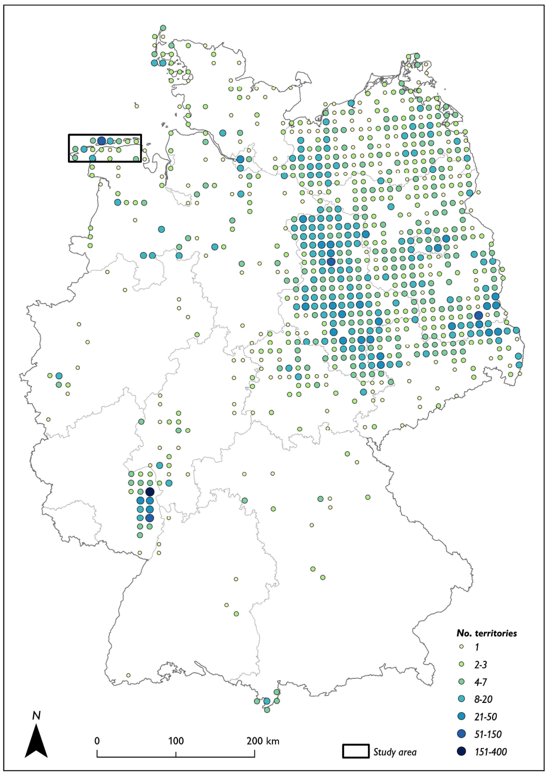

Fig. 1: Location of the study area as well as the distribution and number of territories of the northern Wheatear (*Oenanthe oenanthe*) in Germany based on 10′×6′geographic minute grids. Data Source: Gedeon et al. (2014).

Study area

The study area comprised the East Frisian Islands in the southern North Sea (Lower Saxony, Germany; Fig. 1). An Atlantic climate with a mean annual temperature of 9.6 °C and a mean precipitation of 752 mm characterises the study area (weather station: Norderney; long-term mean: 1981–2010) (Deutscher Wetterdienst, 2018). The East Frisian Islands are sandy barrier islands and are influenced by tides. The main habitats on the islands are beaches, dunes, dry and wet dune slacks as well as salt marshes and tidelands. The most important habitats colonised by Wheatears are dune grasslands typically dominated by *Agrostis capillaris*, *Carex arenaria* and *Corynephorus canescens* as well as different mosses and lichens. Saltmarshes, which are flooded only by high tides, are dominated by *Agrostis stolonifera*, *Festuca rubra*, *Juncus gerardii* and further salt tolerant plants. All eight East Frisian Islands are part of the Wadden Sea National Park of Lower Saxony and the Wadden Sea World Heritage.

The two most intensively studied islands, Norderney and Spiekeroog, have a width of about 2 km. Norderney is approximately 14 km long, with an area of about 25 km^2 (Petersen and Pott, 2005). Spiekeroog is situated 20 km further east and has a length of 10 km and an area of 18 km^2. Norderney is the most important stronghold of the Wheatear in Lower Saxony. In 2015, a total of 179 Wheatear territories were detected on Norderney (Schulze-Dieckhoff, pers. comm., Lower Saxonian Water Management, Coastal Defence and Nature Conservation Agency [NLWKN]), approximately one third of the breeding population of Lower Saxony (Krüger et al., 2014) and more than two thirds of those of the East Frisian Islands (Schulze-Dieckhoff, pers. comm., NLWKN). With an assumed population size of 5,000 individuals, the island is densely populated by European rabbits (*Oryctolagus cuniculus*) (Walter and Kleinekuhle, 2008). In contrast, on Spiekeroog Wheatears breed very rarely and rabbits have been extinct since 1889 (Meyer-Deepen & Meijering, 1979; Schulze-Dieckhoff, pers. comm., NLWKN). The presence/absence of rabbits on Norderney and Spiekeroog is reflected in the vegetation structure with much more open soil on Norderney (Fig. 2, Isermann et al. 2010).

Sampling design

Influence of rabbit abundance on habitat structure and Wheatear populations

Rabbit abundance on the East Friesian Islands was classified into two categories: high (>1 rabbits/ha island area) and low (<0.1 rabbits/ha or even uncolonised) (data source: Peters and Pott, 1999; Hahn, 2006; Walter and Kleinekuhle, 2008). The effects of rabbit abundance on habitat structure were analysed on a representative island for the categories high (Norderney: 1.9–13.4 individuals/ha; Peters and Pott, 1999) and low abundance (Spiekeroog: uncolonised; Walter and Kleinekuhle, 2008). On both islands we randomly selected 15 plots each within the dominant and main breeding habitat of the Wheatear on the East Frisian Islands: dune grassland (cf. section 2.1). In August 2018 we counted the number of burrows within a radius of 5 m around the centre of each plot. Furthermore, we measured vegetation height (cm) at an accuracy of 2.5 cm using a ruler and estimated the cover (%) of bare ground, herbs, mosses, shrubs and litter in an area of 3 m × 3 m. Data on Wheatear territory densities on the East Frisian Islands in 2015 were based on territory mapping (Bibby et al., 2000; Fischer et al., 2005) and provided by Schulze-Dieckhoff (pers. comm., NLWKN).

Habitat preferences of the Wheatear on its abundance hotspot

Plots

On Norderney, the density stronghold of Lower Saxony, we randomly selected 71 quadratic plots with a size of 250 m × 250 m (area: 6.25 ha) within the main breeding habitat of dune grassland (total survey area: 443.75 ha). In these plots we surveyed breeding pairs and habitat characteristics.

Breeding-pair survey

To determine the number of Wheatear breeding pairs per plot, three surveys from the end of May to the end of June 2018 were conducted on all 71 plots (Bibby et al., 2000; Andretzke et al., 2005). During each survey we systematically searched for Wheatear displaying territorial behaviour by following linear transects covering the entire plot. Transect lines were set about 60 m apart from each other. Due to late migrants and a high proportion of unmated, singing males (Currie et al., 2000), the number of Wheatear breeding pairs is often overestimated when conducting regular territory mapping (Bibby et al., 2000; Andretzke et al., 2005). Consequently, in this study the number of breeding pairs was determined only when clear evidence of breeding was available, i.e., the observation of warning or feeding adults. For each breeding territory where warning Wheatears were observed and the nesting site remained unknown, we sought to locate the nests through observing feeding adults. Data on breeding pairs were used for analyses of the habitat preferences of the Wheatear on two different spatial scales: (i) the plot level representing large-scale habitat conditions affecting the breeding density of Wheatears and (ii) the breeding territory level representing small-scale habitat conditions at nest sites.

Environmental conditions at the plot level

At each of the 71 breeding-pair survey plots we measured the vegetation height (cm) and estimated the cover (%) of bare ground and short vegetation (height <5 cm) as potential foraging habitats (cf. Condor, 1989; Low et al., 2010; Van Oosten et al., 2014) on nine systematically arranged subsamples covering the whole plot. Moreover, we counted the number of burrows within a radius of 10 m around the centre of each subsample. For further analyses we used the sum (burrow density) and mean values (all other variables), respectively.

Environmental conditions – breeding territory level
At the breeding territory level environmental conditions were sampled within the (i) breeding territories and controls as well as within (ii) nesting sites and controls. Breeding density within the plots was high and the lowest distance between two nests was only 46 m (mean ± SE: 185.6 ± 9.6). As a result, we analysed the environmental conditions within a radius of 40 m around nests and the centre of controls. This corresponded to a territory size of 0.5 ha, which is the minimum territory size on Central European coasts (Bauer et al., 2012). Controls were randomly selected within the plots using the function "Create random points" in ArcGIS 10.2. Their number was identical to those of the detected nests (*N* = 49). Analysis of environmental conditions of the breeding territories and controls was conducted according to Berg (2008) using the function "Buffer" in ArcGIS 10.2. We calculated the area of the different habitat types using habitat data from the Trilateral Monitoring and Assessment Programme (TMAP) (Wadden Sea National Park of Lower Saxony [WCNPLS] 2004; cf. Tab. 1). For further information concerning the habitat types see Petersen et al. (2014). Moreover, habitat data formed the basis for the calculation of habitat heterogeneity (*H'*) using the Shannon Index (O'Neill et al., 1988).

In order to assess the environmental conditions at the nesting sites, we measured the vegetation height (cm) and cover (%) of the bare ground, as well as the herb layer, mosses, shrubs and litter in an area of 3 m × 3 m around each nest (Tab. 2). We also counted the number of burrows within a radius of 5 m around the nest and measured the distance to the next potential foraging habitat with a vegetation height of less than 5 cm (see above). To document the range of available nesting sites within the breeding-pair survey plots studied, we analysed the same parameters at control samples of equivalent size using the same methods as described for the breeding territories and controls (see above).

Statistical analysis

Differences in environmental conditions between two groups (high vs. low rabbit abundance, breeding territory vs. control and nest site vs. control) were analysed using Mann-Whitney *U* test, because data were not normally distributed (Tab. 1, 2 and 3). At the plot level, we assessed the influence of the sampled environmental parameters (Tab. 4) on Wheatear abundance (breeding pairs/plot) by conducting a generalised linear model (GLM) with Poisson error distribution (cf. Crawley, 2007). At the breeding territory level, we analysed the effects of the sampled environmental parameters (Tab. 2 and 3) on breeding territory occupancy and nest-site occupancy, respectively, via generalised linear mixed-effect models (GLMM) with plot as a random factor (Crawley, 2007). To increase model robustness and identify the most important environmental parameters, we conducted model averaging based on an information-theoretic approach (Burnham and Anderson, 2002; Grueber et al., 2011). Model averaging was conducted using the 'dredge' function (R package MuMIn; Barton, 2016) and included only top-ranked models within ΔAICc <3 (cf. Grueber et al., 2011). To avoid multi-collinearity in the GLMM, Spearman's rank correlations (r_s) were conducted to exclude variables with strong inter-correlations ($|r_s| \geq 0.5$) (Dormann et al., 2013). The area of salt marsh was negatively correlated with those

Tab. 1: Mean values (± SE) of environmental parameters in dune grassland on an island with high rabbit abundance (High Abun; Norderney, n = 15) and uncolonised by rabbits (Uncolonised; Spiekeroog, n = 15). For further explanations see section 2.3.1. Differences between the island with high abundance and the uncolonised island were tested using Mann-Whitney U test. Significance levels are indicated as follows: n.s. P >0.5, * P <0.05, ** P <0.01, ***P <0.001.

Parameter	**Dune grassland**		***P***
	High Abun.	**Uncolonised**	
Burrow density (burrows/100 m^2)	5.6 ± 0.8	0 ± 0	***
Vegetation height (cm)	11.6 ± 1.8	10.9 ± 1.1	n.s.
Cover (%)			
Bare ground	12.8 ± 4.3	3.4 ± 1.1	*
Herbs	54.1 ± 6.3	47.7 ± 4.3	n.s.
Mosses	43.2 ± 7.2	72.1 ± 7.8	**
Shrubs	0.9 ± 0.9	0.9 ± 0.9	n.s.
Litter	19.1 ± 4.5	31.8 ± 5.9	n.s.

of dune grassland (r_s = –0.57, P <0.001) and the cover of mosses was negatively correlated with the cover of the herb layer (r_s = –0.52, P <0.001). Therefore, the variable of salt marsh was excluded from the breeding territory occupancy and moss from the nest-site occupancy analysis. All statistical analyses were performed using R 3.5.1 (R Development Core Team, 2018).

RESULTS

Influence of rabbit abundance on habitat structure and Wheatear populations

Rabbits had a significant influence on the habitat structure of the main breeding habitat of the Wheatear on the East Frisian Islands, dune grassland (Tab. 1). Indeed, burrow density was significantly higher on the island with high rabbit abundance compared to those without rabbits. In addition, high rabbit abundance resulted in significantly greater bare-ground cover and a significantly lower cover of mosses. Moreover, Wheatear abundance was significantly greater on islands with high rabbit abundance relative to those with low abundance (Fig. 3).

Habitat preferences of the Wheatear on its abundance hotspot

Plot level

The habitat structure in the 71 plots was characterised by a high density of burrows (mean ± SE: 5.2 burrows/1,000 m^2 ± 0.4), short turf (height: 11.4 cm ± 0.4), the availability of potential foraging habitats (cover: 11.9% ± 1.0) and some bare ground (cover: 9.5% ± 0.9).

In total, we detected 70 breeding pairs within the 71 plots, resulting in an abundance of 1.6 breeding pairs/10 ha. For 49 of these pairs, the nests were found. All nests, with the exception of one in a niche of an old bunker, were placed in rabbit burrows. Almost 40% of the plots (27 plots) were not occupied by the Wheatear. Within the occupied plots, the number of breeding pairs varied from one to three. According to the GLM analysis, Wheatear abundance at the plots increased with burrow density and cover of potential foraging habitats (Tab. 2, Fig. 4).

Breeding territory level

The dominant habitat type within the Wheatear breeding territories was dune grassland covering on average of 50% of the territories (Tab. 3). High salt marshes (18%) and white dunes (13%) also covered larger parts.

Tab. 2: Results of the GLM (Poisson) analysis (model-averaging): relationship between the abundance of Wheatear breeding pairs per plot and environmental parameters. Model-averaged coefficients (cond. average) were derived from top-ranked models (ΔAICc < 3). R^2_{MF} = McFadden's Pseudo R^2 of averaged model. Significance levels are indicated as follows: n.s. P >0.5, * P <0.05, ** P <0.01, ***P <0.001. R^2_{MF} = 0.21.

Parameter	**Estimate**	**SE**	**Z**	**P**
Intercept	−0.86	0.31	0.32	*
Burrow density	0.02	0.01	1.96	*
Short vegetation	0.04	0.01	2.72	**
Bare ground	0.02	0.02	1.42	n.s.
Vegetation height	−0.04	0.04	0.13	n.s.

Fig. 2: Aerial photographs of dune grassland on Norderney with high abundance of rabbits (left) and Spiekeroog without occurrence of rabbits (right).

Areas of dune grassland and salty dune were significantly higher within the Wheatear breeding territories than at the control. In contrast, the areas of all other habitat types and the habitat heterogeneity did not differ between breeding territories and the control. Based on the GLMM analysis the likelihood of breeding territory establishment increased with the area of dune grassland and salty dunes, too (Tab. 4). The direct vicinity of the nesting sites was characterised by the occurrence of some burrows, short vegetation, a short distance to potential foraging habitats, a high cover of bare ground and mosses, a herb layer with intermediate cover and low shrub and litter cover (Tab. 5, Fig. 4). Aside from shrub cover, all sampled environmental parameters significantly differed between nest site and control. For nest-building, habitats with a higher burrow density, shorter vegetation, shorter distance to potential foraging habitats, higher cover of bare ground and mosses and a lower cover of the herb layer and litter were preferred. The GLMM analysis revealed that the likelihood of nest-building increased with burrow density and decreased with vegetation height (Tab. 4).

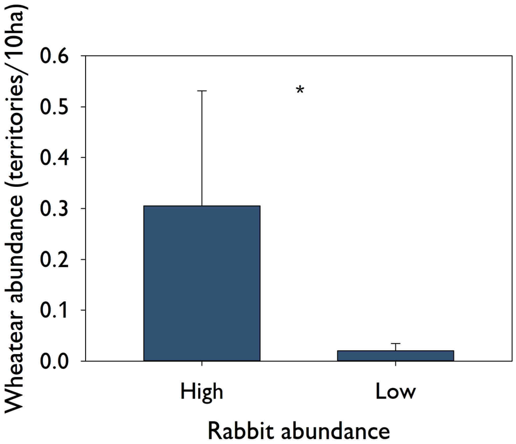

Fig. 3: Mean (SE) Wheatear abundance on the East Frisian Islands with high and low rabbit abundance. High abundance (> 1 rabbits/ha; *N*=3): Baltrum, Borkum and Norderney; low abundance (< 0.1 rabbits/ha or even uncolonised; *N*=5): Juist, Langeoog, Memmert, Spiekeroog and Wangerooge. For further information see method section. Differences between the two abundance categories were tested using Mann-Whitney *U* test: *U*=0.00, **P* < 0.05.

DISCUSSION

Our study indicated that the occurrence of the northern Wheatear on the East Frisian Islands was depending on large populations of the burrowing, herbivorous ecosystem engineer European rabbit. Rabbits were found to have had a considerable influence on the structure of the dune grassland, the main breeding habitat of the Wheatear: high rabbit abundance resulted in greater burrow density and more bare ground. Wheatears were also more abundant on islands with larger rabbit populations. At the plot level,

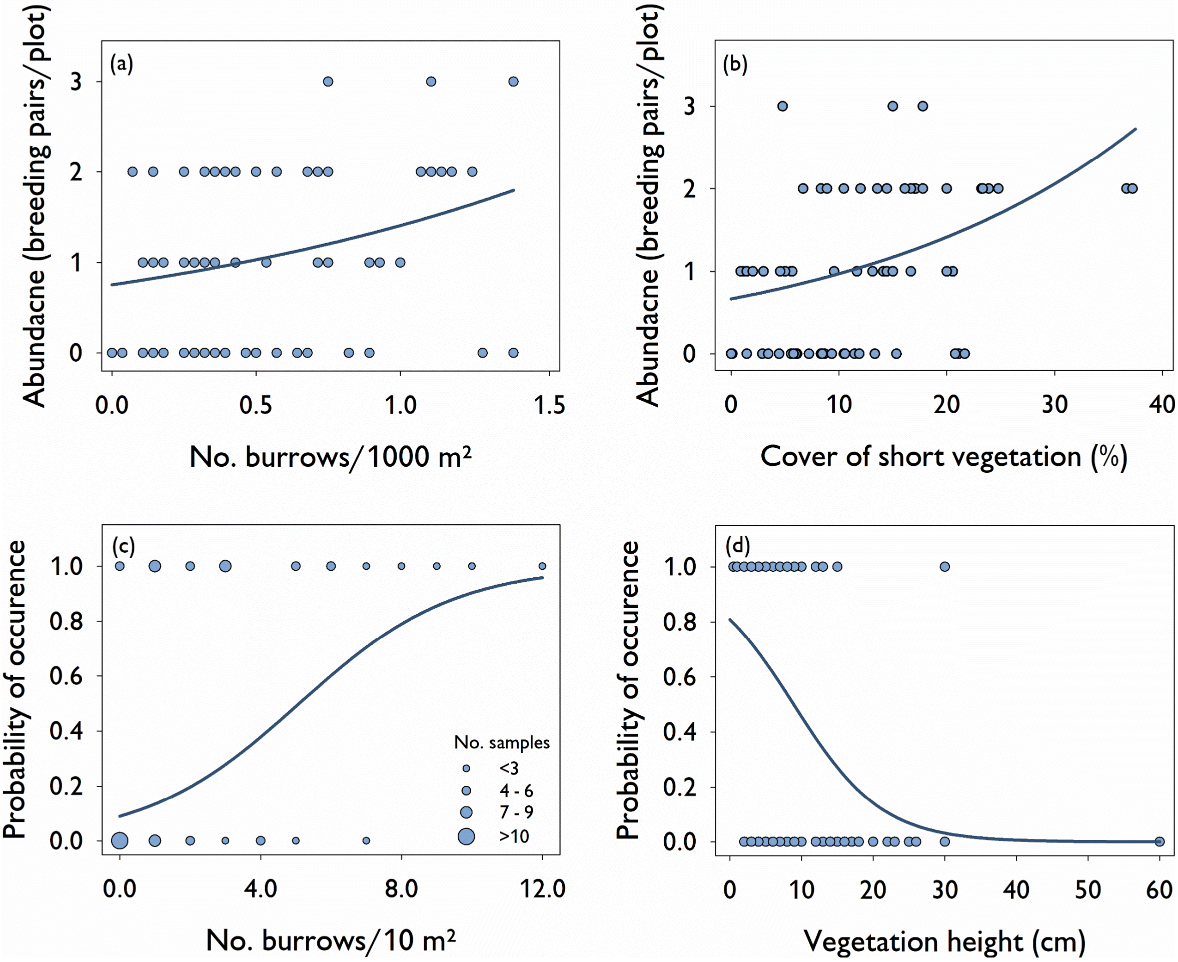

Fig. 4. Results of the GLMM analyses: relationship between abundance (a and b) and occurrence of Wheatear breeding pairs (c and d) with significant predictor variables (see Table 5). The regression slopes were fitted using multivariate GLMM.

Wheatear abundance increased with burrow density and the cover of potential foraging habitats (short vegetation). In addition, the likelihood of nest-building increased with burrow density and decreased with vegetation height. The northern Wheatear breeds in cavities near to the ground (Conder, 1989). In natural habitats above the timber line, potential nesting sites such as rock crevices are usually widespread (Bauer et al., 2012). In contrast, in lowlands the availability of suitable breeding places often constitutes a limiting factor. In our study, all Wheatear nests except one were located within rabbit burrows. Rabbits dig extensive underground burrows ('warrens') for resting during the day as well as for shelter from predators (Wilson et al., 2016). They also create breeding burrows ('nurseries') days, weeks or even month before they are used. Large proportions of these nurseries become abandoned over time and are, hence, available for Wheatears as nesting sites (Wilson et al., 2009; Wilson et al., 2016). Although some authors have reported on Wheatears breeding in rabbit burrows (cf. Conder, 1989; Blüml and Schönheim, 2006), until now a detailed analysis of the importance of rabbit burrows for breeding Wheatears was absent.

In general, information on rabbit burrows as a habitat for other animals remains scarce. In the case of southwestern Europe it has been shown that high rabbit burrow density fosters lizard diversity and density (Bravo et al., 2009; Grillet et al., 2010, Wouters et al. 2012). Furthermore, there appears to be a relationship between the abundance of further cavity-breeding bird

Tab. 4: Results of the GLMM (Poisson) analyses (model-averaging): relationship between breeding territory (a) and nest site occupancy (b) and environmental parameters. Plot was used as a random factor. Model-averaged coefficients (conditional averaged) were derived from top-ranked models (ΔAICc < 3). R^2_{GLMMm} = variance explained by fixed effects, R^2_{GLMMc} = variance explained by both fixed and random effects (Nakagawa et al., 2017), AUC = area under the curve; accuracy of model prediction (Fielding and Bell, 1997). Significance levels are indicated as follows: n.s. $P > 0.5$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Parameter	Estimate	SE	Z	P
(a) Breeding territory				
R^2_{GLMMc} = 0.09–0.34, R^2_{GLMMm} = 0.13–0.37, AUC = 0.78				
Intercept	−0.79	0.47	1.66	n.s.
Dune grassland	0.29	0.14	2.07	*
Salt dune	0.93	0.44	2.08	*
Dune shrub	0.32	0.53	0.61	n.s.
Open dune	1.04	0.83	1.25	n.s.
White dune	0.05	0.18	0.28	n.s.
Bare sand/mud	−0.40	2.87	1.37	n.s.
Dune slack	0.20	0.64	0.31	n.s.
Built-up area	−0.03	0.23	0.13	n.s.
(b) Nest site				
R^2_{GLMMc} = 0.57–0.62, R^2_{GLMMm} = 0.57–0.64, AUC = 0.91				
Intercept	−0.48	0.82	0.58	n.s.
Burrow density	0.46	0.14	3.64	***
Vegetation height	−0.16	0.06	2.51	*
Distance foraging habitat	−0.07	0.05	1.36	n.s.
Bare ground	0.02	0.02	1.53	n.s.
Herb layer	0.01	0.01	0.59	n.s.
Shrubs	0.05	0.04	1.11	n.s.
Litter	−0.04	0.02	1.56	n.s.

species on the East Frisian Islands and rabbit burrow density. Those islands with greater abundance of rabbits have large populations of jackdaw (*Corvus mondula*), shelduck (*Tadorna tadorna*) and stock dove (*Columba oenas*), all of which regularly breed in rabbit burrows (Glue and Scott 1980, Krüger et al., 2014). Furthermore, the use of rabbit burrows as breeding sites has also been reported for the little owl *Athene noctua* (Patterson 1982). Rabbits do not only create nesting sites for Wheatears, but also shape the vegetation structure by digging and grazing (Wilson et al., 2016).

In particular, they suppress succession, reduce herb-layer cover and increase the cover of bare ground, resulting in short and open swards (Foran et al., 1985; Leight et al., 1987; Norbury and Norbury, 1996; Eldridge et al., 2006, Isermann et al. 2010). The influence of rabbits on vegetation structure is also clearly visible when looking at aerial photographs of the two studied islands (Fig. 2). At the plot level, Wheatear abundance increased with the cover of potential foraging habitats (short vegetation), while the likelihood of nest-building decreased with vegetation height due to decreased feeding activity of rabbits (cf. Isermann et al. 2010). In addition, the cover of bare ground and mosses was higher around nest sites compared to the control, while cover of the herb layer and litter as well as distance to foraging habitats was lower. All of these differences in habitat structure indicate breeding Wheatears' preference for short and sparse vegetation. Being primarily a hopping or running bird that is morphologically adapted to foraging on the ground, Wheatears require a fairly firm surface with sparse vegetation, bare ground or rocky terrain in order to move

Tab. 5: Mean values (± SE) of environmental parameters at nest sites (n = 49) and control (n = 49). For further explanations see section 2.3.1. Differences between nest and control were tested using Mann-Whitney U test. Significance levels are indicated as follows: n.s. $P > 0.5$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Parameter	Nest site	Control	*P*
Burrow density (burrows/100 m²)	8.4 ± 0.6	4.5 ± 0.3	***
Vegetation height (cm)	5.8 ± 0.7	12.3 ± 1.3	***
Dist. foraging Hab. (m)	9.0 ± 1.3	14.1 ± 1.0	***
Cover (%)			
Bare ground	25.0 ± 2.9	11.2 ± 2.5	***
Herb layer	52.9 ± 2.9	65.5 ± 4.2	*
Moss	37.8 ± 3.8	26.2 ± 4.4	**
Shrubs	2.1 ± 1.1	3.0 ± 1.5	n.s.
Litter	8.7 ± 1.2	21.5 ± 3.0	**

freely when pursuing arthropod prey (Brooke, 1979; Kaboli et al., 2007). Consequently, Wheatears prefer short vegetation offering good access to prey (Low et al., 2010; Van Oosten et al., 2014) and, hence, pairs that establish their territories in habitats with permanently short swards exhibit superior reproductive performance (Arlt and Pärt, 2007). As a result, Wheatear territory size is known to be negatively correlated with sward height and vegetation cover, implying an adjustment of territory size to hunting success (Tye, 1992; Exnerová et al., 2002).

In our study, Wheatear breeding territory establishment was best explained by the area of dune grasslands and salty dunes. Rabbits prefer such dry, warm and sandy habitats (Wilson et al., 2016). On the East Friesian Islands, dune grasslands and salty dunes represent the main habitats of the European rabbit (Walter and Kleinekuhle, 2008). As a result, we can interpret the preference of the Wheatear for these dune habitats by the high rabbit abundance.

Vegetation structure in the principal Wheatear breeding habitat – dune grassland – differed considerably between the island with high rabbit abundance (Norderney) and its counterpart uncolonised by rabbits (Spiekeroog). Burrow density and cover of bare ground were greater, while cover of mosses was lower on the island with high rabbit abundance. Given that aside from the occurrence of rabbits, the environmental conditions of the two islands were similar (cf. section 2.2), such differences in habitat structure are very likely the result of the grazing and burrowing activities of the rabbits. Surprisingly, there was no difference in the vegetation height (Tab. 1). We assume that this is due to the fact that habitats on Norderney are structurally heterogeneous with short and tall swards (Van Oosten 2014) so that also areas with tall vegetation were sampled. This assumption is congruent with observations of dramatic changes in vegetation structure (taller vegetation and gradual encroachment by shrub and woodland) following the collapse of the United Kingdom's (UK) rabbit populations in the 1950s after the introduction of myxomatosis (e.g. Wilson et al., 2009; Newton, 2017). The same correlation was also described after a decline of the rabbit population in the Netherlands (Drees & van Manen 2005; Drees et al. 2006).

In summary, our study revealed the dependence of the northern Wheatear on large populations of the burrowing, herbivorous ecosystem engineer European rabbit. Through their digging and grazing activities, rabbits create the two key resources for breeding Wheatear: (i) sufficient burrows as potential nesting sites and (ii) availability of short vegetation as foraging habitats. Regarding conservation measures, our study showed that, in addition to the provision of burrows or niches for nesting, the availability of large patches with nutrient-poor, low-growing vegetation is of great importance.

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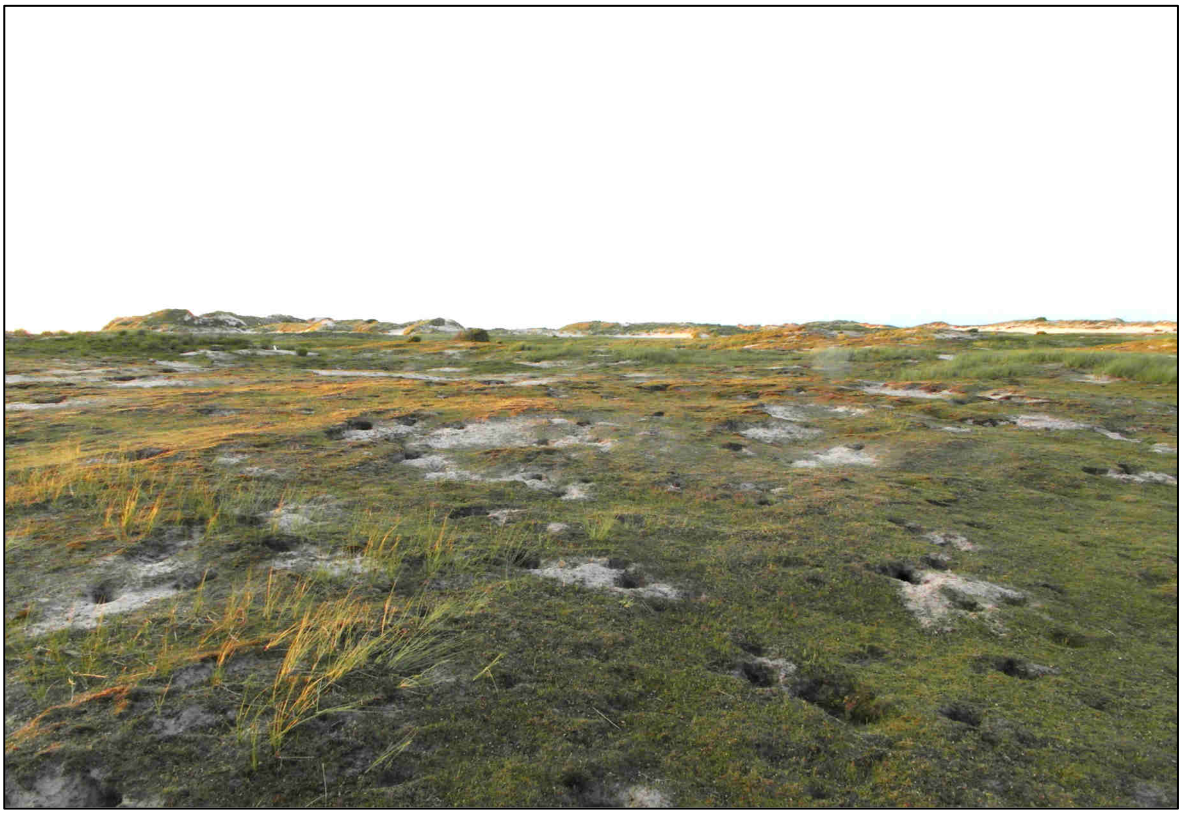
In dune grasslands of the East Frisian Islands, Wheatears (*Oenanthe Oenanthe*) use burrows of the European rabbit (*Oryctolagus cuniculus*) for nesting (Norderney, 29/6/2017).

Fledgling of the Wheatear on the island of Norderney. Fledglings continue to use rabbit burrows as a shelter even after they have left the nest (Norderney, 12/6/2017).



Areas with particularly high rabbit activity can be clearly identified by numerous burrows, open soil and short vegetation (Norderney, 2/6/2017).

Female Wheatear on dune grassland. Areas of such short vegetation are exclusively provided through browsing activities of rabbits. Consequently, rabbits are ecosystem engineers acting as key stone species in grassland habitats (Norderney, 29/07/2017).

(2) Natural coastal dunes on Wadden Sea islands as a refuge for an endangered wader species

STEFFEN KÄMPFER & THOMAS FARTMANN (2022) *Journal of Coastal Conservation* 26: 53.

ABSTRACT

Europe holds globally important populations of breeding waders. However, most of the species are in steep decline, including the Eurasian Curlew (*Numenius arquata*). Here, we studied the breeding-territory and nest-site preferences of a Curlew subpopulation that has, in contrast to the overall trend, been increasing, on the East Frisian Islands (Wadden Sea National Park of Lower Saxony, N Germany). The islands are mostly free from ground predators and intensive agriculture and thus offer the opportunity to examine habitat preferences in largely undisturbed habitats.

Our study revealed that Curlews preferred breeding in habitat mosaics dominated by high marshes and dune grasslands, far from areas with human disturbance. For nest-building, heterogeneous microhabitats with intermediate vegetation cover and height and some bare grounds were preferred. This reflects a trade-off between (i) sufficient shelter for nests and fledglings, (ii) early recognition of predators and (iii) readily available and accessible invertebrate prey. Such heterogeneous habitats, without mammalian predators, are largely missing in the intensively used agricultural landscapes of the European mainland. Consequently, Curlew populations on the mainland are mostly declining. In contrast, those on the East Frisian Islands are stable and, therefore, of prime importance for the protection of the species. Thus, the study highlights the importance of isolated islands providing natural habitats like coastal dunes, which are free from ground predators and extensive human disturbance for the long-term survival of Curlew populations. Based on the results of this study we make suggestions to improve future conservation measures for degraded habitats to boost Curlew populations.

KEYWORDS

Eurasian Curlew (*Numenius arquata)*, grassland management, habitat heterogeneity, land-use change, nest-site preference, vegetation structure

INTRODUCTION

The global decline in biodiversity has reached alarming proportions. Global extinction rates are 1000 times higher than the natural background rate (Pimm et al. 2014). Despite great efforts in nature conservation, there are currently no signs of a trend reversal (Butchart et al. 2010). For terrestrial biomes, land-use change is assumed to be the major driver of the recent biodiversity loss (Sala et al. 2000; Foley et al. 2005; Cardoso et al. 2020). Although farmland is the most important habitat for bird conservation in Europe (Donald et al. 2006; Sutcliffe et al. 2015), farmland exhibits the largest decrease in biodiversity across taxa such as plants, insects, and birds (Vickery et al. 2001; Donald et al. 2006; Flohre et al. 2011).

This decrease also applies to waders, which often occupy man-made landscapes and are among the most threatened birds globally (Birdlife International, 2015). The European Union holds internationally important populations of breeding wader species (BirdLife International, 2004, Keller et al. 2020). However, most of the species are in steep decline and are considered endangered or vulnerable on the European

Red List of Birds (BirdLife International, 2015). Decreasing availability of breeding habitats through agricultural intensification, afforestation, and land abandonment, as well as insufficient reproduction especially due to nest and chick predation, have been identified as the main reasons for declining wader populations (Wilson et al. 2004; Kaasiku et al. 2019; Plard et al. 2019). In the future, climate change is expected to become an additional serious threat, for example through changes in food availability and temporal mismatch (Pearce-Higgins, 2010; Renwick et al. 2012).

The Eurasian Curlew is Europe's largest wader and breeds in the boreal, temperate and steppe zones of Europe and Asia (Brooks et al. 1990; Bauer et al. 2012). The subspecies of the Eurasian Curlew *Numenius arquata arquata* (hereafter referred to as Curlew) breeds in west, north and central Europe to the west of the Urals (Thorup 2006). The Curlew has suffered major range losses and population decline throughout its breeding range (Keller et al. 2020). As more than 75% of the global population breeds in the northern half of Europe, Europe has a great responsibility for the long-term survival of this species (BirdLife International, 2004). Two main reasons have been identified for the decline of the European Curlew population. On the one hand decreasing habitat availability and suitability due to afforestation and intensive agriculture, resulting in homogeneous swards (Berg, 1994; Douglas et al. 2014; Franks et al. 2017). On the other hand, insufficient reproduction due to high egg and chick losses by predators and mechanized management practices (Grant et al. 1999; Zielonka et al. 2019).

Curlews depend on open landscapes with wide visibility unbroken by woodland in dry to wet terrain for nesting (Brooks et al. 1990). The original habitats of the species in Central Europe were bogs, heathlands and poorly drained wetlands, which have largely been destroyed and degraded by human activities like agriculture, drainage and land reclamation. Nowadays, a large proportion of the European and German Curlew population breeds in meadows, pastures and arable fields but still also in (rewetted) raised bogs and fens, heath and dunes (Brooks et al. 1990; Bauer et al. 2005).

While the German breeding population was estimated at 7,000 pairs in the early 1970s, it is now estimated at 3,600–4,800 pairs (Gerlach et al. 2019). This corresponds to a decrease of more than 40% (Hötker et al. 2007). Due to its steep decline during the last decades, the German breeding population is considered threatened with extinction (Ryslavy et al. 2021). However, on the German mainland the decrease has recently been halted in some populations through intensive conservation measures such as marking of nest locations to avoid destruction during agricultural work, electric fencing to prevent mammalian predation, rewetting, and habitat management (Kipp & Kipp, 2003; Rüstringer Heimatbund e.V. & Landkreis Wesermarsch, 2005; Boschert, 2008). Despite further declines outside managed areas, this has led to a stabilization of the German population (Gedeon et al. 2014; Gerlach et al. 2019).

The strongholds of the German Curlew breeding population are the north-western lowlands and the East Frisian Islands (Gedeon, 2014). Colonization of the East Frisian Islands by breeding Curlews started as late as 1938 (Großkopf, 1995). Since then, the population has increased rapidly. Between 2008 and 2017 there have been an average of 102 ± 3 (mean ± SE) Curlew territories on the Islands, of which 16 ± 2 were situated on the island of Spiekeroog (Schulze-Dieckhoff, pers. comm., Lower Saxonian Water Management, Coastal Defence and Nature Conservation Agency [NLWKN], 2018).

So far, the reasons for the different population trends are unknown. However, the lack of mammalian predators and the absence of intensive agriculture on the East Frisian Islands are two possible causes. While several studies have investigated the habitat preferences of Curlews breeding in agricultural landscapes (e.g. Berg, 1992; Valkama et al. 1998), very little is known about the habitat characteristics necessary for breeding in natural habitats on coastal islands. Several authors reported that the highest densities of Curlews on the Wadden Sea Islands occur in dune heath and wet dune slacks (= wet dune valleys) (e.g. Koffijberg et al. 2006). However, there are only very small areas of dune slacks on most East Frisian Islands and their extent has decreased in recent decades due to a lowering of the groundwater caused by drinking water production (Pott, 2006, Geelen et al. 2017). At the same time, however, the number of breeding Curlews has increased (Hötker et al. 2007), which brings into question the importance of dune slacks for breeding Curlews on the East Frisian Islands.

To develop suitable conservation measures designed to counteract the decline of Curlews in Europe, more precise information on habitat preferences is needed urgently (Żmihorski et al. 2018). Therefore, we studied the habitat preferences of a stable Curlew population in natural habitats. The study area, the East Frisian Islands within the Wadden Sea National Park of Lower Saxony, are largely missing mammalian predators and agricultural disturbance. The aim of this study was to investigate habitat composition within territories and vegetation structure at nests in natural largely undisturbed refuge habitats. Based on the results of this study we make suggestions to improve future conservation measures for degraded habitats to boost Curlew population.

MATERIALS AND METHODS

Study area

The study area comprised all the East Frisian Islands on which Curlew's breed (Borkum, Memmert, Juist, Norderney, Baltrum, Langeoog, Spiekeroog; Lower Saxony, Germany). The East Frisian Islands cover an area of about 150 km² and are sandy barrier islands, influenced by tides and characterised by extensive island tails (Groot et al. 2016). The main habitats on the islands are beaches (18%), natural dune grasslands (13%), mudflats (13%), saltmarshes (35%), built-up areas (4%), and dune heath (4%) (Fig. 1). Further habitats that cover smaller areas are copses (3%), white dunes (2%), shrubberies (2%), dune slacks (1%), reeds (1%), semi natural grassland and transition zones between marshes and natural dune grasslands called salty dune (1%) (Petersen & Pott, 2005; Petersen et al. 2014). All the East Frisian Islands are part of the Wadden Sea National Park of Lower Saxony (corresponding to category II of the IUCN Protected Area Classification (Dudley 2013)), and the Wadden Sea World Heritage site (Kalisch 2012). The National Park is divided into three zones of different protection intensity: the core zone, intermediate zone, and recreational zone. During the breeding season, the core and intermediate zone are accessible for humans only on designated roads and paths. Only the recreational zone is fully accessible and open for human activities all year. Dogs are only allowed on a leash. Due to the promotion of eco-tourism such as bird watching (Davenport & Davenport 2006) and intensive public relations work, visitor management and the use of National Park rangers and volunteers to control entry bans, disturbance in protected areas occurs rarely (cf. Kalisch 2012). Only small parts of the islands, primarily saltmarshes, are grazed by livestock.

The East Frisian Islands are principally free of mammalian predators except for domestic cats (*Felis catus*) (Walter & Kleinkuhle, 2008). However, in recent years foxes (*Vulpes vulpes*) were present on the island of Norderney (Andretzke et al. 2017).

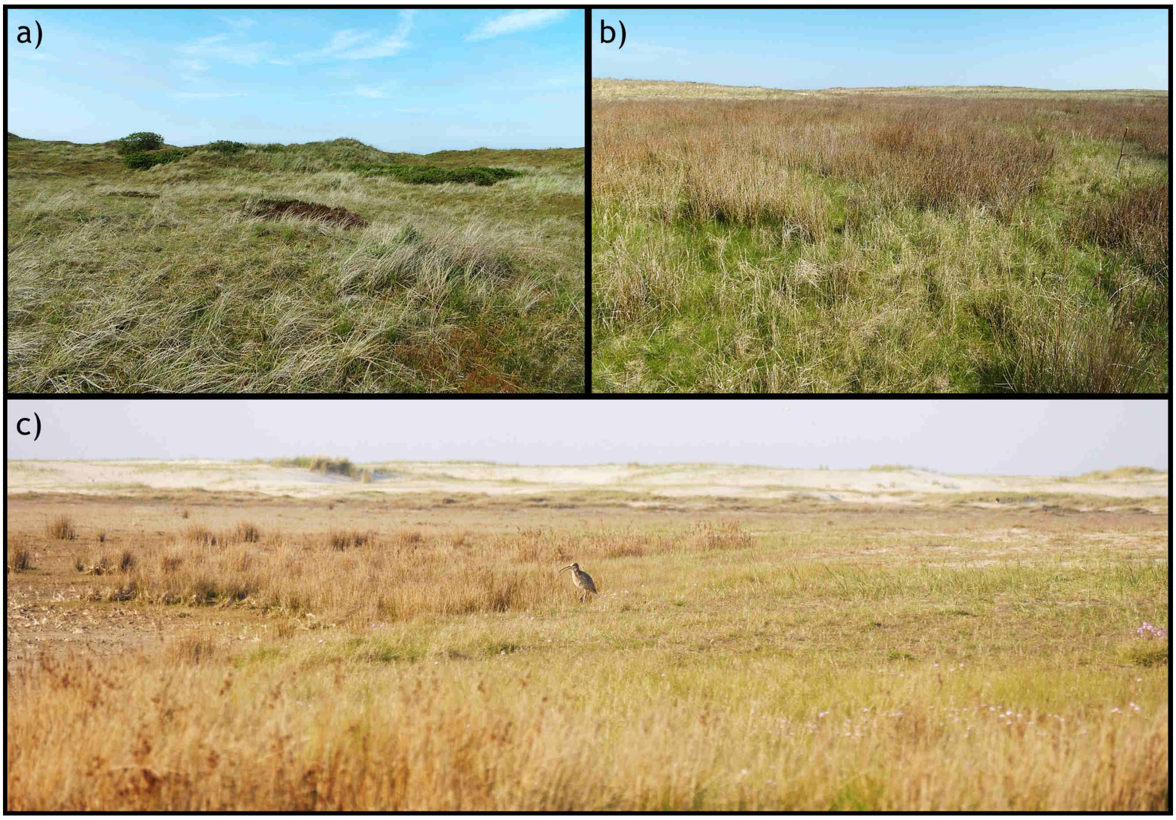


Fig. 1: Photos of typical breeding habitats of the Curlew on the East Frisian Islands: a) dune grassland, b) high marsh, c) salty dune: transition zone between high marsh and dune grassland providing heterogenous vegetation including areas of short vegetation and bare ground as well as high and dense vegetation.

Other mammals that occur on almost all East Frisian Islands and are known to cause clutch loss are common rat (*Rattus norvegicus*) and hedgehog (*Erinaceus europaeus*). Since 2010 a scheme to control population size of these introduced mammals has been carried out on the islands of Borkum, Norderney and Langeoog (Andretzke et al. 2016; Andretzke et al. 2017). By contrast, breeding density of potential avian predators (e.g., Herring gull (*Larus argentatus*), Lesser black-backed gull (*Larus fuscus*), Marsh harrier (*Cricus aeruginosus*) are high on most islands (Gedeon et al. 2014).

A detailed analysis of nest-site preferences was conducted on the island of Spiekeroog, which hosts a large part of the Curlew breeding population on the East Frisian Islands. In addition, the proportion of Curlews, breeding in natural undisturbed habitats within the core zone of the National Park is particularly high there, which enables the investigation of Curlews in low-disturbance, natural habitats without predatory mammals. Spiekeroog is about 2 km wide and 10 km long, producing a total area of 18 km² (Petersen & Pott, 2005).

Sampling methodology

Breeding-territory preferences

To evaluate the habitat preferences of Curlews on the East Frisian Islands, we compared habitat-type composition within Curlew territories with those on the islands in general. Habitat data were available through the Trilateral Monitoring and Assessment Program (TMAP) (Petersen et al. 2014; Wadden Sea National Park of Lower Saxony, 2017). Data on Curlew territories in 2017 were based on territory mapping during six visits (Südbeck et al. 2005; cf. Bibby et al. 2000) and provided by Schulze-Dieckhoff (pers. comm., NLWKN, 2018). For the identification of territories, we paid special attention to repeated observations of territorial behaviour (at least twice seven days apart) such as territory marking by flights as well as copulating, breeding or warning adults or pairs (suspected breeding). Special attention was paid to simultaneous observations for separating different territories situated close to each other. Furthermore, we paid special attention to the observation of breeding adults, distraction display, mobbing of potential avian predators and adults guiding young (confirmed breeding) (Südbeck et al. 2005). Where nests were not found, territory centres were defined as the centre where these behavioural signs were concentrated. After Bauer et al. (2012), minimum territory size of Curlews in north-west Germany is 7 ha. This is in line with the results of five GPS tagged birds breeding on the East Frisian Islands in 2020 (unpublished data 2020, Movebank ID 1126572166). Accordingly, we analysed the habitat composition of an area with a radius of 149 m around each territory centre using the function “Buffer” in software ArcGIS 10.2 (ESRI Inc.) (Kämpfer & Fartmann 2019). In total, we analysed 88 (from all seven islands) and 20 (Spiekeroog) territories, respectively (Fig. 3).

For all territories where nest location has been identified (confirmed breeding) ($N = 46$), we compared habitat-type composition within a radius of 149 m around each Curlew nest with those of randomly selected control territories (without nests) of the same size ($N = 46$). Selection of controls was performed using the function “Create random points” in ArcGis 10.2 and excluded areas that were unsuitable for breeding (beaches, built-up areas, forest, low marshes, and mudflats). Moreover, the Shannon index of habitat types served as a measure of habitat heterogeneity, *H’* (Fartmann et al. 2018, Schwarz et al. 2018) and was calculated by:

$$H' = -\sum_i p_i \cdot \ln p_i \quad \text{with} \quad p_i = \frac{n_i}{N}$$

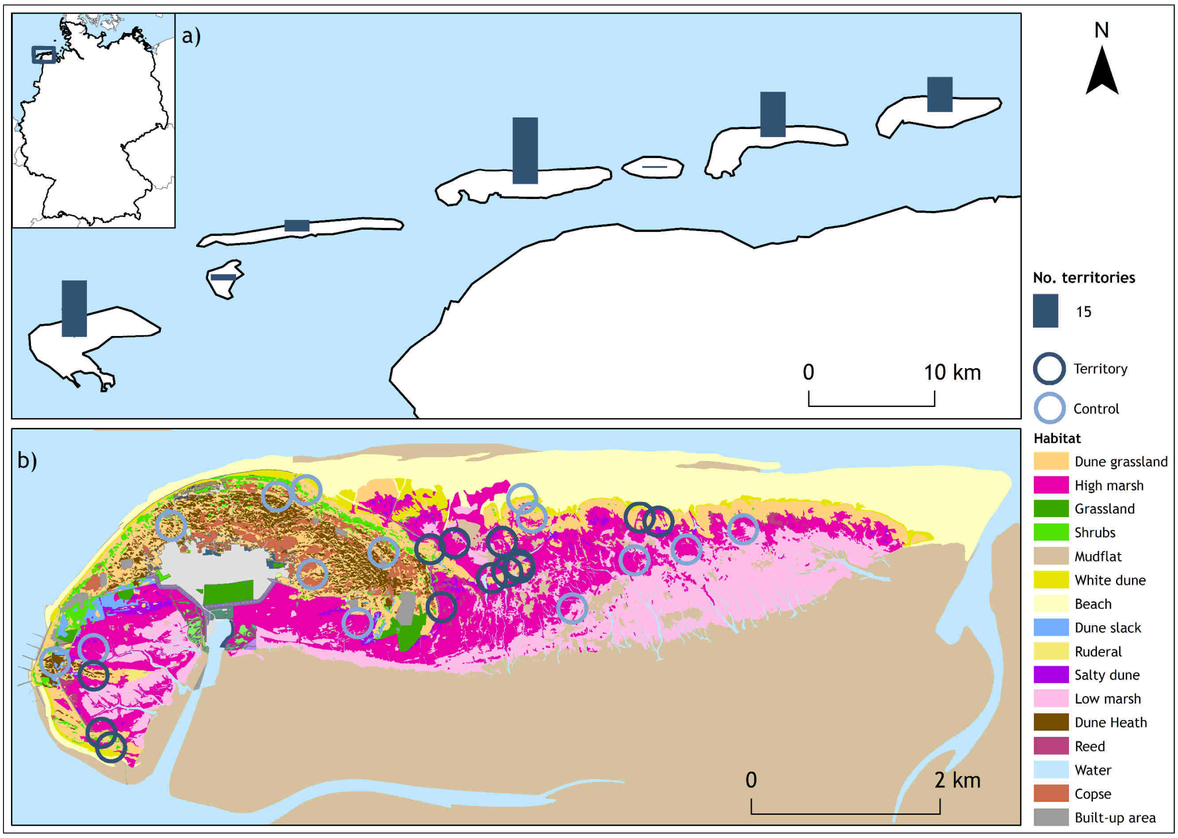


Fig. 2: a) Location of the studied East Frisian Islands (from left to right): Borkum, Memmert, Juist, Norderney, Baltrum, Langeoog, Spiekeroog and average number of territories on different islands between 2007 and 2017 (NLWKN 2018). b) Distribution of habitat types as well as of theoretical territories and controls using the example of Spiekeroog.

where N is the total area of the territory, and n_i is the area of each habitat type in the territory.

Further predictor variables were the closest distance to areas that were frequented by humans (buildings, paths, streets), as a proxy for anthropogenic disturbance, and wetlands (mudflats, standing water, wet dune slacks, tidal creeks), as a measure of proximity to the nearest foraging habitat. Both variables were determined using the function "Nearest" in ArcGIS 10.2.

Nest-site preferences

To assess the vegetation structure at Curlew nesting sites, we searched for nests on the island of Spiekeroog in April and May 2017. Nest sites were identified through observations of territorial behaviour from elevated dunes that indicated confirmed breeding (see above) and a subsequent systematic search for nests. In total, 14 nests out of 20 breeding pairs on Spiekeroog were found and recorded using a GPS device. Vegetation characteristics on the East Frisian Islands are assumed to change only slightly from the breeding period to summer due to (i) environmental stress (dry, nutrient-poor sandy soils), (ii) low competitive power of the perennial plants and (iii) mild climate with early start of the growing season (own observation). To avoid unnecessary disturbance of numerous scarce and threatened breeding birds in the core zone of the national park, vegetation characteristics were, therefore, measured after the breeding season in August/September. We measured the mean vegetation height (cm), at an accuracy of 1 cm using a ruler, and estimated the percentage cover of bare ground, the herb layer, mosses, shrubs, and litter in an area of 2 m × 2 m (finer scale) and 10 m × 10 m (coarse scale) around each nest. All parameters were also recorded at control sites, which were randomly selected within the potential breeding area (see above) using the function "Create random points" in ArcGIS 10.2. To obtain representative controls that cover the entire range of available vegetation structures, we chose a ratio between nest-sites and controls of 1:2.

Statistical analysis

Habitat composition (TMAP) (Petersen et al. 2014) within the territories was compared with the available habitat on the islands, by using Fisher's exact test (McDonald, 2009). Differences in habitat-type composition and vegetation structure (territory vs. control, nest-site vs. control) were analysed using the Mann-Whitney U test, because the data were not normally distributed. The effects of habitat-type composition and distance to relevant habitats on breeding-territory occupancy were analysed by generalised linear mixed-effect models (GLMM) with binomial error distribution (response variable: nest vs. control, predictors: see Tab. 1) and island as a random factor (cf. Crawley, 2007).

To assess the drivers of nest-site occupancy at finer and coarse scale we used generalized linear models (GLM) with binomial error distribution (nest vs. control) and parameters of vegetation structure as predictors (see Tab. 2) (cf. Crawley, 2007). If graphical inspections of the data suggested unimodal rather than linear relationships between the response variable and predictor variables, centred and squared values of the predictors were entered into the full model in addition to the untransformed values (cf. Johnstone, 2017). To increase model robustness and identify the most important environmental parameters, we performed model averaging based on an information-theoretic approach (Burnham & Anderson, 2002; Grueber et al. 2011). Top-ranked models are presented in supplementary Tab. 1. Model averaging was performed using the 'dredge' function (R package MuMIn; Barton, 2019) and included only top-ranked models with ΔAICc <2 (cf. Grueber et al. 2011). To avoid overfitting, maximum number of predictors to be included in a single model was limited to 1/10 of sample (Harrell et al. 1996). To avoid multi-collinearity in the GLM(M), Spearman's rank correlations (r_s) were used to exclude variables with strong inter-correlations ($|r_s| \geq 0.5$) (Grueber et al. 2011). Because the cover of the herb layer was negatively correlated with moss cover both within a radius of 2 m and 10 m around the nests ($|r_s| = 0.69$ and 0.66, respectively), we excluded moss cover from further analysis. All statistical analyses were performed using R 3.5.3 (R Core Team 2020)

RESULTS

Breeding-territory preferences

Habitat composition within Curlew territories and on the islands overall differed significantly (Fig. 3). This was true for all the islands studied. Within Curlew territories on Spiekeroog, high marsh and dune grassland dominated and were overrepresented while, in contrast, low marsh, beaches and mudflats were clearly underrepresented. When considering the habitat composition of all the islands, besides high marsh, and dune grassland, also grasslands were overrepresented in Curlew territories, whereas built-up areas were underrepresented. In addition, despite small proportions of salty dunes on the islands, this type was overrepresented in the territories. Comparisons between territories and controls provided deeper insights into breeding-territory preferences (Tab. 1). However, the proportion of these habitats did not differ between territories and controls. In contrast, Curlews preferred to establish territories in areas with higher proportions of salty dunes and a larger distance to areas that are frequented by humans. Copses and built-up area, however, were avoided. All the other parameters did not differ between territories and controls.

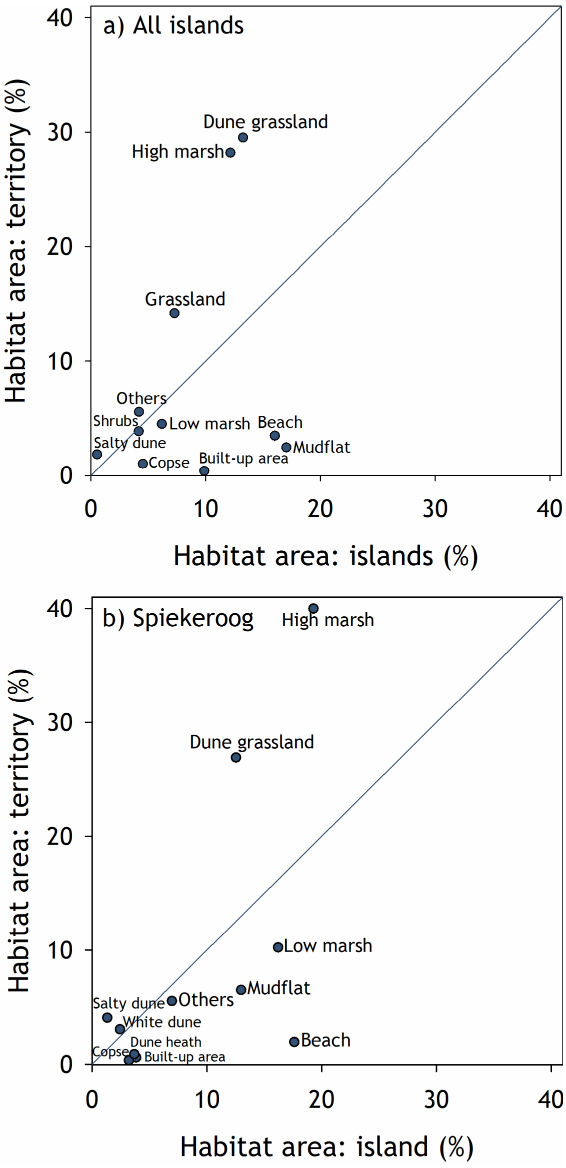


Fig. 3: Proportion of different habitat types within Curlew territories and on the islands, for all East Frisian Islands (a) and Spiekeroog (b), respectively. All islands (a): others = dune heath, dune slack, open water, white dune, ruderal, and reed; Spiekeroog (b): others = dune slack, grassland, open water, reed, ruderal, and shrubs. All islands (a) and Spiekeroog (b): Fisher's Exact Test <0.001.

Based on the GLMM analysis, the likelihood of territory establishment increased with the availability of dune grassland and decreased with those of copses and built-up area (Fig. 4). With an AUC value of 0.88 the model accuracy was high.

Nest-site preferences

The direct vicinity of the nest was almost covered by the herb layer (60%) and the vegetation was nearly 20 cm high (Tab. 2).

Around the nest, at coarse scale, bare ground, mosses, and litter cover were very similar, with nearly 20% in each case. At fine scale, litter covered on average a further 30%, followed by bare ground with 14% and mosses with 11%. Habitats with a higher cover of bare ground were significantly preferred for nest-building, at both spatial scales. At coarse scale, in addition, the cover of the herb layer was significantly lower compared to control. The GLM analysis revealed that at both spatial scales the likelihood of nest-building was highest with increasing amounts of bare ground and an intermediate vegetation height (Fig. 5). The model accuracy was very high with AUC values of 0.87 and 0.89, respectively.

Tab. 1: Mean area (± SE) of habitat types, habitat heterogeneity, distance to human-frequented areas and wetlands for breeding territories (n = 46) and controls (n = 46) on the East Frisian Islands. Differences between breeding territories and controls were tested using the Mann-Whitney *U* test. Significance levels are indicated as follows: n.s. *P* >0.05, * *P* ≤0.05, ** *P* ≤0.01, *** *P* ≤0.001.

Parameter	**Territory**	**Control**	***P***
Habitat type (ha)			
Dune grassland	2.24 ± 0.24	1.66 ± 0.23	n.s.
High marsh	1.83 ± 0.26	1.56 ± 0.30	n.s.
Grassland	0.65 ± 0.27	0.71 ± 0.27	n.s.
Shrub	0.34 ± 0.07	0.45 ± 0.10	n.s.
Mudflat	0.31 ± 0.08	0.14 ± 0.07	n.s.
White dune	0.27 ± 0.08	0.18 ± 0.07	n.s.
Beach	0.24 ± 0.10	0.26 ± 0.11	n.s.
Dune slack	0.20 ± 0.07	0.11 ± 0.05	n.s.
Ruderal	0.17 ± 0.08	0.09 ± 0.05	n.s.
Salty dune	0.17 ± 0.03	0.08 ± 0.04	*
Low marsh	0.15 ± 0.06	0.42 ± 0.13	n.s.
Dune heath	0.11 ± 0.06	0.25 ± 0.10	n.s.
Reed	0.10 ± 0.06	0.12 ± 0.05	n.s.
Open water	0.10 ± 0.04	0.09 ± 0.02	n.s.
Copse	0.08 ± 0.03	0.60 ± 0.15	**
Built-up area	0.03 ± 0.01	0.22 ± 0.08	**
Hab. heterogeneity (H')	1.15 ± 0.06	1.12 ± 0.05	n.s.
Distance to wetland (m)	157.7 ± 20.9	271.2 ± 49.4	n.s.
Distance to human-frequented area (m)	484.7 ± 77.5	439.3 ± 49.3	*

DISCUSSION

Our study revealed that Curlew territories consisted of large proportions of high marshes and dune grasslands, the two dominant habitat types on the East Frisian Islands. However, the most important predictors of territory establishment were a large area of dune grassland and a low extent of copses and built-up area. Microhabitats with an herb-layer characterised by intermediate cover and height as well as some bare grounds were preferred for nest-building. Predation is regarded as one of the major drivers of reproductive failure in birds during the egg and nestling phase (Ricklefs, 1969). One adaption to reduce risk of nest predation is to maintain some view of the surroundings of the nest to facilitate early predator detection (Götmark et al. 1995). The two main habitats within Curlew territories, high marshes and, especially, dune grasslands, provide large areas of low-growing and not too dense vegetation (Petersen & Pott, 2005). Such conditions may facilitate all-round visibility and early predator recognition (Götmark et al. 1995).

However, in salty dunes, the panoramic view is probably even better. High marshes are mostly flat and dune grasslands have a pronounced relief. Despite the generally open habitat structure in both cases, such relief limits distance vision. In contrast, salty dunes usually form small-scale mosaics within high marshes and protrude from them by several decimetres allowing more distant views (Petersen & Pott, 2005). The extent of copses and built-up area were the two other main predictors for territory establishment on the islands. Poor visibility of potential predators is also the most likely explanation for the observed avoidance of copses. Several other studies observed that Curlews and other waders breed less likely near forest edges for the same reason (Berg, 1992; Valkama et al.

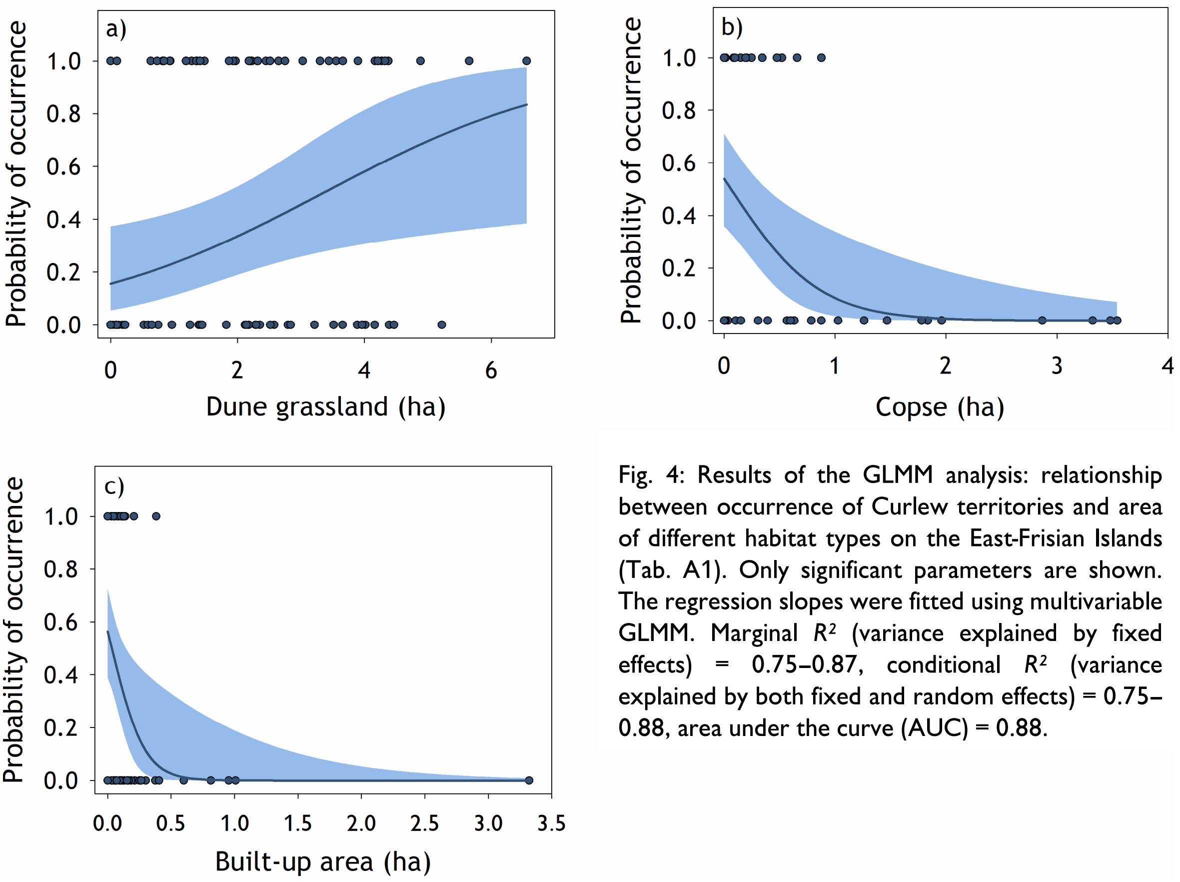


Fig. 4: Results of the GLMM analysis: relationship between occurrence of Curlew territories and area of different habitat types on the East-Frisian Islands (Tab. A1). Only significant parameters are shown. The regression slopes were fitted using multivariable GLMM. Marginal R^2 (variance explained by fixed effects) = 0.75–0.87, conditional R^2 (variance explained by both fixed and random effects) = 0.75–0.88, area under the curve (AUC) = 0.88.

1998, Douglas et al. 2014, Kaasiku et al. 2019). Many wader species are sensitive to disturbance by humans, especially near their nests (Hockin et al. 1992). This is also true for the Curlew (Haworth & Thompson, 1990, Navedo & Herrera 2012); it is known to have very long escape distances (Smit & Visser 1993). In line with this, the amount of built-up area was lower and the distance to roads, paths and buildings was higher in territories than in controls. Additionally, the probability of nest establishment decreased with an increasing extent of built-up area (Fig. 4c).

In Central Europe Curlews mostly nest on grasslands or arable fields in agricultural areas (Berg, 1992, 1994; Valkama et al. 1998). On the East Frisian Islands, however, the role of improved and semi-natural grasslands differed between islands (cf. Fig. 3a and b). Even on islands with larger areas of managed grasslands, they were only used for nesting when land-use intensity was low (own observation), which was the case on the islands of Borkum and Juist. On Borkum, for example, most of the grasslands are grazed with low stocking rates (0.7–1 cattle/ha) and only partly subject to aftermath mowing, promoting the heterogeneous vegetation structure preferred for breeding (Andretzke & Oltmanns 2016).

The nest concealment hypothesis states that more concealed nests are less vulnerable to predation (Filliater et al. 1994). Indeed, several studies have shown that nest concealment usually reduces predation risk (Wiebe & Martin, 1998; Møller, 2018), although other studies found, that this is not a universal pattern (e.g. Koivula & Rönkä 1998; Laidlaw et al. 2020). However, a well-hidden nest hampers all-round visibility and early detection of potential predators (Amat & Masero, 2004). Hence, nest-site selection usually reflects a trade-off between sufficient concealment and a good view for the recognition of predators (Götmark et al. 1995). In line with this, we interpret the preference of Curlews for microhabitats with an herb-layer of intermediate cover and

Tab. 2: Mean values (± SE) of vegetation structure at nest sites (n = 14) and controls (n = 28) at coarse scale (10 m × 10 m) (a) and fine scale (2 m × 2 m) (b), on Spiekeroog. Differences between nest sites and controls were tested using the Mann-Whitney *U* test. Significance levels are indicated as follows: n.s. *P* >0.05, * *P* ≤0.05, ** *P P* ≤0.01, *** *P* ≤0.001.

Parameter	Nest	Control	*P*
a) Coarse scale (10 m × 10 m)			
Cover (%)			
Bare ground	19.6 ± 3.8	6.7 ± 1.8	***
Mosses	17.9 ± 4.4	20.6 ± 6.2	n.s.
Litter	17.9 ± 4.2	26.3 ± 5.0	n.s.
Herb layer	57.5 ± 6.0	74.9 ± 4.3	*
Shrubs	0.2 ± 0.2	0.1 ± 0.0	n.s.
Vegetation height (cm)	18.1 ± 2.5	21.2 ± 2.2	n.s.
b) Fine scale (2 m × 2 m)			
Cover (%)			
Bare ground	13.9 ± 3.3	4.4 ± 1.4	**
Mosses	11.2 ± 5.7	17.5 ± 6.0	n.s.
Litter	30.0 ± 6.2	30.5 ± 5.0	n.s.
Herb layer	59.6 ± 6.5	72.2 ± 5.2	n.s.
Shrubs	0.0 ± 0.0	0.0 ± 0.0	–
Vegetation height (cm)	19.3 ± 2.2	22.6 ± 3.0	n.s.

height, as found in our study, as such a trade-off. Other studies have also shown that Curlews preferred to nest in vegetation that is neither too short nor too high and dense (Valkama et al. 1998; Grant et al. 1999; Johnstone, 2017).

In addition, vegetation density and height influence the availability (Berg, 1993) as well as the accessibility of invertebrate prey (Vickery et al. 2001; Butler & Gillings, 2004; Atkinson et al. 2005). Short swards with patches of bare ground, are preferred foraging habitats of many insectivorous farmland birds (Atkinson et al. 2004; Schaub et al. 2010). While Curlews prefer ragworms outside of the breeding season, ground-dwelling invertebrates are an important food source for adult Curlews and their chicks during the breeding period (Berg, 1993). Therefore, we also attribute the observed vegetation-structure preferences of breeding Curlews to food accessibility. Moreover, short, and scattered vegetation in combination with bare ground might enhance foraging efficiency. It (i) reduces the time needed for predator detection (Whittingham & Evans, 2004), (ii) increases speed of movement during foraging (Butler & Gillings, 2004) and (iii), finally, increases the food uptake of adult Curlews and their fledglings (Devereux et al. 2004).

In summary, on the East Frisian Islands Curlews preferred habitat mosaics dominated by high marshes and dune grasslands, far away from areas with human disturbance for breeding. Although salty dunes usually comprised a small share of breeding territories, they were preferred within breeding habitats. Salty dunes protrude above high marshes by several decimetres, allowing an excellent view into the distance and, hence, early predator detection. Heterogeneous microhabitats with intermediate vegetation cover and height and some bare grounds were preferred for nest-building. This reflects a trade-off between (i) sufficient shelter for nests and fledglings, (ii) early recognition of predators and (iii) high levels of availability and accessibility of invertebrate prey. Such heterogeneous habitats, without mammalian predators and without destructive farming practices, are largely lacking in the intensively used agricultural landscapes of the European mainland (e.g. Berg 1992, 1994; Valkama et al. 1998). Consequently, Curlew populations on the mainland are mostly declining. In contrast, those on the East Frisian Islands are stable and, therefore, of prime importance for the protection of the species. In grasslands, the preferred habitat structures of intermediate vegetation height including areas of bare ground can be achieved by low intensity grazing or mowing (McCracken & Tallowin, 2004). Moderate grazing especially by cattle, can represent a suitable tool in realising such habitats (Devereux et al. 2004). Additionally, small herbivores like hares (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*) can significantly slow down dune

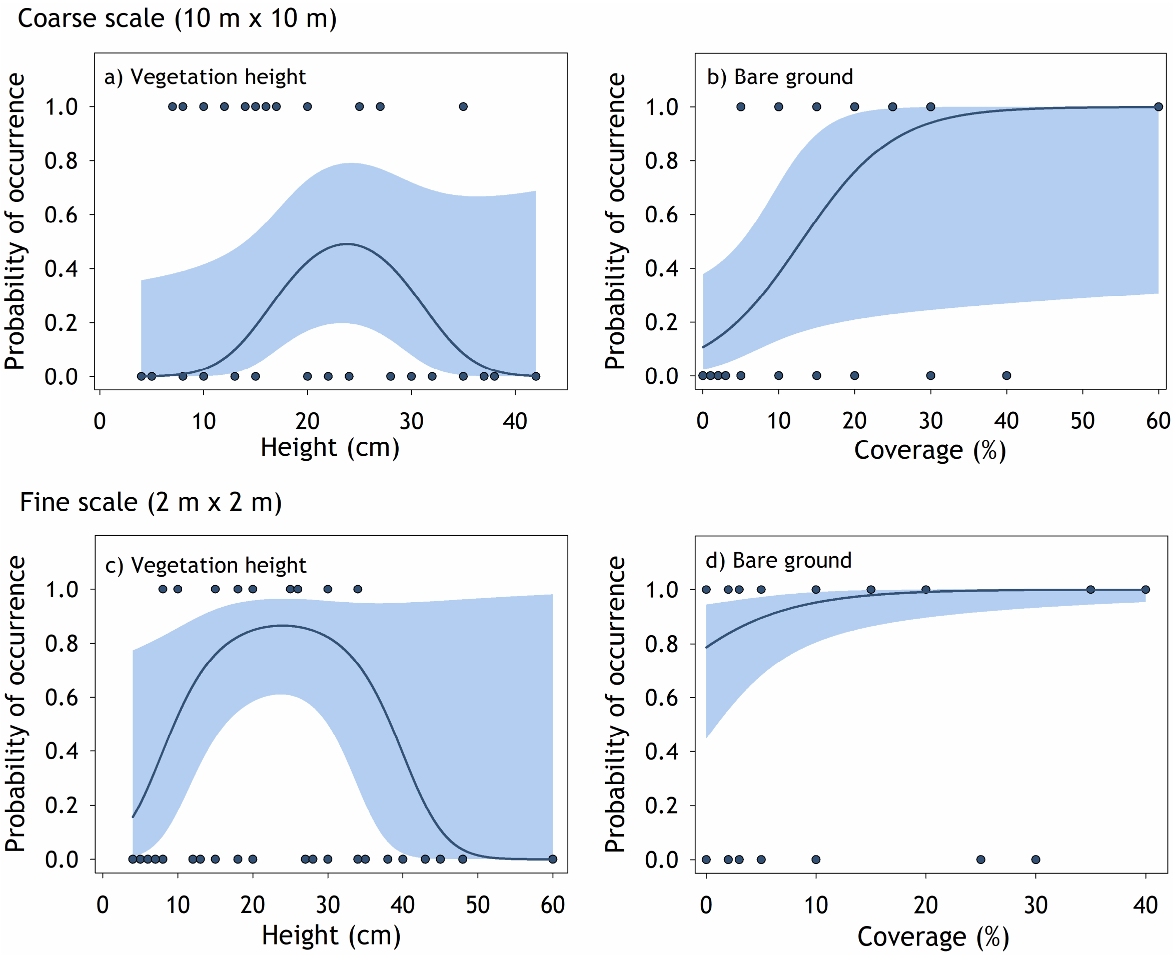


Fig. 5: Results of the GLM analysis: relationship between occurrence of Curlew nests and vegetation structure on Spiekeroog (Tab. A2). Only significant parameters are shown. The regression slopes were fitted using multivariable GLM. McFadden's pseudo R^2 = 0.40, area under the curve (AUC) = 0.87.

succession and provide open areas of short vegetation (Kuijper & Bakker 2003; Kämpfer & Fartmann 2019). Moreover, spatial, and temporal mosaics of different sward heights can be achieved by selective grazing and mowing at different times of the year (Devereux et al. 2004; McCracken & Tallowin, 2004) or through electric fencing in paddock grazing systems (Atkinson et al. 2005). To prevent nest and chick losses due to mowing or trampling by livestock, nests and chicks need to be located before mowing and paddock rotation. Afterwards, these areas must be excluded from agricultural practice until young are fully fledged or have left the area in question. Furthermore, Mandema et al. (2013) found horses to trample significantly more nests than cattle and suggest avoiding grazing by horses in areas with high densities of birds' nests.

Because tall, homogeneous, and dense vegetation is unsuitable for breeding, due to insufficient prey accessibility and restricted bird mobility (Vickery et al. 2001; Butler & Gillings, 2004; Atkinson et al. 2005), the use of fertilizer should be avoided (e.g., McCracken et al. 2004). Due to the Curlew's sensitivity to disturbance, human activities should be reduced to a minimum during the breeding period, e.g., by closing paths and by promotion of nature related eco-tourism (Davenport & Davenport 2006).

The apparently healthy population on the East Frisian Islands highlights the importance of natural habitats with low density of mammalian predators such as islands for threatened species. Since breeding productivity in habitats without mammalian predation is expected to be high, such populations may be important sources that reinforce populations on the mainland. This underlines the importance to retain or even intensify the protection of the Wadden Sea Islands not only in Germany, but also in the Netherlands and Denmark. Despite the great importance of adapted management systems to improve the habitat quality for Curlews breeding in farmland habitats, the preservation and restoration of natural and near-natural habitats should be given high priority.

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APPENDIX

Tab. A1: Results of the GLMM analysis (binomial response variable: presence [n = 46] versus absence [n = 46]): probability of Curlew territory establishment in relation to the area of different habitat types, habitat heterogeneity, distance to human-frequented areas and wetlands on the East Frisian Islands. Island was used as a random factor. Model-averaged coefficients (conditional average) were derived from top-ranked models ($\Delta AIC_C < 2$). R^2_{GLMMm} = variance explained by fixed effects, R^2_{GLMMc} = variance explained by both fixed and random effects (Nakagawa et al., 2017), AUC = area under the curve; accuracy of model prediction (Fielding & Bell, 1997). Low marsh, grassland, ruderal, shrub, open dune, dune slack, mudflat, wetland and distance to human-frequented area were not significant. Significance levels are indicated as follows: n.s. $P > 0.05$, * $P \leq 0.05$.

Parameter	Estimate	SE	Z	*P*
Intercept	0.92	0.59	1.54	n.s.
Built-up area	–9.02	3.71	2.40	*
Copse	–1.85	0.87	2.11	*
Dune grassland	0.67	0.27	2.44	*
R^2_{GLMMm} = 0.75–0.87, R^2_{GLMMc} = 0.75–0.88 AUC = 0.88				

Tab. A2. Results of the GLM analysis (binomial response variable: presence [n = 14] versus absence [n = 28]): probability of Curlew nest-building in relation to vegetation structure at coarse scale (10 m × 10 m) (a) and fine scale (2 m × 2 m) (b), on Spiekeroog. Model-averaged coefficients (conditional average) were derived from top-ranked models ($\Delta AIC_C < 2$). R^2_{MF} = McFadden's pseudo R^2, AUC = area under the curve; accuracy of model prediction (Fielding & Bell, 1997). Litter was not significant (a); herb layer and litter were not significant (b). Significance levels are indicated as follows: n.s. $P > 0.05$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Parameter	Estimate	SE	Z	P
a) Coarse scale (10 m × 10 m)				
Intercept	–9.47	4.50	2.04	*
Vegetation height	0.83	0.41	1.96	*
Vegetation height (centred + squared)	–0.02	0.01	1.97	*
Bare ground	0.17	0.07	2.33	*
R^2_{MF} = 0.40, AUC = 0.89				
b) Fine scale (2 m × 2 m)				
Intercept	–3.96	2.48	1.57	n.s.
Vegetation height	0.44	0.19	2.23	*
Vegetation height (centred + squared)	–0.01	0.00	2.23	*
Bare ground	0.12	0.06	2.14	*
R^2_{MF} = 0.40, AUC = 0.87				

Curlews on a small elevation in dune grassland. Such microrelief offers favourable conditions for early predator detection. (Spiekeroog, 04/07/2019).

Curlew in the transition areas from dune grassland to salt marsh. Natural dynamics of wind and flooding form very heterogeneous vegetation favored by breeding Curlews. Corresponding areas provide both bare ground, short and sparse vegetation for feeding, and areas of tall and dense vegetation for breeding and hiding of chicks (Spiekeroog, 18/05/2019).

(3) Extensive dune grasslands largely lacking human disturbance are an important refuge for a vole-dependent raptor

STEFFEN KÄMPFER, FLORIAN FUMY & THOMAS FARTMANN (under review)

ABSTRACT

Agricultural intensification and abandonment have led to a dramatic decrease of semi-natural grasslands. The Short-eared owl (*Asio flammeus*) is a ground-nesting raptor of open grasslands that has severely suffered from these changes. We studied the habitat preferences of this umbrella species of open grasslands in its last permanent breeding area in Germany (East Frisian Islands, southern North Sea). We analysed the breeding-territory preferences based on 576 territories on six of the islands. Moreover, we assessed nest-site preferences of 13 breeding pairs on the German abundance hot spot, the island of Spiekeroog. Our investigation revealed that the Short-eared owl strongly preferred open dunes for breeding, especially dune grasslands. By contrast, built-up areas and copses were avoided. For nest-building, microhabitats with a high cover of the herb layer and litter resulting in tall vegetation were favoured. By contrast, the vegetation in the wider surrounding of the nest was characterised by more bare ground and shorter vegetation but still a high cover of the herb layer and litter. In conclusion, our study highlights the prime importance of extensive open rough grasslands largely lacking human disturbance as breeding habitats for the Short-eared owl. At the nesting site, tall and dense vegetation with a high cover of litter (i) enhances concealment and (ii) causes a favourable microclimate by protecting fledglings against adverse weather conditions. In the wider surrounding of the nest, shorter vegetation with a pronounced litter layer (i) improves fledgling mobility, (ii) fosters vole abundance and (iii) increases prey accessibility.

KEYWORDS

Conservation management, habitat structure, landscape composition, nest-site preference, Short-eared Owl (*Asio flammeus*), vegetation structure

INTRODUCTION

Grasslands cover more than 20% of the EU-28 land surface and are among the most species-rich ecosystems in Europe (Chytrý et al. 2015, Feurdean et al. 2018, EC 2019, Fartmann 2023). Besides some natural grasslands, such as coastal dunes, most grasslands on the European continent have been shaped by human agricultural activities (Veen et al. 2009, Feurdean et al. 2018). However, agricultural intensification and abandonment have led to a dramatic decrease of these semi-natural grasslands (Bonari et al. 2017, Fartmann 2023). This loss has been associated with a strong decline of species that depend on such grasslands, including many birds (Donald et al. 2006, Marques et al. 2020). Among grassland birds, in particular ground-nesting species have suffered from these changes (Donázar et al. 1997, Heldbjerg et al. 2018, Kamp et al. 2021).

The Short-eared owl (*Asio flammeus flammeus*) is a ground-nesting raptor of open grasslands in the Holarctic (Keller et al. 2020). In the 19th and early 20th century, it was common in cultural landscapes across Western and Central Europe. The species has continually declined since suffering major range losses between 1970 and 1990 (Birdlife International 2004, Keller et al. 2020). Today, the occurrence of the

Short-eared owl is restricted to only a very few remaining strongholds in this part of Europe, such as some low mountain ranges or coastal dunes (Tucker et al. 1994, Newton 2017, Kämpfer & Fartmann 2019a). Accordingly, the conservation status of the Short-eared owl gives cause for concern (Calladine et al. 2012). The same applies to other parts of its range such as Canada (Smith et al. 2019) or the United States of America (Booms et al. 2014, Gahbauer et al. 2021a).

The main threats of the Short-eared owl population in Western and Central Europe are currently considered to be: (i) habitat loss due to agricultural intensification, particularly drainage of bogs, marshes and other wetlands, (ii) increased predation by mammalian mesopredators, (iii) reduced prey availability as a result of shrinking vole populations (*Microtus arvalis*) and (iv) nest destruction through agricultural activities (Bos et al. 2020, Fernández-Bellon et al. 2020, Kämpfer et al. 2022a). Consequently, the Short-eared owl is exposed to similar threats and suffers from comparable population declines as many other ground-nesting grassland birds (e.g. the Hen harrier [*Circus cyaneus*] or many wader species), making it an umbrella species for the conservation of open grassland ecosystems (Booms et al. 2014, Fernández-Bellon et al. 2020, Kämpfer et al. 2022a). Since the development of effective conservation strategies depends on precise knowledge of the species' habitat requirements (Fuller 2003), there is an urgent need to identify the key drivers of territory establishment and nest-site preferences of the Short-eared owl (Fernández-Bellon et al. 2020).

Here, we studied the habitat preferences of the Short-eared owl as an umbrella species of open grasslands. The research was conducted in the last permanent breeding area in Germany, the East Frisian Islands (southern North Sea). The study area is part of the Wadden Sea National Park of Lower Saxony and characterised by vast natural dunes and marshes. The islands are (i) mostly free from predatory mammals, (ii) largely undisturbed by agricultural activities or humans (Niedringhaus et al. 2009) and (iii) exhibit a high breeding success of the Short-eared owl (Kämpfer et al. 2022a). We investigated the breeding-territory preferences of the Short-eared owl between 1996 and 2019 on the basis of 576 territories with confirmed breeding on six of the East Frisian Islands. Moreover, in 2019, we assessed nest-site preferences of 13 breeding pairs on the island of Spiekeroog, the German abundance hot spot. Based on the results of this study, we make suggestions to improve future conservation measures for the Short-eared owl and other bird species of open grasslands.

MATERIALS AND METHODS

Study species

The nominate form of the Short-eared owl (*Asio flammeus flammeus*) has a large Holarctic breeding range (Keller et al. 2020). Breeding abundance, however, varies strongly across its distribution area. In most parts of Europe, the ground-nesting bird has a very local distribution and is quite rare. The majority of the European population breeds in Northern Europe and Russia. By contrast, in Central Europe, higher breeding densities are strongly dependent on an exceptionally high local abundance of voles (*Microtus* spp.). Across its European range, a large variety of open habitats are used for nesting. They comprise natural habitats such as bogs, coastal dunes, marshes, steppes or tundra but also semi-natural ones such as heathlands or young plantations and even agricultural land (Keller et al. 2020). Germany exhibits only a very small population, which is estimated at 50–180 territories (2005–2009) (Gedeon et al. 2014).

In most years, the population size is even at the lower end of this estimate. As a consequence, the species is listed as 'threatened with extinction' in the national red data book (Ryslavy et al. 2020). However, in years with vole outbreaks, the number of territories can strongly increase. The last outbreak was observed in 2019, when more than 200 territories were found mostly in improved grassland (Krüger 2019, Jödicke & Lemke 2020). However, the breeding success was close to zero since most nests were destroyed and fledglings were killed by mowing. Apart from such exceptional years, the occurrence of the Short-eared owl in Germany is mainly restricted to the North Sea coasts of Schleswig-Holstein and Lower Saxony and its Wadden Sea Islands (Gedeon et al. 2014). In recent years, the only permanent breeding area was the East Frisian Islands. Despite typical fluctuations, the number of Short-eared owls breeding on these islands is relatively constant and ranged between 13 and 59 with an average of 32 territories between 1981 and 2019 (Schulze-Dieckhoff, NLWKN 2020). With 10 to 15 breeding pairs per year, the island of Spiekeroog is the abundance hot spot (Fig. 1).

Study area

The study area comprised the East Frisian Islands Borkum, Juist, Norderney, Baltrum, Langeoog and Spiekeroog in the southern North Sea (Lower Saxony, Germany). The islands cover an area of about 120 km² and are sandy barrier islands, influenced by tides. They are characterised by a mild Atlantic climate with a mean annual temperature of 9.6 °C and a mean precipitation of 752 mm (weather station: Norderney; long-term mean: 1981–2010) (DWD 2020).

The islands are dominated by beaches (24%), mudflats (20%), marshes (15%), built-up areas (11%) and dune grasslands (10%) (Petersen & Pott, 2005; Petersen et al. 2014). Further habitats that cover smaller areas are white dunes (4%), shrubs (3%),

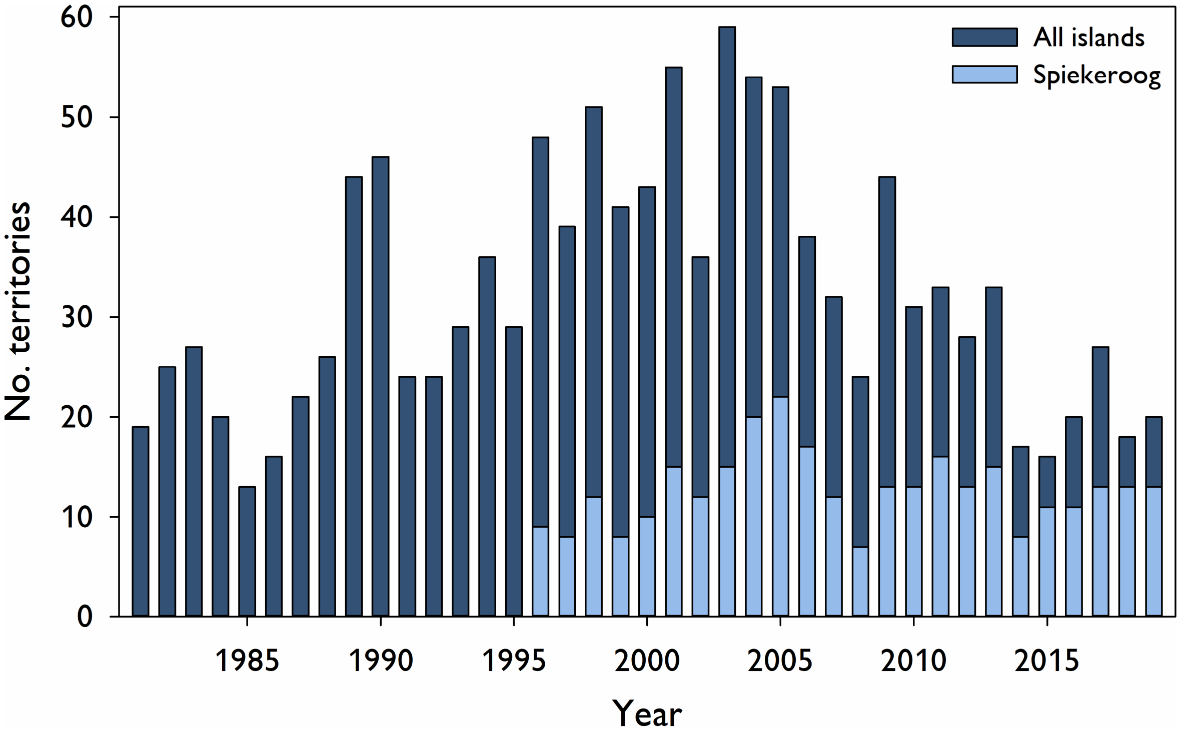

Fig. 1: Population development of Short-eared owls breeding on the East Frisian Islands (1981–2019, dark blue) and on the island of Spiekeroog (1996–2019, light blue). Data provided by M. Schulze-Dieckhoff, NLWKN 2020.

dune heathlands (1%), dune slacks (1%), reeds (1%) and transition zones between marshes and dune grasslands called salty dunes (1%). The East Frisian Islands are part of the Wadden Sea National Park of Lower Saxony (Dudley 2013) and the Wadden Sea World Heritage site (Baird & Asmus 2020). During the breeding season, human access is prohibited in most areas except on designated roads and paths and in small parts of the so called 'recreational zone'. Generally, dogs must be taken on a leash. Disturbance in protected areas occurs rarely thanks to visitor management, intensive public relations work and the use of National Park rangers and volunteers to control entry bans. Only small parts of the islands, primarily salt marshes, are grazed by livestock. Principally, the islands are free of mammalian predators except for Domestic cats (*Felis catus*) (Niedringhaus et al. 2008). However, in recent years, Red foxes (*Vulpes vulpes*) were present on the island of Norderney (Andretzke et al. 2016). Other mammals that occur on almost all East Frisian Islands and are known to cause clutch loss are Common rat (*Rattus norvegicus*) and Hedgehog (*Erinaceus europaeus*). Since 2010, a scheme to control population sizes of these introduced mammals has been carried out on the islands of Borkum, Norderney and Langeoog (Andretzke et al. 2016).

Since the island of Spiekeroog is the German abundance hot spot (Fig. 1), detailed analyses of the vegetation structure at nesting sites were conducted there. Spiekeroog is about 2 km wide and 10 km long and covers an area of 18 km² (Petersen & Pott, 2005).

Sampling design

Breeding-territory preferences

To identify breeding-territory preferences of the Short-eared owl on the East Frisian Islands, we used data from the annual breeding bird monitoring report between 1996 and 2019 provided by the Lower Saxony Water Management, Coastal Defence and Nature Conservation Agency (NLWKN, M. Schulze-Dieckhoff). Territory mapping was carried out according to Südbeck et al. (2005), with six visits between March and June (cf. Bibby et al. 2000). Territories were determined based on observed behaviours interpreted as possible/probable breeding (courtship display, constant perching during daylight periods, repeated observations of pairs) or confirmed breeding (repeatedly carrying prey to an area, giving alarm calls, mobbing potential predators, active nest or young located) (Calladine et al. 2010, Hardey et al. 2013). Since territories based on possible/probable breeding are associated with greater inaccuracies concerning actual nest location, they were excluded from further analyses, resulting in a data set of 576 territories based on confirmed breeding.

To determine preferred breeding areas on the islands, i.e. areas which were repeatedly used for breeding between 1996 and 2019, we conducted a kernel density analysis applying a 100 m × 100 m grid in ArcGIS 10.2 (Silverman 1986). Because the minimum distance between neighbouring breeding pairs was 300 m, we used this as the search radius distance for the calculation of kernel density. Subsequently, the resulting grid data were intersected with habitat data available from the Trilateral Monitoring and Assessment Program (TMAP) (Wadden Sea National Park of Lower Saxony, 2004) and the proportion of different habitats within each grid cell was calculated. We used habitat data from 2004 since this was the middle of the period under study. Furthermore, the vegetation can be assumed to change only slowly due to environmental stress (dry, nutrient-poor sandy soils) and the low competitive power of the dominant perennial plants (cf. Kämpfer & Fartmann 2022b). For the evaluation of the habitats preferred for breeding, all grid cells with a kernel density value of 0 were excluded to prevent zero inflation and to identify preferences within suitable breeding habitats, instead of identifying habitats that are already known to be unsuitable (e.g. beaches or forests).

Nest-site preferences

We conducted a detailed analysis of the preferred vegetation structure for nesting on the island of Spiekeroog. We searched for nests of Short-eared owls from March to July in 2019 in all thirteen territories with confirmed breeding (see section 2.3.1). All nests were marked using a GPS device.

After adults and fledglings have left the nest, we determined the cardinal direction of the nest entrance (0–360°) and measured vegetation characteristics in an area of 2 m × 2 m (fine scale), representing the direct surrounding of the nest, and 10 m × 10 m (coarse scale), representing the surrounding vegetation structure in the breeding habitat. For both spatial scales, we recorded the dominant plant species, measured the mean vegetation height (cm) with an accuracy of 1 cm using a ruler and estimated the cover of bare ground, herbs, mosses, shrubs and litter. Furthermore, we measured vegetation height at the nest in all four cardinal directions by placing a ruler in the nest and measuring vegetation height in north, east, south and west directions. The same parameters were also recorded at randomly selected control sites (hereinafter referred to as 'control'), which were selected by using the function 'Create random points' in ArcGIS 10.2. For the selection of controls, areas that were unsuitable for breeding (beaches, built-up areas, forests, low marshes and mudflats) were excluded. The ratio between nests and controls was 1:2 to cover the entire range of available vegetation structure.

Statistical analysis

All statistical analyses were conducted using the software R 4.0.4. (R Development Core Team, 2021). Vegetation structure data were not normally distributed. Accordingly, differences between nest and control on both spatial scales were analysed using Mann-Whitney *U* test and those between nests on the two different scales by Wilcoxon test since they were not independent from each other. Differences in vegetation height between the four cardinal directions of the nests were tested using ANOVA with Tukey post-hoc test. Mean direction and standard error of nest entrance were calculated using the 'circular' (Agostinelli & Lund 2017) and 'std.error.circular' functions (Flávio & Baktoft 2020).

To evaluate which habitats were preferred for breeding on the islands, we used generalised linear mixed-effects models (GLMMs) with negative binomial error structure using the 'lme4' package of Bates et al. (2015). Within the habitat models, kernel density was used as the response variable, the area of different habitats within grid cells as fixed effects and island as a random effect to account for possible spatial autocorrelation. To assess the effects of vegetation structure on nest-site selection, we conducted generalised linear models (GLMs) with binomial error distribution (nest vs. control) and vegetation parameters as predictors. Predictors were standardised (centred and scaled) to make their effect size comparable (cf. Border & Calladine 2021). If graphical inspections of the data suggested unimodal rather than linear relationships between the response variable and predictor variables, centred and squared values of the predictors were entered into the full model in addition to the untransformed values (cf. Kämpfer & Fartmann, 2022b). Multicollinearity was low for all predictors in all models ($|r_s| < 0.6$)

(Graham 2003). To increase the robustness of models with multiple predictors and to identify the most important variables, we conducted model averaging (full average) based on an information-theoretic approach (Burnham & Anderson, 2002; Grueber et al. 2011). Model averaging was performed using the 'dredge' function (R package MuMIn; Barton, 2020) and included only top-ranked models with ΔAICc <2 (cf. Grueber et al. 2011).

For binomial models, we calculated the area under the curve (*AUC*) as a measure of model accuracy (Fielding & Bell, 1997). Moreover, we calculated the variance explained by the models applying McFadden's pseudo *R*-squared (R_{MF}^2) for GLMs and marginal *R*-squared (R^2_m = variance explained by fixed effects only) and conditional *R*-squared (R^2_c = variance explained by both fixed and random effect) for GLMMs by using the function 'r.squaredGLMM' (Nakagawa et al. 2017).

RESULTS

Breeding territory preferences

Short-eared owl territories were strongly clumped on the islands (cf. the island of Spiekeroog as an example; Fig. 2). The 576 confirmed breeding territories between 1996 and 2019 were located in only 2.5% of all grid cells (*n* = 447). Accordingly, the calculated kernel density was zero in the remaining 97.5 % of the grid cells (*n* = 17,850). Since values of kernel density were high in very few grid cells (maximum 143), these cells can be considered as the breeding hot spots, i.e. they were frequently used and, hence, preferred for breeding (Fig. 2). The amount of dune grassland within grid cells explained most variation in kernel density of breeding territories (Fig. 3). Moreover, and in decreasing order, dune slacks, dune heath, reed, white dunes, salty dunes, reeds and shrubs were preferred for breeding. By contrast, beaches/mudflats and to a lower extent copses and built-up area were avoided.

Nest-site preferences

In 2019, seven of the 13 nests found on the island of Spiekeroog—more than 50%—were located in dune grassland. Of the remaining six, two nests were found in each white dunes and dune heath. The two remaining nests were situated in salty dune and high marsh, respectively. As a result, the dominant plant species at nests were *Ammophila arenaria* (*n* = 10), *Empetrum nigrum* (*n* = 2) and *Juncus maritimus* (*n* = 1). The direct vicinity of the nest (fine scale) was characterised by high cover of the herb layer (mean ± SE: 80 ± 5%) and litter (55 ± 5%) as well as the nearly complete absence of bare ground (1 ± 1%) (Tab. 1). The

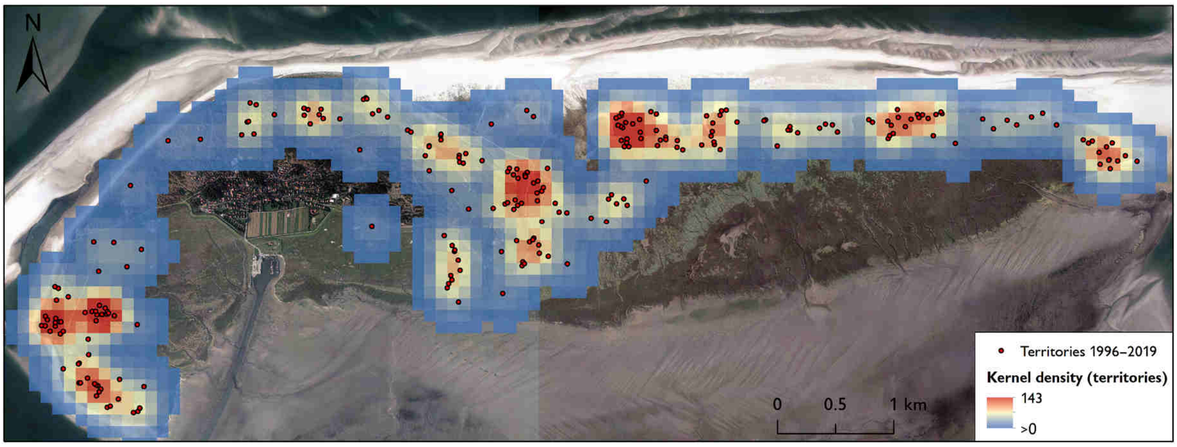

Fig. 2: Kernel density of confirmed breeding territories of the Short-eared Owl between 1996 and 2019, exemplarily shown for the island of Spiekeroog.

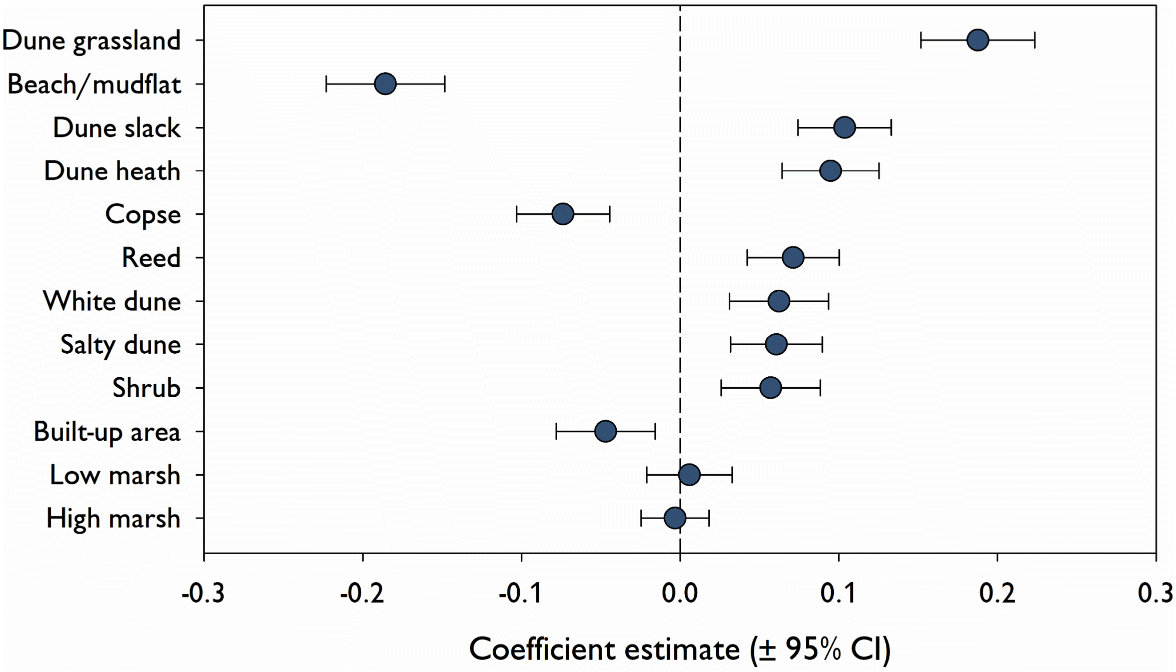

Fig. 3: Relationship between kernel density of breeding territories within grid cells (100 × 100 m) and habitat composition ($N = 447$). Predictors were standardised (centred and scaled) to make their effect size comparable. The effect size of the coefficients ± 95% confidence interval (CI) of the weighted model is shown. Variables whose 95% confidence interval do not intersect the value 0 on the y-axis are significant. For detailed statistics see Tab. S1. $R^2_m = 0.16$, $R^2_c = 0.38–0.39$.

vegetation was tall with a mean height (± SE) of 40 ± 2 cm. Compared to control, the cover of the herb layer and litter were higher, the vegetation was taller and the cover of bare ground was lower. On the coarse scale, the herb layer and litter also covered large parts. In comparison to the fine scale, however, the cover of bare ground was higher and the vegetation was less tall. As has been shown for the fine scale, the cover of bare ground was lower in the adjacency of nests in comparison to control. On both spatial scales, less bare ground and more litter were favoured for nesting (Fig. 4, Tab. S2). Additionally, on the fine scale, taller vegetation was preferred, and a higher cover of shrubs was avoided for nesting. On the coarse scale, an intermediate vegetation height of around 30 cm had a positive effect. Model accuracy (*AUC*: 0.91–0.97) and explained variance in the data set (R^2: 0.43–0.70) were high in both models. The nest entrance was mainly oriented to the east (mean ± SE: 90.3 ± 0.5°). Vegetation height in the four main cardinal directions differed at nests (Fig. 5). It increased from the eastern over the northern to southern and finally the western side. By contrast, there was no difference in vegetation height between the four cardinal directions at control.

DISCUSSION

Our analysis of the long-term data set from the only permanent breeding area of the Short-eared owl in Germany, the East Frisian Islands, revealed that the ground-nesting bird strongly preferred open dunes for breeding, especially dune grasslands and interlinked habitats such as dune slacks and dune heath. By contrast, built-up areas and copses were avoided. For nest-building, microhabitats with a high cover of the herb layer and litter resulting in tall vegetation were favoured (fine scale). By contrast, the vegetation in the wider surrounding of the nest was characterised by more bare ground and shorter vegetation but still a high cover of the herb layer and litter (coarse scale).

The observed preference of Short-eared

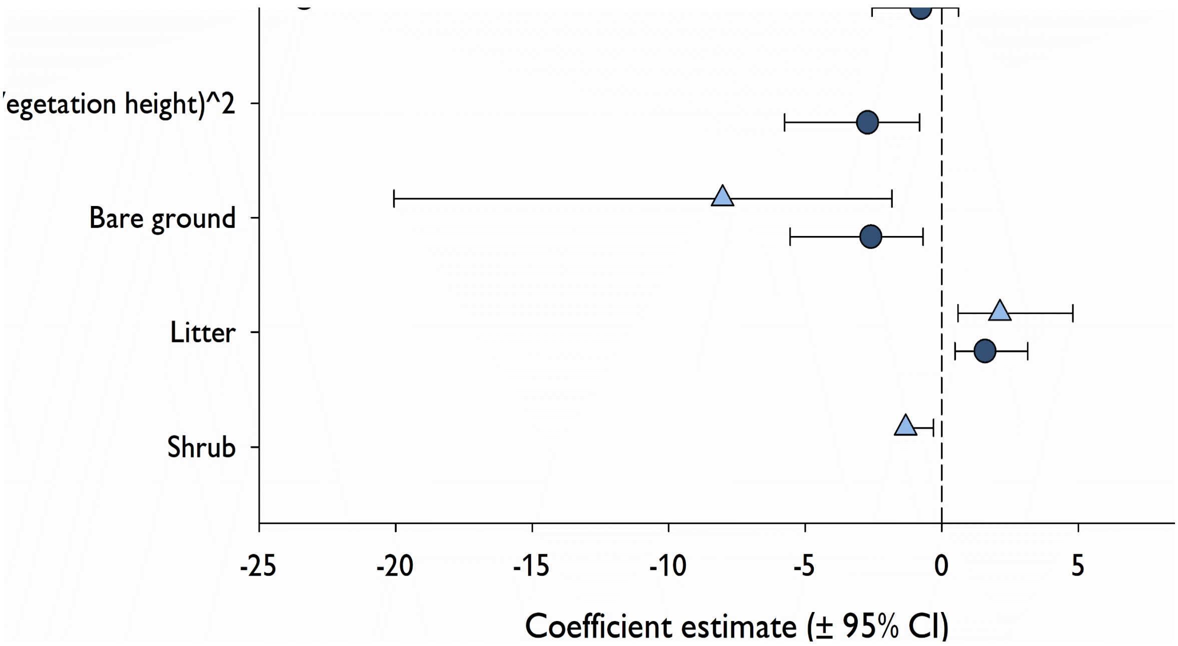

Fig. 4: Relationship between the probability of Short Eared Owl nest-building and vegetation structure on fine scale (2 × 2 m) (R^2_{MF} = 0.70, *AUC* = 0.97) and coarse scale (10 × 10) (R^2_{MF} = 0.43, *AUC* = 0.91). Predictors were standardised (centred and scaled) to make their effect sizes comparable.

owls for dense and tall grassland vegetation rich in litter for nesting is in line with former studies from North America (Holt 1992, Fondell & Ball 2004, Swengel & Swengel 2014, Keyes et al. 2016). According to the nest-concealment hypothesis, more concealed nests are less vulnerable to predation (Filliater et al. 1994, Fartmann et al. 2022). However, support for the nest-concealment hypothesis has been equivocal due to morphological traits and methods used to measure concealment (Borgmann & Conway 2015). Nevertheless, many studies have shown that concealed nests are less prone to predation, especially in ground-nesting birds (Wiebe & Martin 1998; Møller 2018). We assume that besides the dense and tall vegetation, the pronounced litter layer also enhances nest concealment. The colour of litter strongly matches those of the plumage of Short-eared owls (own observation). A recent study of Kämpfer et al. (2022a) determined that a high litter cover fostered the survival of Short-eared owl fledglings and led to an increase in the number of fledged young per nest. The authors also explained this relationship by an improved concealment but additionally by a better shelter against adverse weather (see below) due to the dense litter layer. In

Tab. 1: Mean values (± SE) of vegetation structure at nests (*n* = 13) and controls (*n* = 26) on (a) fine scale (2 m × 2 m) and (b) coarse scale (10 m × 10 m), on Spiekeroog. F = fine scale, C = coarse scale. Differences between nests and controls were tested using the Mann-Whitney *U* test and those between nests on the two different scales by Wilcoxon test since they were not independent from each other. Significance levels are indicated as follows: n.s. *P* >0.05, * *P* <0.05, ** *P* <0.01, *** *P* <0.001.

Parameter	**Fine (2 m × 2 m)**			**Coarse (10 m × 10 m)**			**F vs. C**
	Nest	**Control**	***P***	**Nest**	**Control**	***P***	***P***
Cover (%)							
Bare ground	0.9 ± 0.5	12.6 ± 3.7	**	5.5 ± 1.4	14.0 ± 2.8	*	**
Mosses	28.1 ± 9.2	36.6 ± 8.4	n.s.	43.5 ± 9.8	31.4 ± 7.5	n.s.	n.s.
Litter	55.4 ± 4.9	30.9 ± 4.2	**	45.0 ± 5.0	33.5 ± 3.3	n.s.	n.s.
Herb layer	80.4 ± 5.1	68.2 ± 4.1	n.s.	69.2 ± 5.3	72.5 ± 3.6	n.s.	n.s.
Shrubs	0.5 ± 0.4	2.5 ± 1.7	n.s.	2.1 ± 1.1	5.6 ± 2.4	n.s.	n.s.
Vegetation height (cm)	39.6 ± 2.3	26.3 ± 3.8	**	29.5 ± 2.2	32.5 ± 3.1	n.s.	**

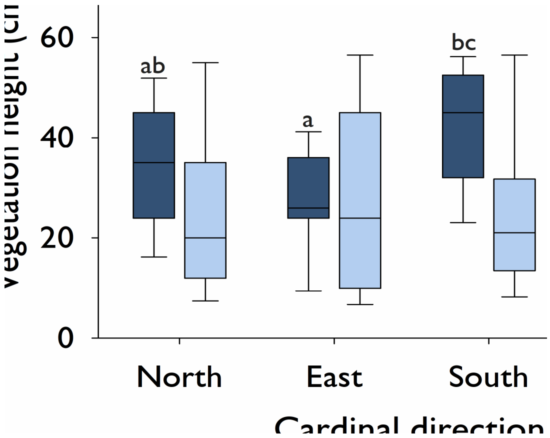

Fig. 5: Vegetation height at the four main cardinal directions at nests (n = 13) and controls (n = 26). Difference between the directions was tested using ANOVA. Nest: F = 7.76, df = 3, P < 0.001; Control: F = 0.05, df = 3, P = 0.98. Different letters indicate significant differences of pairwise comparisons (Tukey test, P < 0.05).

contrast to other ground-breeding birds (e.g. species with deceptive behaviour; Smith et al. 2018), breeding Short-eared owls are known to leave their nests in case of approaching mammalian predators or humans usually only when the potential enemies have nearly reached the nest (Hardey et al. 2013). Consequently, Short-eared owls seem to rely on their high concealment within their nesting site, supporting the nest-concealment hypothesis as well.

Moreover, dense vegetation and litter can have positive effects on nest microclimate and, therefore, reproduction rate by providing shelter from extreme weather such as strong wind, heavy rainfall or intensive solar radiation (Heenan 2013, Fartmann et al. 2022, Kämpfer et al. 2022a). Vegetation height at nests was highest in west and south directions, representing both the main wind direction and the cardinal direction with the most intensive solar radiation in Central Europe (Bauer 1999, Bürger 2003). By contrast, the nest entrance was mostly oriented to the opposite direction (east). Kämpfer et al. (2022a) observed that adverse weather, especially strong winds, affected fledgling survival of Short-eared owls. Consequently, we attribute the preference for tall vegetation in the west and south directions of the nest and the location of the nest entrance in the east as a strategy to cope with the negative effects of bad weather, in particular windy and rainy conditions. Such weather conditions are known to affect coastal areas of the North Sea more regularly than most of the Central European mainland (Bürger 2003).

In the wider surrounding of the nest, an intermediate vegetation height was preferred. Litter cover, however, was still high. Too high and dense vegetation might hamper the mobility of fledglings after leaving the nest (Devereux et al. 2004) and reduce the accessibility of voles for hunting adults (Baker & Brooks 1981, Toland 1987). By contrast, a high cover of litter is known to foster the abundance of voles, the most important prey of Short-eared owls (Amar & Redpath 2005; Huang et al. 2010, Swengel & Swengel 2014, Kämpfer et al. 2022a).

A high food abundance may also explain the observed general preference for dune grasslands. In a recent two-year study on the East Frisian Island of Spiekeroog, Kämpfer et al. (2022a) showed that dune grasslands were characterised by a relatively high vole abundance and the least fluctuating vole population within the investigated habitats. Additionally, dune grasslands usually surmount the surrounding habitats (e.g. dune slacks), which facilitates early predator detection (cf. Kämpfer & Fartmann 2022b).

Based on our study, extensive open rough grasslands are of prime importance as breeding habitats for the Short-eared owl. Similar observations have been made for North America (Wiggins et al. 2004, Swengel & Swengel 2014, Miller et al. 2022). Such habitats do not only provide suitable habitat structures for breeding but also for foraging (Kämpfer et al. 2019, 2022a; see above). By contrast, copses and built-up areas were avoided. Copses hamper access to small mammal prey. Additionally, they can serve as a perch for avian predators (e.g. Carrion crows [*Corvus corone*]), which may result in enhanced nest predation (Andersson et al. 2009). An avoidance of disturbance by human activity has already been shown by Calladine et al. (2010). In general, it can be assumed that the low frequency of human disturbance in the studied national park due to zoning, visitor management and the work of national park rangers favours the Short-eared owl breeding population. This assumption is supported by the findings of Kämpfer et al. (2022a). Although the densities of avian predators (Herring gull [*Larus argentatus*], Lesser black-backed gull [*Larus fuscus*], Carrion crow and Marsh harrier [*Circus aeruginosus*]) were high on the island of Spiekeroog, they detected a very high nest survival rate of Short-eared owls. They explained this pattern by the highly effective defensive behaviour of adult Short-eared owls due to the widespread absence of human disturbance.

In conclusion, our study highlights the prime importance of extensive open rough grasslands largely lacking human disturbance as breeding habitats for the Short-eared owl. The main habitats in our study were dune grasslands and interlinked habitats such as dune slacks and dune heath that provided mosaics of tall and dense vegetation rich in litter for nesting and areas with shorter vegetation but also providing a pronounced litter layer for foraging. At the nesting site, tall and dense vegetation with a high cover of litter (i) enhances concealment and (ii) causes a favourable microclimate by protecting fledglings against adverse weather conditions. In the wider surrounding of the nest, by contrast, shorter vegetation with a pronounced litter layer (i) improves fledgling mobility, (ii) fosters vole abundance and (iii) increases prey accessibility. As a result, the described environmental conditions in the preferred habitats on both spatial scales generally favour higher reproduction rates in the Short-eared owl.

IMPLICATIONS FOR CONSERVATION

Kämpfer et al. (2022a) detected a comparatively high reproduction rate of Short-eared owls (probability of nest survival: 0.9; hatched young per nest: 5.6) on the East Frisian Island of Spiekeroog. They explained the favourable conditions for reproduction on the island by a combination of the following key factors: (i) absence of mammalian mesopredators such as the Red fox, (ii) relatively stable vole populations without cyclic variation, (iii) nearly no disturbance through agricultural measures and (iv) widespread lack of human disturbance due to legal regulations of the National Park. Our study confirmed the latter and, additionally, highlighted the prime importance of large and well-connected open rough grasslands for the establishment of breeding territories of the species. Since habitats meeting the described requirements are very rare in Central Europe due to the dominance of intensive agriculture (Ellenberg & Leuschner 2010) and high density of mammalian mesopredators (Roos et al. 2018), we assume that the availability of suitable habitats is a decisive factor limiting the occurrence of the umbrella species Short-eared owl on the Central European mainland.

Consequently, to promote the species, conservation management should focus on the restoration of extensive und unfragmented rough grasslands. This is especially true for ecosystems where abundance of mammalian mesopredators is naturally low such as bogs, marshes or other wetlands (cf. Border & Calladine 2021) and that are characterised by nutrient-poor soils with low successional speed. The latter is important since under such conditions the preferred vegetation exhibiting a high cover of litter and not too tall vegetation where shrubs are absent can be maintained for longer time periods without management. This assumption is confirmed by the fact that the nutrient-poor dune grasslands on the East Frisian Islands have already hosted strong populations of the Short-eared owl for decades (see section Study species), although they are only affected by weak natural disturbance (e.g. aeolian sand shifts). However, outside national parks, low-intensity grazing and possibly clearing of shrubs are necessary from time to time to reset succession. Such measures are also known to increase habitat suitability for many other grassland species (Kämpfer & Fartmann 2022b, Fumy & Fartmann 2021). By contrast, intensive grazing should generally be avoided. It creates short swards that (i) have a low vole abundance due to the lack of litter (Amar & Redpath 2005, Kämpfer et al. 2022a) and (ii) are unsuitable for nesting (this study). Moreover, in farmland ecosystems, it must be ensured that neither nests nor young birds are harmed by agricultural activities such as mowing (Krüger 2019).

Due to strong competition for land in densely populated Central Europe (Fartmann et al. 2021), the implementation of large-scale habitat management is difficult to achieve and requires long-term approaches. Therefore, besides the development of suitable management measures at the mainland, the continuous protection of the few remaining refuges, such as the East Frisian Islands, should be given highest priority.

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Optimal habitat for Short-eared owls. Mosaic of dune heath, dune grassland and dune slack providing high and dense vegetation with high amounts of litter for breeding and shorter vegetation in the wider surrounding for feeding (Spiekeroog, 28/05/2019).

Fence posts providing a good overview of the breeding territory are regularly used by Short-eared owls (Spiekeroog, 04/07/2018).

Chapter III

Breeding and migration ecology of threatened grassland birds

Curlew (*Numenius arquata*) in low-intensity grassland (Kreis Steinfurt, 04/05/2020).

Chapter III

Breeding and Migration Ecology of threatened grassland birds

Paper 4

Weather conditions determine reproductive success of a ground-nesting bird of prey in natural dune grasslands

Paper 5

Tracking wintering areas and post-breeding migration of a declining farmland bird – An indispensable basis for successful conservation

(4) Weather conditions determine reproductive success of a ground-nesting bird of prey in natural dune grasslands

STEFFEN KÄMPFER, ELIAS ENGEL & THOMAS FARTMANN (2022) Journal of Ornithology 163: 855–865.

ABSTRACT

The Short-eared Owl (*Asio flammeus*) inhabits open grasslands and belongs to the ground-breeding birds that have experienced the most severe declines during recent decades. Here, we studied nest and fledgling survival of the owl species in relation to (i) habitat composition, (ii) vegetation structure, (iii) weather conditions and (iv) vole abundance. The study was conducted on the East Frisian Island of Spiekeroog (southern North Sea, Lower Saxony, Germany), which harbours one of the last remaining permanent populations of the species in Central Europe. With a mean hatching success of 5.6 young per nest (*N* = 34) and an average probability of nest survival of 0.9 (N = 28), values ascertained in this study exceeded those reported in previous research. We attribute this to the special environmental conditions on the island, i.e. (i) the absence of mammalian mesopredators such as the Red Fox (*Vulpes vulpes*), (ii) nearly no disturbance through agricultural measures and (iii) low level of human disturbance due to legal regulations of the National Park. By contrast, the survival of fledglings was lower than survival of nests and varied considerably between the investigated years. Weather conditions were the key driver of fledgling survival. Maximum wind speed and sunshine duration had a negative effect on the probability that chicks successfully fledged. Both lead to reduced hunting success, and the former is also associated with increased costs for thermoregulation. Consequently, increasing frequency of extreme weather events caused by climate change could negatively impact the breeding success of vole-dependent raptors, such as the Short-eared Owl.

KEYWORDS

Barrier Island, breeding success, Common vole (*Microtus arvalis*), Nest/fledgling survival, radio tracking, Short-eared Owl (*Asio flammeus*)

INTRODUCTION

Throughout Europe, agricultural intensification has led to a dramatic decline in biodiversity (Donald et al. 2006; Emmerson et al. 2016, Reif & Hanzelka 2020). Consequently, birds of open grasslands are among the most rapidly declining bird species. The loss is particularly severe in ground-nesting species (Van Turnhout et al. 2010; Kamp et al. 2020). Habitat loss due to agricultural intensification, an increase in nest disturbance through agricultural activities during the breeding season and higher predation rates because of growing populations of mesopredators, such as the Red Fox (*Vulpes vulpes*), are considered to be the main drivers of the sharp decline in ground-nesting birds (Newton 2017; Roos et al. 2018).

The Short-eared Owl (*Asio flammeus*) inhabits open grasslands and belongs to the ground-breeding birds that have experienced the most severe declines during recent decades (BirdLife International 2004). As a result, it is considered a species of conservation concern in Europe (Calladine et al. 2012; Fernandez-Bellon et al. 2020) and threatened with extinction in Germany (Ryslavy et al. 2020). The owl has especially suffered from habitat loss and degradation due to agricultural intensification, increased predation and reduced prey availability (Fernández-Bellon et al. 2020).

Nest and fledgling survival crucially affect population dynamics (Ludwig et al. 2018). Therefore, the identification of the key drivers of reproductive success is decisive for the conservation of threatened species (Green 1999; Bro et al. 2000). This is especially true for species with strong population fluctuations (Nuijten et al. 2020). Populations of the Short-eared Owl are known to heavily oscillate depending on local vole populations (Korpimäi & Norrdahl 1991). However, overall, our knowledge on the environmental parameters that determine reproductive success in this species is scarce (Holt 1992, Fernandez-Bellon et al. 2020). Additionally, habitats of the Short-eared Owl are predicted to become increasingly degraded in some areas in the course of ongoing climate change (Miller et al. 2020). Therefore, there is an urgent need to identify the key drivers of nest and fledgling survival as a basis for the development of effective conservation strategies in times of global change (Holt 1992, Fernandez-Bellon et al. 2020).

Here, we studied nest and fledgling survival of the Short-eared Owl in relation to (i) habitat composition, (ii) vegetation structure, (iii) weather conditions and (iv) vole abundance. The study was conducted on the East Frisian Island of Spiekeroog (southern North Sea, Lower Saxony, Germany), which harbours one of the last remaining consistently occupied populations of the Short-eared Owl in Central Europe. The study area is part of the Wadden Sea National Park of Lower Saxony and the Wadden Sea World Heritage site. It is characterized by natural dunes and marshes free from predatory mammals and largely undisturbed by agricultural activities or humans. The aim of this study was to assess the relative influence of weather and habitat on reproductive success in a breeding population of the Short-eared Owl that does not show the typical strong fluctuations associated with vole cycles.

MATERIALS AND METHODS

Study species

The nominate subspecies of the Short-eared Owl (*Asio flammeus flammeus*) has a large Holarctic breeding range (Keller et al. 2020). However, across its distribution area, abundance of the species varies strongly. In Central Europe, characterized by intensive agriculture (Ellenberg & Leuschner 2010), the species is very rare (Keller et al. 2020) and greater breeding densities are strongly dependent on a high local abundance of Common vole (*Microtus arvalis*) (Gedeon et al. 2014). Within Central Europe, both natural (e.g., bogs, coastal dunes, and marshes) and man-made habitats (e.g., agricultural land) are used for breeding (Keller et al. 2020). Habitat loss and degradation, increased predation and reduced prey availability are considered to be the main threats of the Short-eared Owl in this part of its range (Fernández-Bellon et al. 2020).

The Short-eared Owl is a ground-breeding species. In northern and central Europe nesting usually occurs from March to May, and clutch size ranges from 2 to 8. Eggs are mostly laid at daily intervals, and incubation of eggs takes an average of 27 days. Fledglings leave the nest and hide in the surrounding vegetation at an age of 12–17 days. Their parents continue to feed them until they fledge at the age of 24–27 days (Hardey et al. 2013). On the East Frisian Islands, dune grasslands, dune heath, salt marshes and salty dunes are the main foraging habitats of the species (Kämpfer et al. 2020). For further information about the habitat types see Petersen et al. (2014).

In Germany, population size is estimated to be 50–180 territories (2005–2009) (Gedeon et al. 2014). In years with vole outbreaks, the number of territories can strongly increase (Krüger 2019). For example, in 2019, more than 200 breeding pairs were detected, mostly nesting in improved grasslands. However, in most years, population size is at the lower edge of the population estimate. Within Germany, occurrence of the Short-eared Owl is mainly restricted to the North-Sea coasts and the Wadden Sea Islands (Gedeon et al. 2014, Kämpfer & Fartmann 2020). The only permanent German breeding population with an average of 36 territories between 1993 and 2018 was located on the East Frisian Islands (Kämpfer & Fartmann 2020). Here, the island of Spiekeroog was the abundance hotspot, with 10 to 15 breeding pairs per year. Even in years with low vole abundance, nest camera data revealed that voles are by far the most important food for chicks on this island (Klock 2018).

Study area

The study was conducted on the East Frisian Island of Spiekeroog (southern North Sea, Lower Saxony, Germany). Spiekeroog is about 2 km wide and 10 km long, resulting in a total area of 18 km² (Petersen & Pott 2005). An Atlantic climate with a mean annual temperature of 9.6 °C and a mean precipitation of 752 mm characterise the study area (weather station: Norderney; long-term mean: 1981–2010) (Deutscher Wetterdienst, 2019). The East Frisian Islands are sandy barrier islands and are influenced by tides. The main habitats on the islands are beaches (18 %), natural dune grasslands (13 %), mudflats (13 %), marshes (35 %), built-up areas (4 %), and dune heath (4 %). Further habitats that cover smaller areas are copses (3 %), white dunes (2 %), shrubberies (2 %), dune slacks (1 %), reeds (1%), semi natural grassland and transition zones between marshes and natural dune grasslands called salty dune (1 %) (Petersen & Pott 2005, Petersen et al. 2014). The study area is part of the Wadden Sea National Park of Lower Saxony and the Wadden Sea World Heritage site. During the breeding season, access is prohibited for humans in most areas, except in small parts in the so called 'recreational zone' or on designated roads and paths. Dogs must generally be on a leash. Due to intensive public relations work, visitor management and the use of National Park rangers and volunteers to control entry bans, protected areas are rarely disturbed. Only small parts of the island, primarily salt marshes, are grazed by livestock. The study area is free of mammalian predators except for domestic cats (*Felis catus*) (Walter & Kleinkuhle, 2008), common rats (*Rattus norvegicus*) and hedgehogs (*Erinaceus europaeus*) (Andretzke & Oltmanns 2016).

Sampling design

Nest detection, nest, and fledgling survival

Within the study area, we searched for nests of the Short-eared Owl from March to July in 2011, 2015 and 2017–2019. For the identification of nest sites, we used key behaviours that were indicative of territoriality, such as carrying prey to a potential nest, giving alarm calls, mobbing potential predators, courtship display (wing clapping) and constant perching in the open during daylight periods (indicating a male near an incubating female) (Calladine et al. 2010). During incubation of an average of 27 days (Hardey et al. 2013), all nests found before hatching (n = 28, 511 exposure days) were monitored at 6–9-day intervals to document clutch size, number of hatched chicks and general nest fate, until all fledglings left the nest.

All chicks were banded with an aluminium ring (Ornithological station "Vogelwarte Helgoland") between May and July, right before they left the nest. To improve rediscovery rates of fledglings in their hiding places and to determine their individual fate more precisely, we additionally used coded radio-transmitters (Biotrack ACT-626, 1.3 g), a hand-held antenna (Lotek LiteFlex VHF Yagi) and a receiver (Lotek SRX800). In 2018 and 2019, we radio-tagged 15 fledglings in both years. Radio-tags measured 1.5 × 0.7 cm and were glued on linen fabric of 2.3 × 1.5 cm using universal adhesive (UHU Super Strong) to increase surface area. Subsequently, the radio tags were glued on a feather-free spot on the back of fledglings by applying surgical cement (Perma-Type), which is free from skin-irritating substances and remains flexible even after fast drying. Including material for attachment, tags weighed 2.2 g, while tagged birds weighed 207–386 g (mean: 281 g). Thus, mass of radio tags was at most 1.1% of a bird's body mass and, hence, below the upper recommended load limit of 5% (Kenward 2001). Rediscovered ringed and radio-tagged fledglings are hereinafter termed tagged fledglings. All tagged birds were checked every 5–7 days until their flight ability was large enough to flee from approaching humans and radio tags fell off due to higher mobility of the birds. In this case, fledglings were considered successfully fledged. The geographic position of the tagged fledglings was recorded using a GPS-device. Altogether, 38 tagged fledglings could be included in the analysis of fledgling survival, representing a total of 769 exposure days.

Daily survival rate (DSR) of a nest was defined as the probability that at least one egg within a nest survived a single day (Dinsmore et al. 2002). By contrast, DSR of fledglings considered the survival of each fledgling during a period of 24 hours. The probability of nest survival during the nesting period and fledglings' survival during the fledgling period (in both cases 27 days, Hardey et al. 2013), were calculated as the product of 27 consecutive daily nest survival rates of nests/fledglings (DSR^27) (cf. Dinsmore et al. 2002). Nests for which nest fate or laying date could not be determined unequivocally or those which were found after some of the chicks had already left the nest were excluded from further analysis, resulting in different sample sizes for different parameters (Tab. 1).

Vole abundance

Vole abundance was sampled in 2018 and 2019 within the four main foraging habitats of the Short-eared Owl in the study area: dune heath, dune grassland, salt marsh and salty dune (see 'study area') (Hirschberg 2018; Kämpfer et al. 2020). We randomly selected 12 plots (three per habitat type) using the function 'create random points' in ArcGIS 10.4. For trapping of voles, we arranged 25 Longworth traps in a square grid of 5 × 5 traps, each separated by 10 m (cf. Jareño et al. 2014). Trap deployment was guided by traces, corridors and burrows in an effort to increase probability of catch (Gurnell & Flowerdew 2006). The traps were equipped with an apple (as a water substitute), oats and wheat and were insulated with wood chips to protect the voles from hypothermia (Jareño et al. 2014). Voles were individually marked by fur cutting according to Gurnell & Flowerdew (2006). Trapping was conducted at the end of June, when most of the breeding owls were rearing young and the need for food was particularly high. The traps were opened 8 hours after placing them in the plot and from then on left open for 24 hours. During this period, traps were checked every 8 hours. The number of captures per plot was converted to the number of captures per 100 trap nights (recaptured individuals were not included) (cf. Steen & Gibbs 2004).

Environmental parameters

To determine the environmental drivers of nest and fledgling survival, we used data on (i) habitat type, (ii) vegetation structure and (iii) weather. We analysed habitat composition within the home range of tagged fledglings. Home range was determined by applying the minimum-convex-polygon (MCP) method (White & Garrot 1990) using the function 'minimum bounding geometry' in ArcGIS 10.4. The resulting polygons were intersected with habitat data available through the Trilateral Monitoring and Assessment Program (TMAP) (Wadden Sea National Park of Lower Saxony, 2017). The proportion of each habitat type within the home range was then calculated for every tagged bird. Furthermore, we measured mean vegetation height (accuracy: 1 cm) using a ruler and estimated the percentage cover of bare ground, herb layer, mosses, shrubs and litter in an area of 10 m × 10 m around each nest in June. Weather data comprised maximum wind speed (m/s), mean wind speed (m/s), precipitation sum, sunshine duration, temperature, and relative humidity per day (weather station island of Norderney, 20 km west of the study area, German Meteorological Service [DWD 2020]).

To test the effects of habitat composition and vegetation structure on the number of successfully fledged young per nest, we also applied the methods described above for the tagged fledglings for each individual nest. However, the assessment of the home range was based on the location of all fledglings per nest and not only a single bird.

To assess the impact of habitat structure on vole abundance, we measured vegetation height (accuracy: 1 cm) as well as the percentage cover of bare ground, herb layer, mosses, shrubs and litter in three subplots of 3 m × 3 m size within each of the 12 plots in which small mammal trapping was conducted in June 2018 (see ‘sampling design’). For further analysis, we used the mean of the three subplots.

Statistical analysis

All statistical analyses were conducted using the software R 4.0.3. (R Development Core Team, 2021). To account for undetected nests in survival estimates and to incorporate explanatory variables that may explain variation in nest and fledgling survival, daily survival rates (DSR) were modelled by applying nest-survival models (NSMs) in the program ‘MARK’ (Dinsmore & Dinsmore 2007; Cooch & White 2019). Analysis was performed using the R-interface ‘RMark’ version 2.2.7 (Laake 2020). Since for the evaluation of nest DSR nest age (laying date) must be determined accurately (Dinsmore & Dinsmore 2007), it was calculated based on nest-monitoring, (hatching date and incomplete clutches) assuming a mean incubation period of 27 days with eggs laid at daily intervals (see ‘study species’).

In models for DSR of fledglings, we used habitat compositions of the home range as individual covariates, vegetation structures as grouped covariates and weather data as time-specific covariates (see ‘sampling design’) (Dinsmore et al. 2002). Moreover, we incorporated nest age, the number of nest siblings as well as linear and quadratic time trends and year, to account for possible annual variation, in the models (Dinsmore et al. 2002).

To avoid overfitting, firstly, four different NSMs of fledgling survival were conducted: (i) a breeding-biology model incorporating age and time dependent effects as well as number of siblings, (ii) a habitat-type model with the cover of different habitat types as predictors, (iii) a vegetation-structure model including vegetation height and cover of different vegetation layers and (iv) a weather model (Tab. 2). Finally, a synthesis model was generated including all significant predictors of the preceding four models.

To evaluate those variables that influence the number of successfully fledged birds per nest, we used generalized linear mixed-effects models (GLMMs) applying the 'lme4' package of Bates et al. (2015), with binomial error distribution and a logit link function. We used the proportion of the number of successfully fledged and died fledglings per nest as the response variable applying the function cbind() (cf. Schöll & Hille 2020), and the cover of different habitat types within the home range of the fledglings of each nest and vegetation structure as predictors. Additionally, we incorporated 'year' as a random effect (cf. Crawley, 2007).

To increase model robustness and identify the most important parameters in NSMs and GLMMs, we performed model averaging based on an information-theoretic approach (Burnham & Anderson, 2002; Grueber et al., 2011). Model averaging was performed using the 'dredge' function (R package MuMIn; Bartón, 2019) and included only top-ranked models with ΔAICc <2 (cf. Grueber et al., 2011). The maximum number of predictors to be included in a single model was limited to 1/10 of the sample size (Harrell et al. 1996). To avoid multi-collinearity in the models, Spearmen's rank correlations (*r*) were used to test for strong inter-correlations ($|r| \geq 0.6$) (Dormann et al. 2013). Because the cover of the herb layer and mean vegetation height were intercorrelated ($r = 0.63$, $p < 0.001$) and mean daily wind speed was intercorrelated with maximum wind speed ($r = 0.78$, $p < 0.001$), only one of the respective variables was included in the models. Based on AICc values, models including vegetation height and maximum

Tab. 1: Egg-laying date, clutch size, hatching success, nest and fledgling survival of Short-eared Owl breeding pairs in different years. *N* = number of nests considered for the respective analysis; laying date: Julian day (January 1st = 1); DSR = daily survival rate: probability that a nest/fledgling survives a single day; PNS/PFS = probability of nesting/fledgling survival: probability that a nest/fledgling survives the nesting/fledgling period of 27 days.

Year	**Egg-laying date**		**Clutch size**		**Hatching success**			**Nest survival**			**Fledgling survival**		
	Mean ± SE	***N***	**Mean ± SE**	***N***	**Mean ± SE**	%	***N***	**DSR**	**PNS**	***N***	**DSR**	**PFS**	***N***
2011	115 ± 2.1	5	6.3 ± 2.4	7	6.0 ± 2.4	95	6	1 ± 0	1 ± 0	4	·	·	·
2015	114 ± 4.3	2	6.7 ± 0.5	4	·	·	·	1 ± 0	1 ± 0	2	·	·	·
2017	138 ± 2.8	7	5.4 ± 1.8	9	4.4 ± 1.7	84	9	0.993 ± 0.007	0.82 ± 0.16	7	·	·	·
2018	107 ± 1.3	8	6.2 ± 2.1	9	5.7 ± 1.9	89	9	1 ± 0	1 ± 0	7	0.962 ± 0.010	0.35 ± 0.01	18
2019	115 ± 2.3	9	7.1 ± 2.2	10	6.1 ± 1.9	86	10	0.992 ± 0.006	0.83 ± 0.15	8	0.983 ± 0.007	0.64 ± 0.10	20
Total	**118 ± 3.0**	**31**	**6.3 ± 1.1**	**39**	**5.6 ± 1.0**	**88**	**34**	**0.996 ± 0.002**	**0.90 ± 0.07**	**28**	**0.973 ± 0.006**	**0.48 ± 0.08**	**38**

Tab. 2: Results of the NSMs: relationship between daily survival rate of Short-eared Owl fledglings and environmental parameters. Daily survival rate: probability that a fledgling survives a single day. Model-averaged coefficients (full average) were derived from top-ranked models (ΔAICC < 2). Significance levels are indicated as follows: n.s. *P* >0.05, * *P* ≤0.05, ** *P* ≤0.01, *** *P* ≤0.001.

Variable	Est.	SE	*Z*	*P*
(a) Breeding biology				
Intercept	4.29	2.76	1.56	n.s.
Year 2019	0.78	0.58	1.33	n.s.
Time	−0.02	0.08	0.27	n.s.
I(time^2)	0.00	0.00	0.17	n.s.
No. siblings	−0.01	0.06	0.15	n.s.
(b) Habitat type				
Intercept	3.02	0.44	6.78	***
Salty dune	8.70	4.26	2.04	*
Dune grassland	1.16	0.55	2.03	n.s.
Dune heath	0.81	3.68	0.22	n.s.
White dune	−0.10	0.44	0.23	n.s.
High marsh	−0.09	0.44	0.20	n.s.
Copse	−0.25	1.58	0.16	n.s.
Shrub	0.21	1.50	0.14	n.s.
(c) Vegetation structure				
Intercept	2.13	0.75	2.34	**
Litter	0.03	0,01	2.29	*
Veg. height	0.01	0.01	0.55	n.s.
Bare ground	0.03	0.06	0.51	n.s.
Shrub layer	−0.01	0.03	0.29	n.s.
(d) Weather				
Intercept	23.47	7.33	3.20	**
Sunshine	−0.80	0.30	2.68	**
Wind speed	−0.73	0.24	3.07	**
Precipitation	−0.10	0.23	0.42	n.s.
(e) Synthesis				
Intercept	23.25	7.49	3.10	**
Salty dune	6.68	4.75	1.41	n.s.
Sunshine	−0.81	0.31	2.63	**
Wind speed	−0.74	0.24	3.13	**
Litter	0.00	0.01	0.38	n.s.

wind speed performed better compared with models including herb layer and mean wind speed. Consequently, in each case the latter was excluded from the analysis.

To test for differences in vole abundance between years and habitat types, we used a two-way repeated-measures ANOVA with a Bonferroni *t*-test. The effect of vegetation structure on vole abundance was analysed using GLMM as described above, with 'vole abundance' as the response variable, 'vegetation structure' as predictors and 'biotope type' as a random effect.

RESULTS

Nest and fledgling survival

Overall, in the five study years, 39 owl nests were found before the chick rearing stage (Tab. 1). Mean clutch size varied between 5.4 (2017) and 7.1 (2019) with an average of 6.3 eggs per nest. Probability of nest survival during the nesting period was very high and ranged between 0.82 and 1 (mean: 0.9). The egg-laying period varied from March 24th to June 15th (probably a second brood since it only contained three eggs) with April 26th as the median laying date (Tab. 1).

Out of 202 eggs, 178 hatched successfully (88%, Tab. 1), 14 eggs remained in the nest with intact surface, one chick died during hatching, three eggs were found destroyed in the surrounding of the nest and six eggs disappeared for unknown reasons. Hatching success ranged between 4.4 (2017) and 6.1 (2019) with a mean of 5.6 hatched young per nest. Fledgling survival was much lower than nest survival and differed strongly between the two study years. In 2018, the probability of the fledglings to became fully fledged was 0.35, while in 2019 the probability was almost twice as high at 0.64.

Among the five NSMs, the breeding-biology model was the only one that failed to detect significant predictors of fledgling survival (Tab. 2). Daily fledgling survival increased with the area of salty dunes in the home range (habitat-type model), the cover of litter around the nest (vegetation-model) a low daily sunshine duration (weather

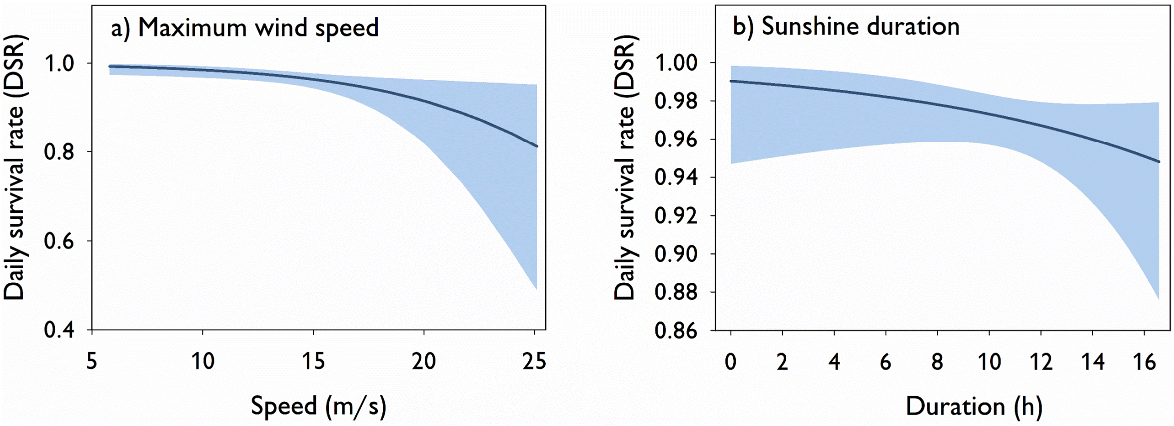

Fig. 1: Results of the synthesis NSM: relationship between daily survival rate of Short-eared Owl fledglings and significant environmental parameters. Daily survival rate: probability that a fledgling survives a single day. Note the different scales in the Y-axis. For detailed results see Tab. 2e.

and a low daily maximum wind speed (weather model). In the synthesis model, only the two weather variables, sunshine duration and wind speed, had a significant influence on fledgling survival (Tab. 2, Fig. 1). By contrast, the number of successfully fledged young per nest only increased with the cover of litter within the home range of the fledglings (Tab. 3, Fig. 2).

Tab. 3: Results of the GLMMs: relationship between the number of successfully fledged young per nests and habitat type and vegetation structure. Model-averaged coefficients (full average) were derived from top-ranked models (ΔAICC < 2). R^2m = variance explained by fixed effects, R^2c = variance explained by both fixed and random effects (Nakagawa et al., 2017). Significance levels are indicated as follows: n.s. $P > 0.05$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Variable	**Est.**	**SE**	***Z***	***P***
(a) Habitat type				
Intercept	−1.64	0.80	−2.06	n.s.
Dune grassland	−0.01	0.02	0.37	n.s.
White dune	0.00	0.01	0.21	n.s.
Built-up area	−0.02	0.08	0.19	n.s.
Salty dune	−0.00	0.01	0.09	n.s.
Copse	0.02	0.11	0.21	n.s.
Low marsh	−0.00	0.01	0.02	n.s.
(b) Vegetation structure ($R^2m = 0.31$, $R^2c = 0.31$)				
Intercept	−1.64	0.80	−2.06	*
Litter	0.04	0.02	2.23	*

Vole abundance

Vole abundance was almost three times higher in 2019 than in 2018 (Fig. 3). Salty dunes had the highest abundance and dune heath/grassland the lowest; salt marshes had an intermediate position. Abundance of voles in the plots increased with the cover of the litter (Tab. 4, Fig. 4).

Tab. 4: Results of the GLMMs: relationship between the abundance of voles (*Microtus arvalis*) and vegetation structure. $N_{plots} = 12$. The model containing litter and habitat type (random factor) was the only model within $\Delta AIC_C < 2$. R^2_m = variance explained by fixed effects, R^2_c = variance explained by both fixed and random effects (Nakagawa et al., 2017). $R^2m = 0.44$, $R^2c = 0.91$; * = $P \leq 0.05$.

Variable	**Est.**	**SE**	***Z***	***P***
Intercept	−2.38	1.21	−1.96	*
Litter	0.07	0.02	3.08	*

DISCUSSION

Both predation of eggs and nestlings, especially by mammalian mesopredators, are considered important drivers of reproductive failure in ground-nesting birds (Roos et al. 2018). This also applies for the Short-eared Owl (Fondell & Ball 2003). Further threats causing loss of eggs and nestlings in this owl are agricultural measures such as mowing and human disturbance (Wiggins 2004, Fernandez-Bellon et al. 2019).

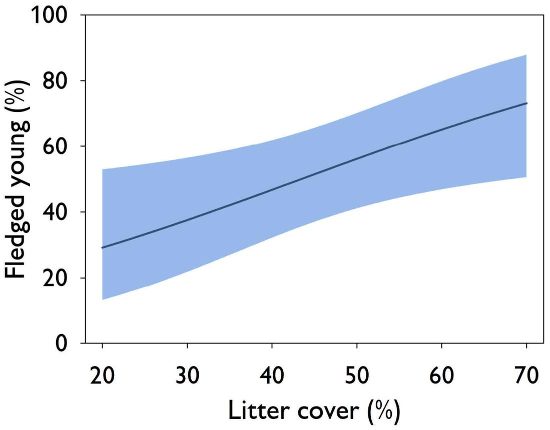

Fig. 2: Results of the GLMMs: relationship between the number of successfully fledged young per nest and significant environmental parameters (litter cover). For detailed results see Tab. 3.

In our study, hatching success and nest survival of the Short-eared Owl were extraordinarily high. With a mean hatching success of 5.6 young per nest ($N = 34$) and an average probability of nest survival of 0.90 ($N = 28$), our values from the East Frisian Island of Spiekeroog exceeded those reported in other studies (Pitelka et al. 1955; Holt 1992). We attribute this to the special environmental conditions on the island, i.e. (i) the absence of mammalian meso-predators such as the Red fox (*Vulpes vulpes*), (ii) nearly no disturbance through agricultural measures and (iii) a lack of human disturbance due to legal regulations of the National Park on large parts of the island. Predatory birds are also known to cause egg and nestling loss (Roos et al. 2018). Herring gull (*Larus argentatus*) and Lesser black-backed gull (*Larus fuscus*) are numerous, and Carrion crow (*Corvus corone*) and Marsh harrier (*Circus aeruginosus*) are regular breeding birds in the study area (Gedeon et al. 2014). All four species have been identified as predators of Short-eared Owl eggs or nestlings in other study areas (Holt 1992; Wiggins 2004). We explain the virtual absence of predation through birds by the highly effective defensive behaviour of adult owls in habitats that are largely free of disturbance by humans. During field work, we regularly observed defensive behaviour, especially against carrion crows and marsh harriers but also gulls. In all observed cases the owls successfully expelled the predatory birds. By contrast, in environments where humans regularly disturb breeding owls, the nests are no longer protected by defending adults and, therefore, predation rates may increase. Consequently, we assume that the National Park concept including zoning and visitor management as well as the use of National Park rangers to control entry bans is

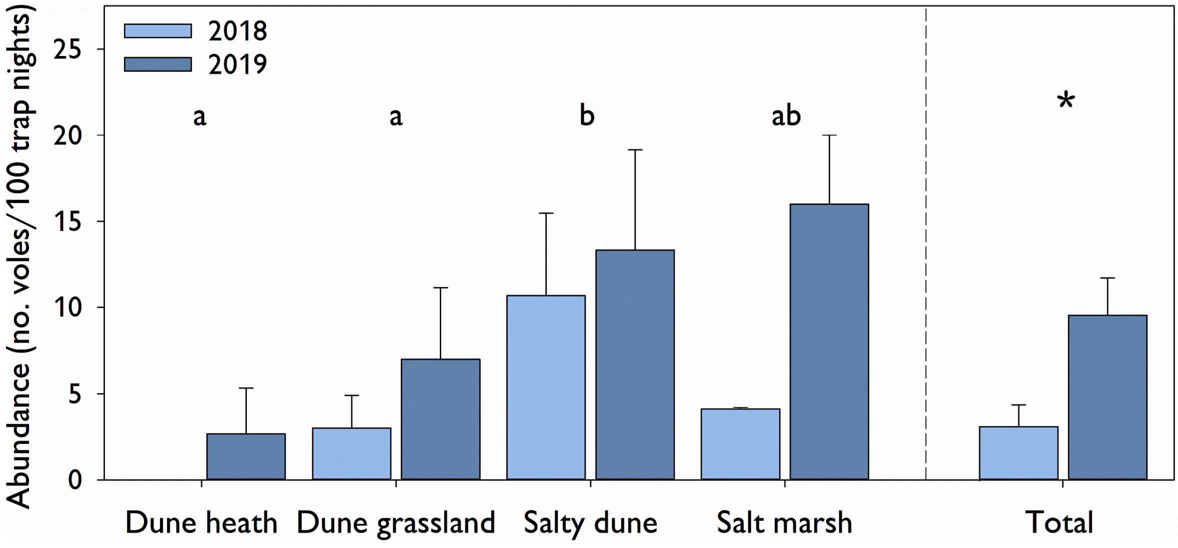

Fig. 3: Abundance (individuals per 100 trap nights) of voles (*Mircrotus arvalis*) in the four main foraging habitat types of the Short-eared Owl in 2018 and 2019. Differences were tested using two-way repeated-measures ANOVA with a Bonferroni *t*-test. Different letters indicate significant differences between vole abundance in the habitat types (habitat types: $F = 8.1$, $P \leq 0.01$; year: $F = 6.3$, $P \leq 0.05$).

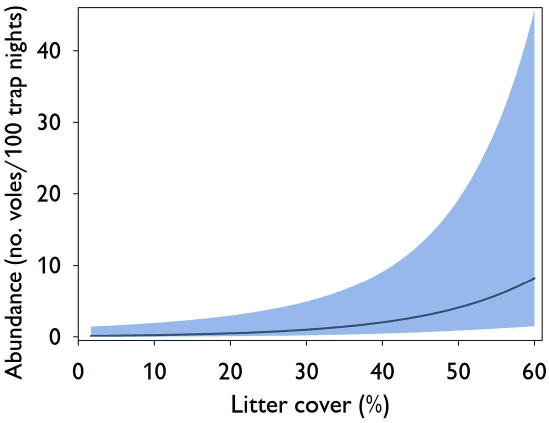

Fig. 4: Results of the GLMM: relationship between the abundance of voles (*Microtus arvalis*) and significant environmental parameters (litter cover). For detailed results see Tab. 4.

another important tool to secure successful reproduction of the Short-eared Owl. In contrast to hatching success and nest survival, the survival of fledglings was lower and, additionally, differed between the two years. Weather conditions were strongly associated with fledgling's survival and were, therefore, likely a key driver. Both maximum wind speed and sunshine duration had a negative effect on the probability that chicks successfully fledged. Van Manen (2001) observed that Long-eared owls hunted most effectively at a wind speed of about 4 m/s. At higher wind velocity, the amount of prey caught decreased. Windy conditions are well known to hamper prey detection (Bradley et al. 1997) and hunting success (Fisher et al. 2004) in birds of prey. This is especially true for owls for which acoustic prey recognition plays an important role (Van Manen 2001; Kouba et al. 2017). Besides food shortage for the fledglings, periods of windy weather are also associated with increased costs for thermoregulation (Tatner 1989, Bakken et al. 2002). Both result in increased mortality of the fledglings.

The negative relationship between sunshine duration and fledgling survival can probably also be explained by a reduced hunting success (Wróbel & Bogdziewicz 2015). Foraging of Short-eared Owls is most efficient when it coincides with peaks in vole activity (Reynolds & Gorman 1998). Several studies have shown that increased cloud cover and darker conditions enhance activity of small mammals (Vickery & Bider 1981; Brown 1988; Stokes et al. 2011). The authors assume this activity pattern to be an adaptation to avoid predation through predators that use visual prey detection.

Additional predictors of fledgling survival were the area of salty dunes within the home range of fledglings and the cover of litter around nests, both fostered survival rates. Salty dunes, the transition zone between high marshes and dune grasslands, usually form small-scale mosaics within high marshes and protrude them by several decimetres (Petersen & Pott 2005). Therefore, they are probably important refuges during storm surges in winter, facilitating a high abundance of voles. Indeed, salty dunes had the highest vole abundance in our study. Moreover, salty dunes surmount the surrounding high marshes and may thereby favour distant views and early predator detection.

Both the survival of fledglings and the number of successfully fledged chicks per nest increased with the cover of litter around the nest. Vole abundance was positively related to litter cover in our study. This aligns with previous findings that especially voles prefer dense herbaceous vegetation with a pronounced litter layer (Huang et al. 2010). Moreover, Short-eared Owls are known to depend on taller vegetation with high amounts of litter for nesting (Holt 1992; Swengel & Swengel 2014; Kämpfer et al. 2013). It is very likely that high amounts of litter facilitate concealment of nests and fledglings, resulting in lower predation rates (Martínez et al. 1998). Consequently, we attribute the positive effect of litter cover on fledgling survival to a (i) higher food supply due to higher prey densities in the proximity of the nests and (ii) lower predation risk due to enhanced concealment of fledglings.

Survival of fledglings was almost two times higher (0.64 vs. 0.35) and abundance of voles nearly three times higher in 2019 than in 2018. However, surprisingly, the year had no effect on survival rates in our study. Short-eared Owls are known to be highly dependent on vole abundance (Korpimäki & Norrdahl 1991; Johnson et al. 2013), resulting in unpredictable invasions in years of vole outbreaks (Kleefstra et al. 2015, Krüger 2019, Škorpíková et al. 2020). By contrast, on the East Frisian Islands, the number of breeding pairs is relatively constant (Kämpfer & Fartmann 2020, Kämpfer et al. 2013). There are two possible explanations for the low variation in population size of Short-eared Owl on the islands: (i) the presence of sufficient alternative prey, such as birds, or (ii) relatively low fluctuations in vole abundance. Indeed, on islands in the Dutch Wadden Sea, where voles are absent, the owl diet consists of up to 90% of waders and songbirds (Schaub & Klaassen 2020). However, in our study area, even in years with lower vole abundance, such as 2018, fledglings were almost exclusively fed with voles (93%, $N = 42$; data of nest cameras) (Klock 2018). Accordingly, the first assumption must be rejected. By contrast, Knipping et al. (2020) did not observe any cyclic variation in vole abundance on the East Frisian Islands over a period of six years, which points to the second explanation. Accordingly, for the Short-eared Owl, the availability of voles seems to be sufficient even in years with relatively low abundance, if weather and habitat conditions are favourable (see above). However, further research is necessary and should include long-term monitoring of vole populations as well as the effects of storm surges on vole abundance.

In conclusion, our study highlighted the prime importance of natural barrier islands largely free of human disturbance and mammalian mesopredators for the survival of a threatened ground-breeding bird of prey. So far, the availability of voles was considered the main predictor of reproductive success in the Short-eared Owl (Korpimäki & Norrdahl 1991; Johnson et al. 2013). Our study, however, now revealed that extreme weather events, here periods of strong wind, were the key driver of reproductive failure. Consequently, climate change might threaten vole-dependent raptors, such as the Short-eared Owl, not only by alterations in temperature and precipitation (Miller et al. 2020), habitat degradation (Miller et al. 2020) or trophic interactions like dampening of vole cycles (Millon et al. 2014) but also through extreme weather events, which are predicted to increase due to climate change (IPCC 2021). To assess the potential impacts of climate change on birds of conservation concern more precisely and to develop suitable adaptation strategies, further research on the effects of extreme weather events is urgently needed.

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STATEMENTS AND DECLARATIONS

Competing Interests

The authors declare that they have no competing interest.

Ethical approval

The National Park was accessed under licence of the National Park Administration of the Wadden Sea National Park of Lower Saxony (01.1-22242/23-1.0(6-14)). Permits for catching, ringing and radio tagging were granted by the Lower Saxony Water Management, Coastal Defence and Nature Conservation Agency (D7.2220/VB_2018) and the Lower Saxony State Office for Consumer Protection and Food Safety (33.19-42502-04-18/2786).

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APPENDIX

Tab. A1: Top ranked models ($\Delta AIC_C < 2$) applied for model-averaging for consecutive models.

Top-ranked models	Df	LogLik	AICc	*Delta*	*Weight*
(a) Breeding biology					
Year	2	−50.30	104.62	0.00	0.27
Null	1	−51.87	105.75	1.14	0.15
Year + no. siblings	3	−50.18	106.40	1.78	0.11
Year + time + I(time^2)	4	−49.19	106.45	1.83	0.11
(b) Habitat type					
Salty dune	2	−48.48	100.98	0.00	0.26
Salty dune + dune grassland	3	−47.98	102.00	1.01	0.16
Salty dune + dune heath	3	−48.16	102.36	1.38	0.13
Salty dune + white dune	3	−48.19	102.41	1.43	0.13
Salty dune + high marsh	3	−48.26	102.55	1.57	0.12
Salty dune + copse	3	−48.35	102.74	1.76	0.11
Salty dune + shrub	3	−48.37	102.78	1.80	0.11
(c) Vegetation structure					
Litter	2	−48.75	101.52	0.00	0.45
Litter + veg. height	3	−48.60	103.24	1.71	0.19
Litter + bare ground	3	−48.62	103.27	1.75	0.19
Litter + shrub layer	3	−48.71	103.46	1.93	0.17
(d) Weather					
Wind speed + sunshine	3	−40.84	87.72	0.00	0.72
Wind speed + sunshine + precipitation	4	−40.76	89.58	1.87	0.28
(e) Synthesis					
Wind speed + sunshine + salty dune	4	-37.86	83.78	0.00	0.83
Wind speed + sunshine + litter	4	−39.43	86.93	1.98	0.17

Typical habitat of the Short-eared owl in natural dune grasslands. High amounts of litter increased the survival probability of fledglings (Spiekeroog, 11/05/2019).

Habitats with high litter coverage not only provide good camouflage of breeding adults and chicks but also enhance food availability, since the abundance of voles as the main prey of Short-eared owls, increases with higher litter cover (Spiekeroog, 04/07/2018).

(5) Tracking wintering areas and post-breeding migration of a declining farmland bird – An indispensable basis for successful conservation

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ABSTRACT

Many farmland birds, such as the Eurasian Curlew (*Numenius arquata*; hereafter Curlew), are in steep decline. So far, decreased reproduction and, hence, an insufficient number of offspring to compensate for adult mortality has been considered the main driver of the recent population collapse. However, despite extensive conservation measures in most breeding areas, there are no signs of a general reversal of the population trend. Accordingly, conservation has to focus on decreasing adult mortality outside the breeding areas as well. For Curlews breeding in NW Germany, ring recoveries suggest that the main wintering areas are the coastlines of western France and southern England. However, such data are often biased in space and time. Here, we used GPS tracking to investigate the wintering areas and post-breeding migration of Curlews of the main German breeding population based on large sample size. Altogether, we tagged 86 adult breeding birds at 23 subareas across a transect of about 250 km (in length) in NW Germany. Curlews started post-breeding migration right after finishing breeding or attempting to breed, which was mainly in mid-June. We identified the coastlines of Great Britain/Ireland, western France and the Netherlands, in particular the Rhine-Meuse-Delta and the Wadden Sea, as the main wintering areas of Curlews breeding in NW Germany. We found a latitudinal structuration of migration, with birds nesting further north using more northerly wintering areas. However, in some cases, wintering areas of birds of the same subpopulation were located more than a thousand kilometres apart from each other. All three main stopover areas identified by our study (German/Dutch Wadden Sea, Dutch Rhine-Meuse-Delta, French Normandy) overlap in large parts with the main wintering areas. Since Curlews spend most of the year outside their breeding areas, and wintering and stopover areas also suffer from rapid environmental change, conservation has to additionally focus on these areas. Nearly one third (29%) of the tracked birds wintered in France or used French stopover areas. Accordingly, they might potentially be affected by a resumption of hunting, which is currently in discussion in France. Our study provides an important basis for the protection of wintering and stopover areas of the main German breeding population but also for other wader species migrating along the East Atlantic Flyway.

KEYWORDS

Bird hunting, Eurasian Curlew (*Numenius arquata*), GPS tracking, movement ecology, stopover area, threatened species

INTRODUCTION

Across the northern hemisphere, farmland birds are in steep decline (BirdLife International 2017, Stanton et al. 2018, Correll et al. 2019, Keller et al. 2020, Reif & Hanzelka 2020). Among them are many wader species, such as the Eurasian Curlew (*Numenius arquata*; hereafter referred to as Curlew) (Roodbergen et al. 2012). A large proportion of the Curlew population in Europe breeds in agricultural grasslands and arable fields (Brooks et al. 1992, Bauer et al.

2005, Silva-Monteiro et al. 2021). The European population has decreased by 25–29% in three generations (BirdLife International 2021). As a result, the species is now considered near threatened in Europe (BirdLife International 2021). The German breeding population is estimated at 3,600–4,800 pairs (Gerlach et al. 2019) and has declined by more than 40% since the early 1970s (Hötker et al. 2007, Gedeon et al. 2014). Accordingly, the species is even considered threatened with extinction in Germany (Ryslavy et al. 2020).

So far, decreased reproduction and, hence, an insufficient number of offspring to compensate for adult mortality has been considered the main driver of the recent Curlew population collapse (Roodbergen et al. 2012). The low reproduction rates are particularly attributed to (i) high nest and chick losses by mammalian predators and (ii) intensive agricultural management practices (Grant et al. 1999, Zielonka et al. 2020). Consequently, in many European countries, extensive and costly conservation measures have been implemented to increase reproductive success in Curlew populations. Such measures include nest marking to avoid destruction by farming activities, electric fencing of nests and surrounding habitats to prevent mammalian predation, rewetting of grasslands and further measures to promote habitat quality in the breeding habitats (Kipp & Kipp 2003, Düttmann et al. 2006, Junker et al. 2006, Boschert 2018). In a few protected areas, these measures have been successful in fostering reproductive output and, thus, compensating for adult mortality (Gedeon et al. 2014; Gerlach et al. 2019). However, in most breeding areas, there are no signs of a general reversal of the population trend.

Despite the ongoing decline, the Curlew is still listed in the EU Birds Directive as a game bird in Denmark, France, Ireland and the United Kingdom (Brown et al. 2015). However, hunting bans were established in all these countries between 1982 and 2019 and remain in place. Nevertheless, four cases of illegal killing of GPS-tagged Curlews have been documented in France in 2022 (unpubl. data). Moreover, France is currently considering a reintroduction of Curlew hunting at the wintering areas based on a national adaptive harvest management plan (AEWA Eurasian Curlew International Working Group 2019). Any future hunting of migrating and wintering Curlews, however, should not jeopardize the achievements of the extensive conservation measures in the breeding areas. Consequently, there is an urgent need to know (i) which proportion of the different Curlew breeding populations winters in or migrates through France and (ii) where exactly the wintering and stopover areas are located in France.

In wader species with a large breeding area, timing, stopovers and wintering areas of migrating birds can considerably differ between breeding populations or even within one breeding population (Hooijmeijer et al. 2013, Loonstra et al. 2019, Verhoeven et al. 2021). This is also true for the Curlew (Pederson et al. 2022). Breeding birds from Ireland appear to be largely resident, while most Curlews breeding in Britain seem to be short-distance migrants that winter in SW Britain, Ireland and France (Bainbridge & Minton 1978). By contrast, Curlews nesting in subarctic regions are long-distance migrants with important wintering areas in the Wadden Sea and along the Atlantic coasts of western Europe (Bocher et al. 2017, Schwemmer et al. 2021, Pederson et al. 2022).

The German Curlew breeding population consists of two subpopulations: a small one in southern Germany and a large one in northern Germany (Gedeon et al. 2014). For Curlews breeding in NW Germany, ring recoveries suggest that the main wintering areas are the coastlines of southern England and western France (Bairlein et al. 2014). However, ring recoveries are subject to heterogeneities in ringing effort and of recovery probability in space and time (Korner-Nievergelt et al. 2010). Consequently, it is unclear whether these ring recoveries fully represent the current migration routes of the NW-German breeding population, i.e. the main wintering and stopover areas. Additionally, it has been shown that the ongoing climate change (IPCC 2021) has already had strong effects on post-breeding migration of many migratory birds (Potvin et al. 2016, Illán et al. 2022). Accordingly, recent shifts in wintering and stopover areas also seem possible for Curlews.

In this study, we investigated the wintering areas and post-breeding migration of Curlews of the main German breeding population based on a large sample size of GPS-tagged individuals. To obtain a representative overview, we tagged a total of 86 adult breeding birds over two consecutive springs at 23 subareas across a transect of about 250 km (in length) in NW Germany. So far, conservation efforts for the rapidly declining Curlew have mainly focused on measures within the breeding areas. However, wintering areas and migration routes of migratory birds are also affected by rapid environmental change, e.g. climate change or plans for anticipating an open hunting season for Curlews in France (see above). Our study provides an important basis not only for the protection of wintering and stopover areas of the main German breeding population but also for other wader species migrating along the East Atlantic Flyway.

MATERIAL AND METHODS

Study area

The study was carried out in the German Federal States of Lower Saxony, Bremen, and North Rhine-Westphalia (NW Germany). To obtain a representative overview of the migratory behaviour of Curlews breeding in NW Germany, we tagged 85 adult breeding birds in spring 2020 and 2021 at 23 subareas (mean ± SE: 3.8 ± 0.7 birds per subarea) across a transect of about 250 km (in length) ranging from the Wadden Sea islands in the north to the Westphalian Basin in the south (Fig. 1). Breeding habitats of Curlews on Wadden Sea islands were dominated by mosaics of high marshes and natural dune grasslands (Kämpfer & Fartmann 2022). By contrast, breeding habitats at the mainland were characterized by different types of agricultural grasslands, which were primarily used for haymaking and silage production (Blickensdörfer et al. 2022). In these mainland breeding habitats, usually conservation measures for nesting waders were conducted. These measures ranged from simple protection of nest sites through marking and fencing of nests to rewetting of grasslands in combination with an adapted grassland management (EEA 2019).

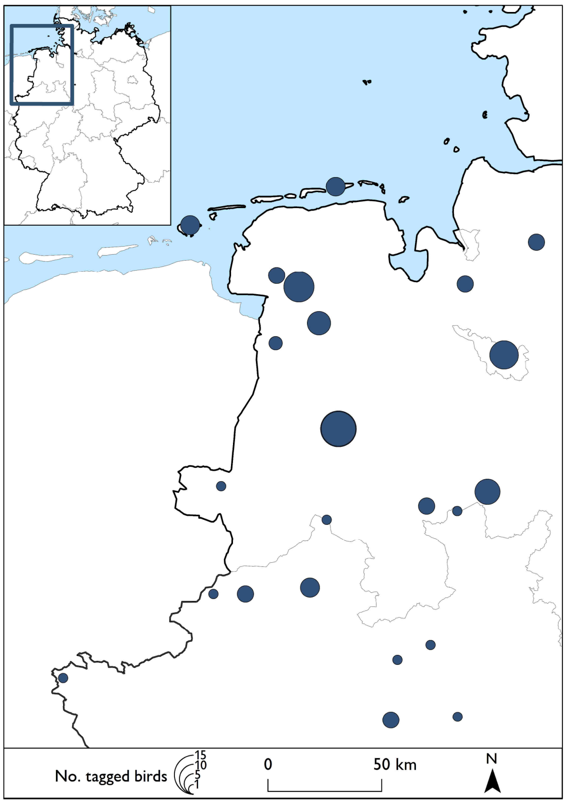

Fig. 1: Overview of the 23 subareas in NW Germany where Eurasian Curlews were tagged. *N* = 86.

Tagging

In both 2020 and 2021, Curlews were caught with a clap net on the nest between late April and the beginning of June (Fig. 1). Trapping was performed when the birds had been incubating for at least two weeks to minimize the risk of clutch abandonment. We (i) measured body weight and bill length, (ii) marked the birds with metal rings ("Vogelwarte Helgoland") and in 2021 additionally with colour rings and (iii) equipped them with solar-powered GPS backpack tags with GSM data transmission (type Ornitrack 10 by Ornitela, 10 g). The tags were attached using a breast harness (cf. Thaxter et al. 2014, Schwemmer et al. 2021). Tag weight was 1.7% of the bird's body mass at maximum, which was clearly below the recommended load limit of 5% (Cochran 1980, Kenward 2001). After tagging, Curlews were immediately released into their nesting habitats.

In the present study, we additionally incorporated tracks of one bird that was caught with mist nets at its wintering area in 2019 in the National Nature Reserve of Moëze-Oléron near La Rochelle (France). This bird nested in 2020 on the Wadden Sea island of Spiekeroog, which is part of our study area. It was equipped with the same tag as used in our study (cf. Jiguet et al. 2021a). However, the tag was fitted with a silicone leg-loop harness and the bird additionally received colour rings.

All tags were programmed to record geographic positions every 10 minutes. Data were stored in the Movebank database (www.movebank.org). We used bill length to determine the sex of each individual according to Summers et al. (2013). From 68 of all 86 tagged birds, we gathered additional information on nesting success based on observations in the field. Nests were considered successful when breeding pairs raised at least one fledgling (Steenhof & Newton 2007).

Post-breeding migration and wintering

We defined the start of post-breeding migration (= migration departure) as the timestamp of the last location that was less than 1 km away from the recorded nest before the bird had moved at least 50 km away from the nest. We assigned all locations of post-breeding migration to four different regions: (i) the Netherlands (NL), (ii) Great Britain and Ireland (GB/IE), (iii) France including the Channel Islands (FR) and (iv) the Iberian Peninsula (Spain and Portugal, ES/PT) (overlay with the map 'countries' in R-package 'rworldmap', South 2011). Locations of individuals on the water were attributed to the nearest of the four regions.

To determine wintering areas, we first extracted all areas after migration departure where a bird stayed within a radius of 10 km for at least 3 days. The last of those before 31 August was defined as the wintering area. For the arrival timestamp, we used the first location in the wintering area with GPS speed below 1m/s. Based on the location and date of migration departure and arrival in the wintering area, we calculated the migration distance (Vincenty's distance) and duration. Additionally, we extracted stopover areas. A stopover area was defined as an area along the migration route where Curlews stayed for at least 6 hours in an area with a radius of less than 10 km. The first/last location in this area with a speed below 1 m/s, indicating that the bird was on the ground, was considered as the entry and exit timestamp, respectively, of the stopover.

Statistical analysis

We performed all statistical analyses using R 3.6.1 (R Core Team 2021). The effects of (i) breeding success and sex on migration departure and of (ii) sex on the number of stopovers and migration duration were analysed by using generalised linear mixed-effects models (GLMM; R package 'lme4', Bates et al. 2015). The effects of (i) migration distance on the number of stopovers, (ii) migration distance and the number of stopovers on migration duration and (iii) geographical latitude of the nesting site on latitude of the wintering area were assessed by using linear mixed-effects models (LMM) or GLMMs depending on the distribution of the data. For GLMMs with a discrete response variable, we applied Poisson linkage. Continuous response variables were modelled using gamma error structure. Differences in migration distance, migration duration and the number of stopovers between the four groups of wintering areas were assessed by GLMMs using Tukey's test as a post-hoc test (R package 'multcomp', Hothorn et al. 2008).

In all models, subarea (Fig. 1) was used as a random effect to account for potential spatial autocorrelation. Variance explained by fixed effects (marginal *R²*) and variance explained by both fixed and random effects (conditional *R²*) were calculated according to Nakagawa et al. (2017) using the function 'r.squaredGLMM'.

Tab. 1: Results of LMMs and GLMMs: Relationship between migration departure (a), migration duration (b, c, d) and number of stopovers (e, f), respectively, and predictor variables. R^2_m= variance explained by fixed effects, R^2_c = variance explained by both fixed and random effects (Nakagawa et al. 2017). n.s. = not significant, ** $P \leq 0.01$, *** $P \leq 0.001$.

Model (response ˜ explanatory)	**Parameter**	**Estimate ± SE**	**z/t**	**P**
a) Migration departure (day) ˜ sex*breeding success (GLMM¹)				
R^2_m= 0.30, R^2_c= 0.43	Intercept	3.32 ± 0.04	73.94	
	Breeding success (successful)	0.17 ± 0.05	3.50	***
	Sex (male)	0.16 ± 0.05	3.40	**
b) Migration duration (days) ˜ migration distance (GLMM²)				
R^2_m= 0.01, R^2_c= 0.06	Intercept	1.41 ± 0.25	5.61	
	Distance (km/100)	0.04 ± 0.02	1.70	n.s.
c) Migration duration (days) ˜ no. of stopovers (GLMM²)				
R^2_m= 0.36, R^2_c= 0.41	Intercept	0.52 ± 0.15	3.39	
	No. of stopovers	0.63 ± 0.07	9.61	***
d) Migration duration (days) ˜ sex (GLMM²)				
R^2_m= 0.01, R^2_c= 0.03	Intercept	1.95 ± 0.19	10.15	
	Sex (male)	−0.29 ± 0.23	−1.29	n.s.
e) No. of stopovers ˜ migration distance (LMM)				
R^2_m= 0.17, R^2_c= 0.21	Intercept	0.46 ± 0.30	1.54	
	Distance (km/100)	0.13 ± 0.03	4.11	***
f) No. of stopovers ˜ sex (GLMM¹)				
R^2_m= 0.02, R^2_c= 0.05	Intercept	0.54 ± 0.13	4.03	
	Sex (male)	−0.27 ± 0.18	−1.48	n.s.

1 Poisson error structure

2 Gamma error structure

RESULTS

Tagging statistics

From 86 tagged individuals, 39 were females and 47 males. Of the 68 tagged birds for which breeding success was determined, 23 successfully raised at least one chick (breeding success: 38%).

Wintering areas

The tracked Curlews used four different wintering areas along the coastline of the North Sea and Atlantic Ocean: (i) Great Britain/Ireland (44%, 38 out of 86 birds; not only southern England but also Ireland, northern England and Wales), (ii) France/Channel Islands (29%, 25 birds; mainly Brittany), (iii) the Netherlands (16%, 14 birds; particularly the Rhine-Meuse-Delta and the Wadden Sea) and (iv) the Iberian Peninsula (9%, 8 birds) (Fig. 2). One female, which bred on the Wadden Sea island of Spiekeroog, did not migrate and stayed there after both breeding seasons (2020/21 and 2021/22).

Geographical latitude of the nesting site was related to the latitude of the wintering area; i.e. birds nesting further north used more northerly wintering areas (Fig. 3). However, birds that had nested only a few kilometres apart from each other showed marked differences in their wintering areas. While some birds migrated to the nearby Netherlands, others wintered in Ireland or the Iberian Peninsula (Fig. 2).

Post-breeding migration

Migration departure at the breeding area varied from June 1 to July 11 in 2020 and from May 17 to July 22 in 2021. However, in both years, the departure peak was mid-June (Fig. 4). The GLMMs revealed that sex and breeding success affected the timing of departure (Tab. 1a). Females departed on average seven days earlier than males, and birds that did not breed successfully left the breeding area on average eight days earlier than birds of successful pairs.

For shorter tracks, birds used the most direct route between the breeding and wintering areas (Fig. 2). Birds migrating to the Netherlands either crossed overland or went along the coastline to the Rhine-Meuse-Delta. Those wintering in Great Britain/Ireland crossed the North Sea and then flew over the country if heading for Wales or Ireland. Birds wintering in France/Channel Islands moved along the coastline after leaving the Netherlands. Those that wintered at the French Biscay Bay coast already turned south in Normandy or eastern Brittany and flew overland, thus using the 'beeline' route. Birds that continued their migration to the Iberian Peninsula mainly crossed the Golf of Biscay and then migrated along the Iberian Atlantic coast.

The average (± SE) migration distance was 789 ± 45 km (Fig. 5a). However, migration distance varied strongly and ranged from 99–2,119 km. Almost 50% of the birds reached their wintering area in less than three days, and the average (± SE) migration duration was 6.3 ± 0.8 days (Fig. 5b). Overall, however, duration also varied widely with a range of 0.3–30.4 days. Two birds, for instance, although wintering in the nearby Netherlands, stayed at a stopover not far away from the breeding ground for 28 and 19 days, respectively. As a result, the duration of post-breeding migration was not affected by the distance between breeding and wintering area or by the birds' sex (Fig. 5b, Tab. 1b and d). However, it increased with the number of stopovers (Tab. 1c). Birds arrived at the wintering areas mainly in mid-June (mean: June 23) with arrivals varying between May 31 and July 24.

Approximately three fourths of the tagged birds (72%, 62 out of 86 birds) used up to five stopover areas during their migration and stayed there between 0.4–27.9 days (mean ± SE: 2.7 ± 0.4 days). The mean (± SE) number

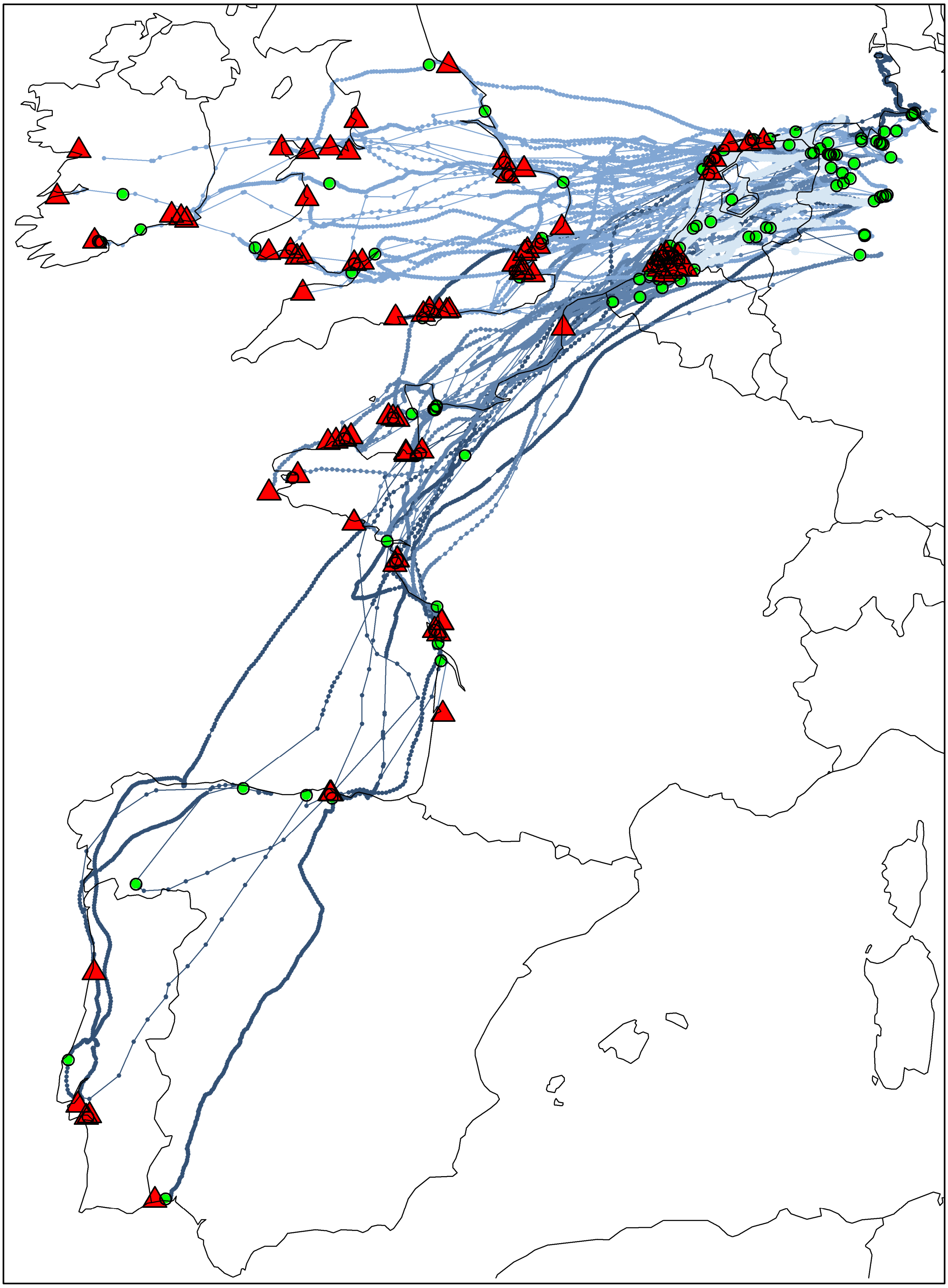

Fig. 2: Tracks of post-breeding migration of tagged Eurasian Curlews breeding in NW Germany. *N* = 85. Wintering area: red triangle, stopover: green dot.

of stopovers was 1.5 ± 0.2 (Fig. 5c). The three most important stopover areas were (i) the Wadden Sea (GER, NL) for birds migrating to Great Britain/Ireland, (ii) the Rhine-Meuse-Delta (NL) for birds wintering in the Netherlands, France/Channel Islands and Iberian Peninsula and (iii) the coast of Normandy (FR) for birds heading to western France and the Iberian Peninsula. Not surprisingly, the number of stopovers differed with the distance of the wintering area to the breeding area (Tab. 1e): It was lowest for birds wintering in The Netherlands and highest for those spending the winter at the coasts of the Iberian Peninsula (Fig. 5c). By contrast, sex-specific differences in the number of stopovers failed to appear (Tab. 1f).

DISCUSSION

Wintering areas

Along the coasts of the North Sea and Atlantic Ocean, we identified three main wintering areas of Curlews breeding in NW Germany: (i) England, Wales and Ireland, (ii) France/Channel Islands and (iii) the Netherlands, here especially the Rhine-Meuse-Delta and the Wadden Sea. Additionally, some birds wintered along the Atlantic coast of the Iberian Peninsula and one single individual did not migrate at all and stayed next to its breeding site at the German Wadden Sea. Overall, our findings expand the knowledge about wintering areas of Curlews of the NW-German breeding populations based on ringing recoveries, which identified the coastlines of southern England and western France as the most important wintering areas (Bairlein et al. 2014).

We consider four possible explanations for the different results of our study with GPS-tagged birds compared to the findings of previous ringing analyses. First, the identification of new wintering areas can partly be due to a higher sample size, i.e. 86 birds in our study versus 52 observations in Bairlein et al. (2014). Second, ring recoveries are subject to heterogeneities in ringing effort and of recovery probability in space and time (Korner-Nievergelt et al. 2010). Accordingly, the results are often biased. Third, in recent decades, several short-distance migrants (e.g. the Northern Lapwing [*Vanellus vanellus*]) have shifted their wintering areas northwards due to global warming (Lehikoinen et al. 2013, Potvin et al. 2016, Illán et al. 2021). Hence, the increased number of birds wintering more northerly in the Wadden Sea may also indicate northward shifts of the wintering area due to climate change. Fourth,

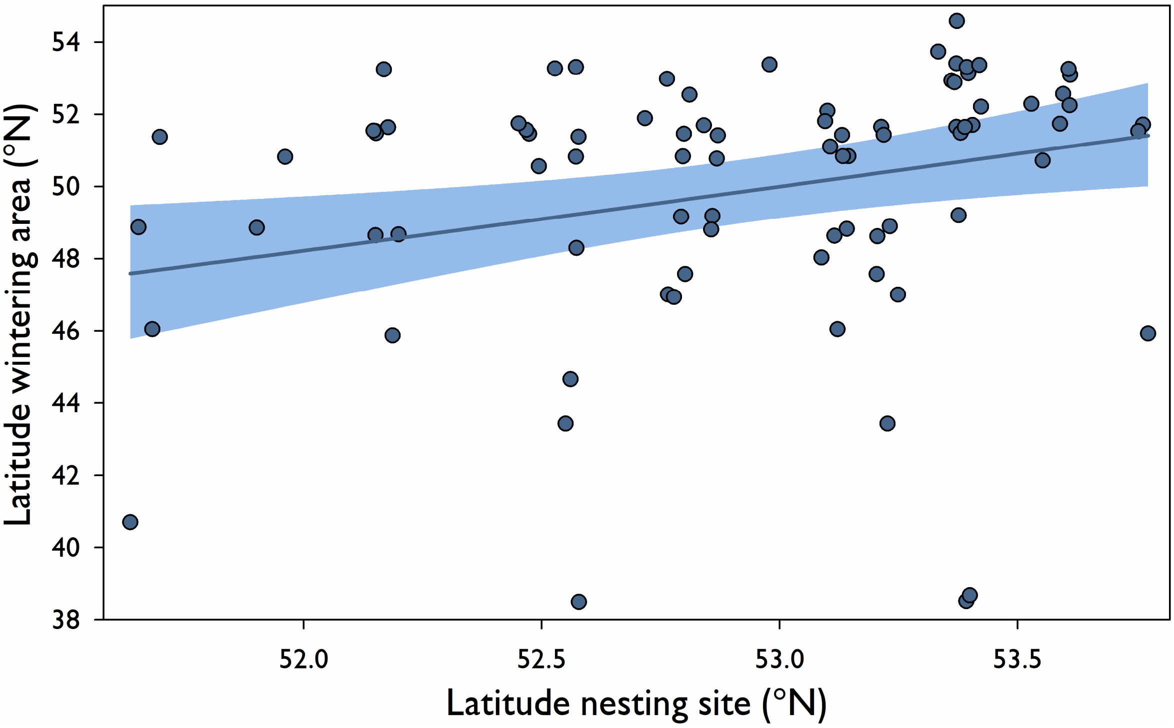

Fig. 3: Relationship between latitude of nesting site and wintering area of tagged Eurasian Curlews breeding in NW Germany. N = 85. GLMM (Poisson error structure): latitude breeding area – estimate ± SE: 0.36 ± 0.13, z/t: 0.43, ** P ≤0.01.

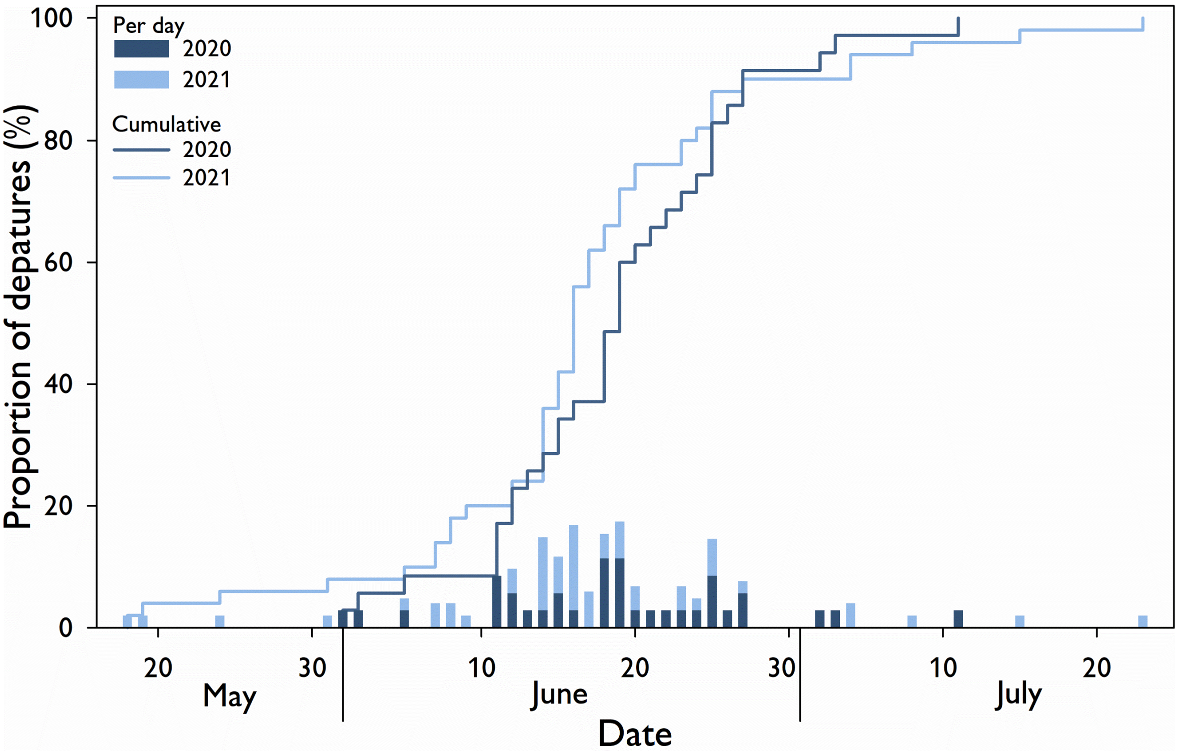

Fig. 4: Departure of post-breeding migration of tagged Eurasian Curlews breeding in NW Germany. $N_{2020} = 35$, $N_{2021} = 50$.

adult survival is likely to differ between Curlew wintering areas. In 2022, at least four tagged Curlews were illegally killed in northern France (Normandy, Haut de France) (unpubl. data). As a result, different adult survival in the wintering areas might lead to a shift towards wintering areas with higher survival rates. However, further research on this topic is urgently needed.

In general, geographical latitude of the nesting site was related to the latitude of the wintering area; i.e. birds nesting further north used more northerly wintering areas. In line with this, a tracking study with Curlews of the breeding population of southern Germany identified wintering areas at the Atlantic coasts of southern France, the Iberian Peninsula and Morocco (LBV 2022, Pederson et al. 2022). As a result, the wintering areas of NW- and S-German breeding populations only partly overlap.

Despite the general relationship between the geographical latitude of the nesting site and wintering area, some birds of the same local breeding population differed markedly in their wintering area. Similar observations have been obtained for Black-tailed Godwits (*Limosa limosa*) in the Netherlands (Verhoeven et al. 2021). Since individuals of the same subpopulation are expected to share some genetic background, especially in species with high nest-site fidelity such as the Curlew (Valkama et al. 1998), our findings raise the question of the underlying processes of these individual differences. Tracking over multiple years or even lifetime tracking in combination with ontogenetic experimental approaches can help to untangle the mechanisms behind this variation in wintering areas (Verhoeven et al. 2021).

Post-breeding migration

Curlews breeding in NW Germany started post-breeding migration right after finishing breeding or attempting to breed, which was mainly in mid-June. The timing of migration departure in our study corresponded well with the arrival dates of colour-marked individuals in a wintering area in Great Britain (Sanders & Rees 2018) and GPS-tracked Curlews breeding across other parts of Europe (Schwemmer et al. 2021, Pederson et

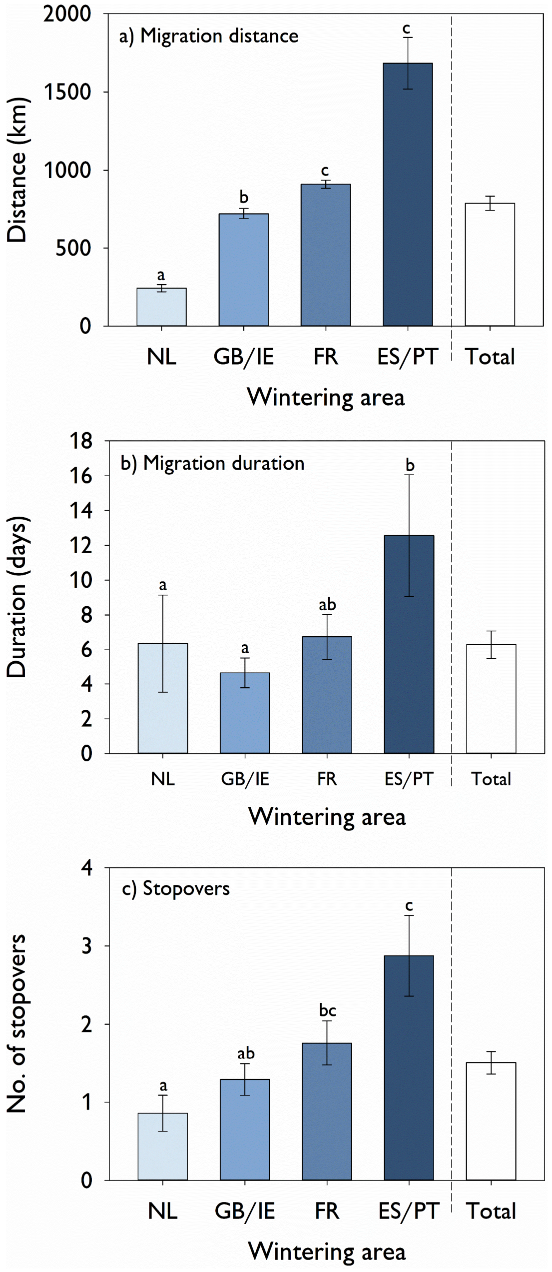

Fig. 5: Migration distance (a), migration duration (b) and number of stopovers (c) of tagged Eurasian Curlews breeding in NW Germany depending on the wintering area. NL: the Netherlands, GB/IE: Great Britain and Ireland, FR: France and Channel Islands, ES/PT: Spain and Portugal (Iberian Peninsula). Differences between groups were tested using GLMMs and Dunn's test as a post-hoc test. Different letters indicate significant differences between groups (* $P \leq 0.05$).

al. 2022). As in other wader species (Carneiro et al. 2019), female Curlews have been observed to leave their chicks earlier than males (Currie et al. 2008). In accordance with this, we detected the same sex-specific difference in the Curlews of the NW-German breeding population.

The migration routes of many tagged Curlews followed the coastlines. Possible explanations for this behaviour are (i) the high availability of foraging habitats along the coasts (Masero et al. 2000) and (ii) geographical cues that facilitate orientation during migration (Alerstam 1996, Meyer et al. 2000). However, we also observed overland flights, which significantly reduced the migration distance and enabled an early arrival at the wintering areas.

In our study, the average migration duration was about 6 days, and almost 50% of the tagged birds even reached their wintering area in less than three days. Early arrival at the wintering areas has the advantage that the birds can occupy and defend the most suitable foraging habitats against newcomers (Pederson et al. 2022). However, some birds migrated over several weeks, while others made the same distance in just a few days. Strong individual differences in migration behaviour have already been obtained in other wader species (Hooijmeijer et al. 2013, Loonstra et al. 2019, Verhoeven et al. 2021, Pederson et al. 2022). Besides individual fitness (Anderson et al. 2019, Jiguet et al. 2021b) and initial fuel reserves before departure, habitat quality—including prey availability at stopovers—is also an important factor that determine the number of stopovers to reach the wintering areas (Anderson et al. 2021). Stopovers are also known to be important (i) for recovery after strenuous migration, (ii) to avoid adverse environmental conditions for flight and (iii) for further reasons such as minimising predation, spatio-temporal adjustments or social interaction (Linscott & Senner 2021, Schmaljohann et al. 2022). However, for a better understanding of the use of certain stopovers by Curlews in general and the marked individual differences in particular, further studies are needed.

The mean (± SE) migration distance between nesting sites and wintering areas in our study

(789 ± 419 km) was three times shorter than for Curlews that breed in Russia and winter in the German Wadden Sea (2,339 ± 612 km) (Schwemmer et al. 2021) and even four times shorter compared to birds nesting in other parts of Europe (Estonia, Poland, S Germany) (3,362 ± 1,351 km) (Pederson et al. 2022). This confirms the high variability of migratory behaviour of different Curlew breeding populations, ranging from residents in Ireland (Wernham et al. 2002) to long-distance migrants in Russia (Pederson et al. 2022).

IMPLICATIONS FOR CONSERVATION

Despite extensive conservation measures in German breeding areas, most Curlew populations are still in decline (Gedeon et al. 2014, Gerlach et al. 2019). Since Curlews spend most of the year outside their breeding area (Bauer et al. 2005, Bairlein et al. 2014) and wintering and stopover areas also suffer from rapid environmental change (see Introduction), conservation efforts should additionally focus on these areas (Schuster et al. 2019). Based on our study, the coastlines of Great Britain/Ireland, western France and the Netherlands are the main wintering areas of Curlews breeding in NW Germany. We identified the Wadden Sea, the Rhine-Meuse-Delta and the coasts of the French Normandy as the most important stopover areas for this breeding population. Since Curlew breeding populations are declining in many European countries, the consideration of a resumption of Curlew hunting in France during the migration period and in winter (see AEWA Eurasian Curlew International Working Group 2019) deserves further attention. The increasing number of wintering Curlew in Great Britain during the 1980s and early 1990s, for instance, can at least partly be explained by the cessation of hunting in the early 1980s: it reduced adult mortality and led to a decrease of disturbance of wintering Curlews (Taylor & Dodd 2013, Woodward et al. 2022). The latter is known to be an important factor for the carrying capacity of waterfowl wintering areas (Madsen & Fox 1995).

In general, an increase in adult mortality must be compensated by higher reproductive success to maintain a stable population size. A resumption of Curlew hunting in France will currently affect about 29% of the birds of the NW-German breeding population, whereby the effect may be different between subpopulations. Moreover, there are reports of Curlew poaching in France despite the current hunting moratorium (Jiguet et al. 2021c). In northern France (Normandy, Haut de France) in particular, where hunting on the coast is traditional and open in August, one month earlier than on the mainland, there are indications of high hunting pressure. Moreover, the species appears sensitive to wind farm collision (Jiguet et al. 2021a, Schwemmer et al. 2022), which could further jeopardize conservation efforts on breeding grounds. In Lower Saxony, productivity in different subpopulations currently ranges between 0.18–0.84 fledged chicks per breeding pair (C. Peerenboom, NLWKN unpubl. data). However, in most subpopulations, productivity is below 0.45 chicks per pair. According to a long-term study on the productivity of a Curlew population in North Rhine-Westphalia, it is suggested that a minimum of 0.41 fledged chicks per breeding pair is required for a stable population. In summary, we conclude that most Curlew subpopulations breeding in NW Germany are currently incapable of compensating for higher adult mortality (e.g. by hunting).

Further research is necessary to secure long-term survival of Curlew populations. Regarding influences of Curlew hunting, comparative survival analyses should be carried out for adult and juvenile birds as it is likely that unexperienced juvenile Curlews might suffer a higher mortality risk when they arrive in the wintering areas in August, when the hunting season is already open in France. Therefore, tracking of juvenile birds is important, which we have started in 2022. Detailed studies on the habitat quality at stopover and wintering areas for Curlews are urgently needed as well. The same is true for the underlying processes behind the individual differences in migration behaviour of birds of the same subpopulation. Global warming is rapidly accelerating and changing environmental conditions (IPCC 2021). Accordingly, it is likely that climate change will affect Curlew migration routes in general and the importance of the current stopover and wintering areas in particular. Therefore, research on this topic is also required. Overall, such research will be an important basis to predict the ability of Curlews to track current and future environmental change (Senner et al. 2020; Verhoeven et al. 2021).

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A large proportion of the Curlews breeding in Northwest Germany use the few remaining areas of low-intensity grasslands for nesting. Most of these are managed applying agri-environmental schemes (Diepholzer Moorniederung, 17/06/2021).

Some Curlews in Northwest Germany use freshly sown maize fields for breeding, which are mostly unvegetated and very open during territory establishment (Landkreis Diepholz, 20/05/2021).

Chapter IV

Synthesis and perspectives

Short-eared owl in the blue sky of Spiekeroog (15/08/2018).

SYNTHESIS AND PERSPECTIVE

Habitat characteristics of natural grassland refuges

The studies on habitat and nest-site requirements of threatened grassland birds highlight the general importance of open dune grasslands as habitats for threatened species. However, the detailed analyses have shown that the investigated species preferred different vegetation structures. The Wheatear as an insectivorous songbird preferred highly disturbed habitats characterised by huge amounts of open soil and very short and sparse vegetation. In the study area, such habitats are almost exclusively provided by rabbits due to grazing and digging activities. Furthermore, Wheatears used rabbit holes for nesting, resulting in a strong dependence on rabbit activity. In this way, the rabbit acts as an ecosystem engineer providing holes for nesting and early successional stages with sparse and short vegetation for foraging of ground-dwelling species (Paper 1).

In a comparable way, Curlews preferred areas providing some bare ground for territory establishment but intermediate vegetation structure for nesting. This can be explained by a trade-off between concealment and shelter for breeding, and early predator detection, and food availability. Consequently, Curlews preferred heterogenous vegetation structures. These provide areas of open soil and short vegetation for feeding and chick rearing but also areas of intermediate vegetation height for breeding and hiding of chicks (Paper 2).

In contrast, Short-eared owls preferred high and dense vegetation for nest building surrounded by intermediate vegetation for foraging. Moreover, litter turned out to be a crucial habitat requisite (Paper 3). Huge amounts of litter at nest sites might be preferred for concealment and shelter from extreme weather. In line with this, vegetation at nests was highest in the dominant wind direction. Our study showed that particularly strong winds severely impacted the survival of the Short-eared owls' fledglings probably by reducing hunting success and vole availability while increasing the juvenile food requirements for thermoregulation (paper 4). This indicates that an increasing frequency of extreme weather events, as expected with ongoing climate change, could negatively impact the breeding success of vole-dependent raptors, such as the Short-eared owl. Against this backdrop, the preference for high and dense vegetation rich in litter can be interpreted as an adaption to reduce energetic costs from weather events. At the same time, voles also preferred a pronounced litter layer, resulting in higher food availability in habitats with high litter coverage. Accordingly, litter seems to be a key resource for breeding Short-eared owls and probably other raptors feeding on voles. Despite their preference for high and dense vegetation for breeding, the owls preferred intermediate vegetation height outside the nesting area, which might be explained by reduced prey accessibility and fledglings' mobility in too dense and high vegetation.

All investigated species have in common that they avoided late successional stages like shrubs and copses. In this way, despite differences in nest-site preferences, all species profited from nutrient-poor conditions and relatively high dynamic due to the influence of tides and wind. Additionally, some species were favoured by European rabbits acting as ecosystem engineers, which provide early successional stages and slow down succession to unsuitable woody habitats. The avoidance of areas frequented by humans revealed for Curlew and Short-eared owl highlights the importance of large undisturbed areas for ground breeding species. Therefore, it can be assumed that both species profit from legal regulations and visitor management in the study area. At the same time, the very high hatching success revealed in paper 4 is an impressive indication of the importance of breeding habitats with low predation pressure and low human disturbance for ground-breeding species.

In conclusion, we found threatened breeding birds to profit from nutrient-poor conditions and relatively high natural dynamics. Both result in sparse and open vegetation structures and extensive areas of early successional stages which are crucial for feeding of many threatened bird species.

Nonetheless, we also found evidence for the high importance of intermediate stages of succession such as rough grassland providing high coverage of litter for concealment of breeding adults and fledglings and for enhanced food availability for raptures feeding on voles (paper 4).

The extensive availability of these conditions in the study area seems to be the outstanding characteristic making the East Frisian Islands an important refuge for threatened breeding birds. The high habitat quality of the investigated islands is also underlined by the fact that one of the tagged Curlews wintered in its breeding area on the island of Spiekeroog, which was not described so far (Paper 5). This observation raises the interesting question of whether wintering in the breeding areas of the Wadden Sea has only occurred in recent years due to climate change or whether it has been overlooked for methodological reasons. Apart from that, the study basically confirms the great importance of France as a stopover and wintering area for Curlews breeding in Northwest Germany. Almost one third of the population uses stopovers or wintering areas in France and would therefore be potentially affected by a resumption of hunting in France. On the other hand, the study revealed a higher proportion of the tagged birds to winter in the Netherlands and Ireland than expected based on ring recoveries. This might be an indication that climate change already affects the ecology of species in the study area. Consequently, there is an urgent need for further research to predict the ability of species to track current and future environmental changes (Senner et al. 2020; Verhoeven et al. 2021). Results of such research should be considered in future conservation measures.

In contrast to the East Frisian Islands, the above-mentioned conditions are rare in the intensively used agricultural landscape on the mainland, which makes the discrepancy of breeding densities of threatened species on the islands and the mainland comprehensible. Therefore, the consequent protection of the refuge habitats on the islands but also along the migration routes and wintering areas is crucial for the preservation of the threatened species and should be of high priority for their conservation (Watson et al. 2018). At the same time, the restoration of degraded habitats based on the example of the habitats preferred in the refuges is urgently needed to enhance habitat availability and suitability on the mainland.

Implications for conservation

The preservation of intact, natural habitats should be of high priority for biodiversity conservation because they can harbour important source populations (Watson et al. 2018). Because such habitats are very rare after centuries of human-caused land-use change in the course of the industrial revolution, increasing attention is paid to the active (re)creation of functioning ecosystems. Nonetheless, such measures need templates of intact and suitable habitats, which can be found in last refuges like National Parks to derive promising conservation strategies (Watson et al. 2018).

Based on the findings of this thesis, large-scale measures providing heterogenous grasslands are considered the key to the conservation of threatened ground-breeding species like Wheatear, Curlew, and Short-eared owl. Various management measures can be considered to (re)create open grassland areas with suitable habitat characteristics that are comparable to the natural habitats examined here. Generally, measures should aim to create grassland habitats providing extensive areas of open and short vegetation but also intermediate stages of succession, namely rough grasslands with high and dense vegetation and especially high coverage of litter. Because the small-scale presence of both, open ground and dense vegetation are required to meet habitat requirements for breeding and feeding, habitat heterogeneity in the form of small-scale combinations of different successional stages seems to be crucial for the (re)creation of high-quality habitats. Because all investigated species avoided copses and shrubs, the dominance of late successional stages should be prevented.

Corresponding habitats might be created through low-intensity land use applying agri-environmental schemes (Früh-Müller et al. 2019, Tyllianakis & Martin-Ortega 2021) that should encompass rotating fallows (high and dense vegetation rich in litter and voles) (Amar & Radpath 2005) and areas of higher land-use intensity featuring disturbance like mowing or grazing (open-soil, short and sparse vegetation) (Schwarz & Fartmann 2022). Agricultural measures like mowing or grazing should include the protection of nest sites through adapted management periods to avoid nest destruction and disturbance (Grüebler et al. 2012, Franks et al. 2017). Besides agricultural measures, natural dynamics or the presence of ecosystem engineers can help to preserve early successional stages and areas of short and sparse vegetation (paper 1, Streitberger & Fartmann 2013, Streitberger et al. 2018). Where possible and present, both should be included in conservation concepts to use synergies and minimise financial costs. For the implementation of such measures, nutrient-poor habitats with slow succession and areas with naturally low density of (meso)predators like bogs, heath, or wetlands, should be preferred (Border & Calladine 2021).

The presented studies indicate that climate change already affects the investigated species through the increasing frequency of extreme weather events with negative impacts on fledglings' survival (Paper 4). Moreover, paper 5 shows that a resumption of Curlew hunting in France would affect a relevant proportion of the population studied and should therefore be prevented. In addition, it provides evidence of changes in migration ecology such as wintering areas. Prospective conservation measures should therefore include strategies that anticipate future environmental changes like climate change (Mawdsley et al. 2009). At the same time, this highlights the need for consequent political action to counter climate change and (by that) biodiversity loss. Despite further gaps in knowledge about the connection between human activity and the loss of biodiversity, current scientific knowledge has long been sufficient to take countermeasures (Buxton et al. 2021). Now, there is an urgent need for action (Turney et al. 2020).

To bring about a global trend reversal on the ongoing loss of biodiversity, a comprehensive change towards an economy considerate of the planetary boundaries and question the paradigm of economic growth seems vital and indispensable (Rockström et al. 2009, Díaz et al. 2019, Otero et al. 2020). Therefore, a significant part of society must be made aware of the interaction of human activities and loss of biodiversity to work towards its conservation (Rousseau & Deschacht 2020). Increasing passion for the beauty of our planet and biodiversity will help further this goal. Here, refuges like the East Frisian Islands can play a central role to create and promote enthusiasm and awareness through public relations work. Experiencing the impressive beauty of a landscape like the Wadden Sea islands as I did during the research for this thesis, will inspire enthusiasm about its protection and preservation.

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Different stages of Short-eared owl brood (in rows from left to right): 1st row: adult owl guarding nest, well camouflaged adult bird on the nest, 2nd row: nest with nine eggs in vegetation dominated by *Ammophila arenaria*, recently hatched young and eggs in the nest, 3rd row: fledglings of different ages in the nest, portrait of an almost fledged young bird, 4th row: young bird about to fledge, fledged young in threatening gesture.

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Kruckenberg, H., Kämpfer, S., Düttmann, H. & T. Fartmann: Satellitentelemetrie von Brachvögeln aus der nordwestdeutschen Population 2020-2021. 13th Seabird and Coastal Bird Conservation Colloquium of the German Seabird Conservation Group, Amrum (11/2022).

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Hölzel, N., Frenzel, M., Gottbehüt, K., Kämpf, I., Kämpfer, S., Kuzmin, I., Mathar, W., Reinhard, A., Tolstikov, A., Tupitsin, S., Weking, S. & J. Kamp (2013): Land-use change and biodiversity in Western Siberia: Implications for Conservation. International conference "Ecology and Management of Natural Resources" of the Tyumen State University, Tyumen, Russian Federation (09/2013)

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Oberdiek, N.,Kämpfer, S., Dierschke, J. & K. Jeromin (2011): Zur Situation der Sumpfohreule (*Asio flammeus*) in Niedersachsen und Schleswig Holstein. 27th Annual Meeting of the Deutsche Arbeitsgemeinschaft zum Schutz der Eulen, Marsberg-Bredelar (10/2011)

Erklärung über Eigenständigkeit der erbrachten wissenschaftlichen Leistung

Hiermit erkläre ich, Steffen Kämpfer, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe. Die aus anderen Quellen direkt oder indirekt übernommenen Daten und Konzepte sind unter Angabe der Quelle gekennzeichnet.

Bei der Auswahl und der Auswertung des folgenden Materials haben mir die nachstehend aufgeführten Personen in der jeweils beschriebenen Weise geholfen.

Artikel 1

Kämpfer, S. & T. Fartmann (2019): Breeding populations of a declining farmland bird are dependent on a burrowing, herbivorous ecosystem engineer. *Ecological Engineering* 140: 105592.

Thomas Fartmann: Redigieren des Artikels. Anteil: 20 %

Artikel 2

Kämpfer, S., & T. Fartmann (2022): Natural coastal dunes on Wadden Sea islands as a refuge for an endangered wader species. *Journal of Coastal Conservation* 26: 53.

Thomas Fartmann: Redigieren des Artikels. Anteil: 20 %

Artikel 3

Kämpfer, S., Fumy, F. & Fartmann, T (2023): Extensive dune grasslands largely lacking human disturbance are an important refuge for a vole-dependent raptor. *Global Ecology and Conservation*

Florian Fumy: Unterstützung Datenanalyse, Redigieren des Artikels. Anteil: 10 %

Thomas Fartmann: Redigieren des Artikels. Anteil: 15 %

Artikel 4

Kämpfer, S., Engel, E. & T. Fartmann (2022): Weather conditions determine reproductive success of a ground-nesting bird of prey in natural dune grasslands. *Journal of Ornithology* 163: 855– 865.

Elias Engel: Unterstützung Datenerhebung Kleinsäugeruntersuchung (2018), Unterstützung Auswertung Kleinsäugeruntersuchung. Anteil 15 %

Thomas Fartmann: Redigieren des Artikels. Anteil: 10 %

Artikel 5

Kämpfer, S., Kruckenberg, K., Düttmann, H., Kölzsch, A., Jiguet, F., Bocher, P. & Fartmann, T. (2023): Tracking wintering areas and post-breeding migration of a declining farmland bird – An indispensable basis for successful conservation. *Global Ecology and Conservation*.

Helmut Kruckenberg: Datenerhebung, Redigieren des Artikels. Anteil: 10 %

Heinz Düttmann: Redigieren des Artikels. Anteil: 15 %

Andrea Kölzsch: Datenauswertung, Redigieren des Artikels. Anteil: 15 %

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Thomas Fartmann: Redigieren des Artikels. Anteil: 10 %

Weitere Personen waren an der inhaltlichen materiellen Erstellung der vorliegenden Arbeit nicht beteiligt. Insbesondere habe ich hierfür nicht die entgeltliche Hilfe von Vermittlungs- bzw. Beratungsdiensten (Promotionsberater oder andere Personen) in Anspruch genommen. Niemand hat von mir unmittelbar oder mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen. Die Arbeit wurde bisher weder im In- noch im Ausland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde vorgelegt.

(Ort, Datum, Unterschrift)